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Whitcombe, Robert Peter

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THE BIOLOGY OF *APIS* SPP. IN OMAN WITH SPECIAL REFERENCE TO *APIS FLOREA* FAB.

by

ROBERT PETER WHITCOMBE

being a thesis presented in the candidature
for the degree of Doctor of Philosophy, in
the Zoology Department of the
University of Durham, 1984

وَأَوْحَىٰ رَبُّكَ إِلَى ٱلنَّحْلِ أَنِ ٱتَّخِذِي مِنَ ٱلْجِبَالِ
بُيُوتًا وَمِنَ ٱلشَّجَرِ وَمِمَّا يَعْرِشُونَ × ثُمَّ كُلِي مِنْ كُلِّ
ٱلثَّمَرَاتِ فَٱسْلُكِي سُبُلَ رَبِّكِ ذُلُلًا يَخْرُجُ مِنْ بُطُونِهَا
شَرَابٌ مُخْتَلِفٌ أَلْوَانُهُ فِيهِ شِفَاءٌ لِلنَّاسِ إِنَّ فِي ذَٰلِكَ
لَآيَةً لِقَوْمٍ يَتَفَكَّرُونَ ×

Your Lord inspired the bees, saying: "Build your homes in the mountains, in the trees, and in the hives which men shall make for you. Feed on every kind of fruit, and follow the trodden paths of your Lord." From its belly comes forth a fluid of many hues, a medicinal drink for mankind. Surely in this there is a sign for people who reflect.

The Koran, Chapter of the Bee (No.16) : 68-69.

The biology of *Apis* spp. in Oman with special reference to *Apis florea* Fab.

by Robert P. Whitcombe

ABSTRACT

In northern Oman, *Apis florea* is widely distributed and is managed for honey production on a small scale; *Apis mellifera jemenitica* is kept in log hives in the Jabal al-Akhdār. *Florea* nest-sites were investigated. Avoidance of exposed positions in date-palms and preferential selection of sites in the SE sector of trees indicated that a microclimate which facilitated thermoregulation and foraging was important. Some *florea* keepers also considered nest-site orientation and exposure important and sited colonies accordingly. Omani methods of *florea* management are described, especially of one man who kept up to 30 colonies, moving them between shady date-garden in summer and a sunny location in the plains in winter.

Florea foraging activity and brood-nest thermoregulation were adapted to a higher range of ambient temperatures (T_A) than *jemenitica*. The lower threshold for flight was c. 18°C for *florea*, 12°C for *jemenitica*; peak activities were at c. 30°C and 22°C respectively. *Florea* brood-rearing, particularly in small colonies, diminished during winter and this was attributed to poor thermoregulation at low T_A; brood-rearing in summer continued at higher levels despite floral dearth.

Floral calendars for 3 habitats are presented; flowering patterns and *florea* and *mellifera* foraging strategies are discussed. Adequate (*florea*) colony development by April, for swarming and exploitation of the main *Acacia tortilis*/*Prosopis cineraria* honey flow, depended on the use of many minor forage sources in early spring. A second developmental peak and honey flow came in October/November from *Ziziphus spina-christi*. Records of Omani-managed *florea* and colonies in hives indicated an increased absconding tendency in summer: causes of absconding (predation, microclimate, dearth) are discussed.

Hives to prevent *florea* absconding and facilitate honey extraction met with mixed success. It seems that certain adaptations of *florea* to tropical environments makes them less well suited to management.

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Hawasina and Hamoud Ali Sālim at Khabura also deserve special mention, as does an anonymous carpenter at Bidaya for his assistance in making *Apis florea* hives.

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At Durham University, Hazel Burt, Dr Ann Greatrex and Dr Judy Turner helped with pollen analyses, Andrew Wood and Nicholas Aebischer with statistics and computing and Adil Abdul-Wahid with certain Arabic terms. Technical assistance came from John Richardson, David Young and David Hutchinson, the last-mentioned making the photographic plates of the line drawings in this thesis. Dr Shirley Goodyer, Zak Erzinçlioğlu and other research workers and staff offered useful comments and advice during the research as did Professor F. Ruttner of the Institut für Bienenkunde (German Federal Republic). In particular, Dr John Free (Rothamsted Experimental Station) gave me much encouragement and guidance in the U.K. and Oman on how to tackle this study of honeybees. Many thanks to all these people.

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CHAPTER I

GENERAL INTRODUCTION : LITERATURE ON *APIS FLOREA*, ITS NATURAL HISTORY AND THE DISTRIBUTION AND ORIGINS OF OMANI HONEYBEES

1. Status of ecological research on honeybees

Wilson (1971) recognized 3 overlapping phases of research into social insects, (i) natural history, (ii) physiology and (iii) population (colony) biology/ecology. Progress on these 3 aspects has not been evenly balanced for honeybees. In 1976, shortly before my arrival in the Sultanate of Oman to investigate the biology and management of the sub-species of *Apis mellifera* L. named *jemenitica* by Ruttner (1975) and, in particular, of *Apis florea* (Fabricius) the Little or Dwarf honeybee, J. Louveaux wrote: "When considering the astonishing mass of scientific work devoted to (honey) bees, one is hit by the disproportion which exists between the innumerable investigations in the fields of physiology and behaviour and those, very much rarer, which concern ... ecology .... especially if one takes account of their huge geographical distribution. This includes temperate climatic zones as well as semi-arid, sub-tropical or tropical zones and offers, consequently, a large variety of ecological conditions."

Some of the gaps in our knowledge of the ecology of temperate and tropical *Apis mellifera* are now being filled (see Winston *et al* 1983 for a recent review) but thorough research on nearly all aspects of the biology of *Apis florea*, including its ecology, is still scarce and much of our present understanding of this species is drawn by inference from studies on *Apis mellifera*. Seeley (1983) gives the most modern review of the ecological adaptations of all 4 *Apis* species and he stresses the importance of predation in moulding the nesting and defensive behaviour of the 3 Asian honeybees, *Apis dorsata*, *Apis cerana* and *Apis florea*.

So, despite *Apis florea* having been referred to in over 100 publications (Free 1981),detailed work on all of Wilson's (1971) 3 phases was still urgently required in Oman and in the other parts of its range. Laboratory facilities not being readily available in Oman and because *Apis florea* physiology could be studied elsewhere, my research was concentrated primarily on stage (i) natural history but also on (iii) ecology and on *Apis florea* management. This was appropriate because of the extreme nature of the Oman environment, which could be expected to reveal particularly clearly any special adaptations of *Apis florea* and because northern Oman was the only place in which *Apis florea* was known to be managed for honey production (Dutton & Simpson 1977; Dutton & Free 1979; Williams 1979).

For brevity, *Apis florea, Apis dorsata, Apis cerana, Apis mellifera* sensu lato and *Apis mellifera jemenitica* have been referred to in the text of this thesis as *florea, dorsata, cerana, mellifera* and *jemenitica* respectively.

2. Main sources of reference on *Apis florea* and Oman

Crane (1967, 1978) and Morse (1970) have published comprehensive bibliographies on *florea* and Free (1981, 1982) has reviewed the bulk of this literature and pointed out the fragmentary nature of the information on the biology of this species. I believe that, in part, this must be due to the tendency of *florea* to abscond when disturbed and to the low yield of honey per colony and because these two properties in turn have meant that *florea*, unlike *mellifera, cerana* and *dorsata*, has not been a major honey source (except in Oman) though its honey is widely esteemed (Muttoo 1956; Crane 1975a).

An outline of the natural history of *florea* is given in the next section (3), but for the aspects of the biology of *florea* that are covered in this thesis, the pertinent literature is discussed in more detail in the appropriate chapters. For aspects not covered, Free's (1981, 1982) reviews should be consulted. Since Free's papers, however, the results of a major investigation on the defensive strategies of *cerana, dorsata* and *florea* in Thailand have been published (Seeley 1982b, 1983; Seeley *et al* 1982). The main paper (Seeley *et al* 1982) contains much new information on *florea*; the data had been systematically gathered and analysed which was not the case with many of the earlier *florea* studies. Seeley *et al*'s field work overlapped in time and scope with my work in Oman, but our findings and conclusions have not all been the same. However, it has been useful to be able to compare the two studies and to consider whether or not the apparent differences are genuine and, if so, do they reflect divergent adaptations to contrasting conditions in Oman and Thailand.

The only other Ph.D. thesis on *florea* (Akratanakul 1977) was also based on investigations in Thailand. The ecological aspects of the thesis were primarily descriptive and have been superseded by Seeley *et al* (1982) while the behavioural aspects concerned subjects not tackled in detail in my thesis; repeated comparisons of the results of the two theses have therefore not proved necessary.

Hawley (1977), Gallagher & Woodcock (1980), Durham University (1978-198?) and the Journal of Oman Studies and its Special Reports on the 1975 and 1977 Oman Flora and Fauna Surveys provided essential background information on the Sultanate of Oman, especially its physical, biotic and cultural environment; they set the scene for this research so that the study could be viewed in a local context. Additional literature of relevance was traced through various bibliographies on Oman (King & Stevens 1973; Shannon 1978; Düster 1980; Clements 1981). Appendix II gives details of atmospheric temperature and relative humidity in northern Oman, the former being of particular importance to *florea*, and Appendix III provides a guide to the flora, including honeybee plants.

3. *Apis florea* natural history

Based on my own observations in Oman and supplemented by descriptions in the literature, the principal features of the *florea* colony and its life cycle are outlined here. The basic characteristics (caste system, developmental cycle of individuals, colony reproduction, nutrition ie nectar and pollen, wax comb and so on) appear to be much the same as for *mellifera* as described by Butler (1974), Free (1977) and many others. However there are also numerous differences in detail, some of which may be of ecological significance, and these will be considered throughout the thesis.

The single comb nest of *florea* is usually attached to twigs or branches of trees, to the roofs of small caves or to buildings, but not in (near) completely enclosed sites like those used by *mellifera*. The cells of the upper portion of the wax comb, close to the supporting structure, are generally extended for honey storage so that the thickness of the comb near the support may be 3.5 - 6.2cm, individual cells reaching a depth of 3.0 - 4.0cm (Franssen 1932; Thakar & Tonapi 1962; Sakagami & Yoshikawa 1973). In Oman I recorded honeycomb thicknesses of 10.5cm and individual cells 5.4cm deep. Below the honeycomb pollen is stored in a band of 1 - 4 or more cells and below this the worker brood is reared in cells 6.9 to 9mm deep and 2.7 to 3.1mm in diameter (Franssen 1932; Thakar & Tonapi 1962; Sakagami & Yoshikawa 1973). In Oman cells were approx. 9mm in depth and were 3.1 - 3.3mm in diameter; most combs were constructed so that the cells were vertically-sided, as Morse (1983) found for *florea* elsewhere in Asia.

The worker eggs, larvae and pupae (in sealed cells) often occurred in a pattern of concentric rings and according to Sandhu & Singh (1960) in India the total development period from egg to adult was 20 - 22 days (mean 20.68). From photographic recordings on a strong colony in April - May 1980, not yet fully analysed, my impression was that the development period in Oman could be a little shorter, perhaps 18 - 20 days.

During seasons of abundant forage and when a colony is strong, drones are reared in larger cells below the worker brood. After the emergence of the adult drones, wax would often be deposited around the periphery of the cells, restricting the entrance and making them circular rather than hexagonal in appearance; honey was sometimes stored in these empty cells. Akratanakul (1977) too has observed these two traits in Thailand. My observations in Oman also indicated that, unlike worker brood cells which would be used several times over, each drone cell was only used once for brood and new drone comb would be constructed if a colony went through two swarming phases in a season.

Swarm queen cells were usually attached to the lower edge of drone comb ; Akratanakul (1977) found 3 - 13 queen cells per colony of 22 examined, but up to 15 - 20 have been recorded (Ghatge 1949). Colonies that have lost their queen may produce up to 19 emergency queen cells by extending worker brood cells (Sakagami & Yoshikawa 1973; Akratanakul 1977; Free & Williams 1979); if the queen is not replaced, "laying workers" usually develop within the colony (Kshirsagar *et al* 1980; my own observations).

One colony I had in an experimental hive (No. 5) did build c. 17 queen cells directly onto the lower edge of the worker comb, producing no drone cells at all, but on the infrequent occasions that I saw such queen cells (attached to worker comb) they were usually few in number (eg 1 or 2) and on small colonies that I deduced had been recently established. By marking queens with paint I have confirmed Akratanakul's (1977) observation that it is the old one that leaves with a colony's prime swarm, and before the emergence of new queens (as in *mellifera*) and therefore I believe that these queen cells attached to the worker comb of small colonies were not swarm cells, but supersedure cells for the replacement of an old queen.

During the summer, some *florea* colonies in Iran were estimated to have populations of 30,000 workers (Tirgari *et al* 1969), but Seeley *et al* (1982) measuring that of 12 colonies in Thailand found a mean and standard deviation of 6271 ± 4957. In Oman, a medium-large sized colony (28.5cm high by 28.8cm wide with the bees, the comb 25.5cm by 26cm without) that I sacrificed on 5.viii.80 contained 6,165 workers, 77 drones and 1 queen (40 workers and 21 drones had been removed 6 days earlier) and from measurements of the weight of the bees in this and other colonies, I believe that the 30,000 estimate of Tirgari *et al* represents an exceptional rather than typical colony population.

The bees form a "curtain", 1 - 3 or more workers thick, that envelopes the comb in strong colonies. In Thailand Seeley *et al* (1982) consider that this "curtain's" primary function is to protect the colony, its brood and honey, from predators, but as discussed in Chapters II and V its role in brood thermoregulation may be as, if not more, important in Oman. Whatever its functions, the curtain makes observations on the brood and food stores and on the behaviour of adult workers and the queen beneath, extremely difficult without some interference to the colony. In contrast, the forage communication dances are readily visible; they are usually performed on the near horizontal platform provided by the top ("crest") of the honeycomb and have been described and investigated by Lindauer (1957), Akratanakul (1977), Free & Williams (1979) and Koeniger *et al* (1982).

Little is known about the swarming process in *florea* (Free 1981) though in Oman large colonies are reported to produce up to 8 swarms a year (Dutton & Free 1979). Akratanakul (1977) reported an "interim" cluster site for a reproductive swarm 20m from the parental nest, but made no further observations so it may even have stayed at this site; as discussed in Chapter VI, I came cross only one likely, but circumstantial, instance of an interim cluster site, so more evidence is required to confirm the existence of such behaviour and establish its frequency. Likewise the absconding behaviour of *florea* is poorly understood, though the prevalence of this trait has been widely reported in the literature; I have made some preliminary observations on the behaviour of colonies prior to swarming and absconding, but they are not presented here.

As considered in Chapter VI, there has been confusion as to whether swarming and absconding by *florea* extends to long distance migration as in *dorsata* (Koeniger & Koeniger 1980) or is a purely local phenomenon. Statements such as Thakar & Tonapi's (1962) : "*A. florea* is highly migratory. They periodically migrate between plains and adjacent low hills according to seasonal variations in forage availability ... They are essentially adapted to plains up to 1500 or 2000ft though they may be rarely seen migrating up to 4000 to 5000ft in hills, Muttoo 1956" are potentially misleading without supporting evidence and details of the distances travelled, particularly when the author quoted (Muttoo 1956) gives no data either. "This bee *(florea)* is common in the plains of India, up to about 1500 feet (500 metres). It migrates up to 4000 feet." Whether the absconding of *florea* involved long distance migration in Oman was also not clear, though it was inferred in the reports of Dutton & Free (1979) and Williams (1979). That local movements of less than 500m do occur has been indicated adequately (Tirgari *et al* 1969; Tirgari 1971) but this is not migration as I understand it. Diminution in the supply of forage, temperature changes and invasion by enemies have been invoked as causes of absconding (Free 1981).

4. Previous studies on honeybees in Oman

4.1 *Apis mellifera jemenitica*

In northern Oman *jemenitica* is kept in cylindrical hives (sing. "tubl", pl. "tubūl"), hollowed out from sections of date-palm trunk, under a traditional form of management outlined by Dutton & Free (1979) and Williams (1979). Until the advent of beekeeping programmes in the 1970s, *jemenitica* in Dhofar was entirely wild, but nests were robbed for their honey, especially in the hills (Berkeley 1979). Lorimer (1908) reported that beeswax was exported from the region. Both populations of *jemenitica* have been the subject of modern apicultural projects involving Langstroth hives and this work has been described by Manley (1978, 1980), Berkeley (1979) and Dutton *et al* (1982). Various unpublished reports to the Oman Ministry of Agriculture and Fisheries and Durham University by A. Berkeley, M. Manley, P. Boyles and J. Karpowicz contain further information. More detailed research on *jemenitica* in Oman, particularly its biometrics but with initial observations on its ecology and suitability for beekeeping, is given in Dutton *et al* (1981).

4.2 *Apis florea* (with records of attempted management in India)

Prior to 1977, attempts at managing and hiving *florea* had only been recorded from India (for references and discussion see Free 1981; Whitcombe 1982a and b; this thesis Chapter VIII), but it appeared that none of the "experiments" met with much success and that the techniques employed were not adopted more widely. Dutton & Simpson (1977) gave the first authentic report of a man successfully managing colonies of *florea* for their yield of honey and this was in Oman at the SE corner of the Arabian peninsula and at the western end of the species' range. Dutton & Free (1979) and Williams (1979) made further observations on the practices of the bee-keeper, Humayd bn Sulayman al-Shimili, and Free & Williams (1979) made preliminary investigations on aspects of *florea* colony biology.

Humayd brought wild colonies to his village from nearby mountains, installing them in artificial caves, cavities in ruined buildings and in trees. A split stick, usually a section of date-palm frond ("zoora"), was used to support the comb but the method had disadvantages in that when the honey crop was removed, the wax comb was crushed and discarded and not re-united with the brood comb. Furthermore, the *florea* in Oman, as elsewhere, exhibited the absconding habit so to maintain and increase the number of his colonies the beekeeper needed to discover and collect more wild ones; nevertheless it was said that colonies with queen cells could be divided and that this helped to prevent swarming.

Dutton & Free (1979) described a preliminary attempt to induce a colony to use separate frames for honey and brood (one above the other); it showed some promise but the bees absconded. The beekeeper gave some indication of the seasonal patterns of colony movement/migration and of the main brood rearing and swarming seasons (Spring and Autumn). The main honey harvests followed these and were associated with the "semra" tree *Acacia tortilis* and "sidra" tree *Ziziphus spina-christi*, respectively; lucerne (*Medicago sativa*) and newly mature dates "rutub" were also thought to be sources of "nectar". Identifying the sources of forage for *florea* and *jemenitica* in Oman was to be one of the important objectives of this study (Chapter VII). For these plants, authors of latin names, details of distribution and so on are not given in the text but can be found in Appendix III. Where known, Omani names for such plants and of other organisms and artefacts associated with beekeeping and of relevant geographical terms, have been translitterated from the Arabic and given within quotation marks.

The biological investigations of Free & Williams (1979) were primarily concerned with the behaviour of individual bees eg of foragers and their dances on return to their nest, and with the role of pheromones (natural and synthetic) in attracting workers to the nest, in marking sources of forage, in colony defence and in the response of workers to the queen. Though the continuation of such work was of practical and academic interest, I had no synthetic pheromones available and chose not to follow up these investigations in any detail. However, Free & Williams' observations on absconding were pertinent to this ecological study of *florea* and were a stimulus to the research presented on this topic in Chapter VI.

Some preliminary findings of my research have already appeared in press (Whitcombe 1980, 1982 a and b, 1984; Dutton *et al* 1982) and in unpublished reports to the Oman Ministry of Agriculture and Durham University.

5. World distribution of *Apis florea* and the other *Apis* species

Florea has a tropical and sub-tropical distribution from Indonesia in the east, through south-east Asia and the Indian sub-continent to Pakistan and southern Iran in the west (Stitz & Szebe 1933; Maa 1953; Pourasghar 1979). A. Abdul-Wahid (pers. comm.) states that it also occurs in Basra, southern Iraq, and it has recently been recorded on the southern coast of the Arab Gulf at Abu Dhabi island (Brown & Hamer 1983). Though specimens of *florea* from "Muscat" were reported over 50 years ago (Dover 1929) and Shepherd (1961) tells of being entertained with wild honey (which must have come from *florea*) in the Wadi Jizzi, northern Oman, no details of its presence in Arabia were known until the report of Dutton & Simpson (1977) about its use for honey production in the Dhahira region of Oman.

Crane (1983a) gives a map showing the approximate world distribution of *florea*, and of *mellifera, cerana* and *dorsata* in their native ranges. *Mellifera* is widely distributed with various races native to Europe, Western Asia and Africa, while *cerana* occurs in eastern Asia, including India and Pakistan; both species occur in temperate, sub-tropical and tropical climates. *Dorsata* has a tropical and sub-tropical distribution similar to that of *florea*, but does not occur so far west, being absent in Iran.

6. Distribution and origins of the honeybees of Oman

6.1 *Apis mellifera jemenitica*

The surveys that were performed throughout the period of field work, with assistance and additional information coming from A.G.M. Berkeley and M.J.D. Manley in particular, have elucidated the distribution of *jemenitica* and *florea* in Oman (Figure 1.1). Major Omani place names mentioned in the thesis are also given in Figure 1.1, while Bartholomew (1977), Hunting (1977) and Oxford University Press (1980) show further names and features; smaller places are given on 1:500000, 1:250000 and 1:100000 maps prepared by the UK Ministry of Defence.

Other than the wild population in Dhofar, *jemenitica* was restricted to the central region of the Jabal Akhdār where the highest mountains, up to 3,000m, occur. The colonies were nearly all kept in date-log hives at sites in the villages and along wadis, mostly at lower altitudes (300 - 1,000m). At Shurayjah and Al Yayna (alt. c. 2,000m) near Sayq, empty hives were found (palm-logs split in half, length-ways, to facilitate transport by donkey, date-palms being absent in situ). The demise of the honeybees was attributed by the Omanis to the effects of bombing during the "Jabal War" in the 1950s (see Shepherd 1961 for personal account), the hives being partially buried in rock falls, and/or to the use

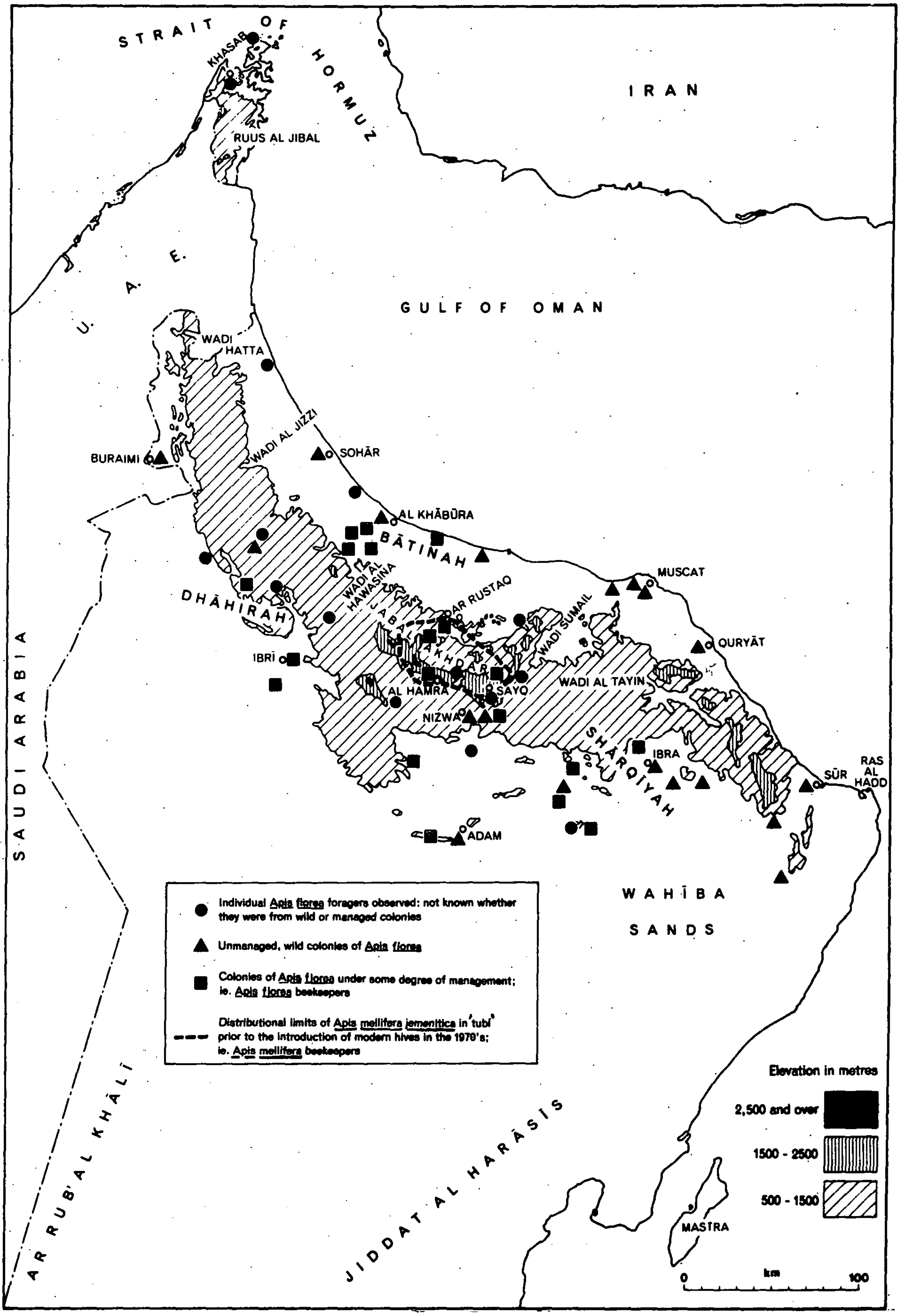


Figure 1.1 Distribution of honeybees, *Apis florea* and *Apis mellifera jemenitica*, and bee-keepers in northern Oman as determined between December 1977 and August 1980.

of insecticides for control of pests of agriculture and/or public health; mismanagement and dearth of forage and water, due to drought/temporary cessation of irrigation supply, were other possibilities. That *jemenitica* can survive in this region is indicated in Chapter V. Very few colonies of *jemenitica* were known to exist in the wild anywhere in northern Oman.

It was at one time considered possible that this population of *jemenitica* in northern Oman might be a survivor of an earlier, slightly wetter period and that it was now restricted to this mountain region which experiences rather higher rainfall (Horn *et al* 1977; Horn & Nielsen 1977a; Gallagher & Woodcock 1980). Certain components of the vegetation of the higher parts of the Jabal Akhdār appear to have a floristically homologous equivalent in the western Himalayas/east Afghanistan and some plants and communities are identical or closely related to ones in Iran, pointing to close biogeographical affinities between the lands across the Gulf (Mandaville 1977; Miller & Whitcombe 1983). Therefore a relict population of *mellifera* of Iranian origin, associated with an equivalent relict flora, was not inconceivable. However, morphometric studies (Dutton *et al* 1981; Ruttner 1981) have in fact shown that the honeybees of Yemen and Oman were of the same race, *jemenitica*, and had African affinities; they were not related to the *mellifera* found in Iran. Thus their biogeographical origin is similar to that of much of the southern Arabian butterfly fauna which is more African than Oriental in composition (Larsen 1984).

Yet the view of some local inhabitants was that *jemenitica* had been imported and it has come to light, from an old document referred to by Wilkinson (1977), that the bees were not native but allegedly introduced to northern Oman during the rule of Imām/Sultan Saif ibn Sultan (1688-1711). As discussed in Whitcombe (1984) the bees would almost certainly have been brought to Rustaq from North or South Yemen, where there is a long history of bee-keeping and the bees are kept in hollow logs or pipes similar to those used in northern Oman (eg Strabo ?7A.D.;

Pliny the Elder 23-79 A.D.; Ingrams 1936; Bodenheimer 1951; Serjeant & Doe 1975; Mandaville 1981; Jaycox 1983 a and b). It is most unlikely that the bees were brought from Dhofar, for though this southern region of Oman is closer than the Yemens, there is no history of beekeeping with the indigenous *jemenitica* which have been entirely wild there until recently (Berkeley 1979; Dutton *et al* 1981).

6.2 *Apis florea*

In contrast to *jemenitica*, colonies of *florea*, both wild and managed, were found to be widely distributed over northern Oman, from Musandam in the north where honey is taken from wild colonies (M. Gallagher and T. Larsen, pers. comm.), to near the limits of cultivation in the south (Bilad Bani Bu Hassan, Ja'alān region). No *florea* colonies or foragers were found on visits to Sayq (2,000m) and surrounding villages in 1978 and 1979 and it was assumed that temperatures below 0°C in winter (Horn *et al* 1977) prevented survival of *florea* at this altitude. However, a colony that was taken and kept there in an experimental hive (No. 9) survived from 23.xii.79 till about 21.iii.80 when the bees were said to have absconded. Though not rearing brood on 17/18.ii.80 when it was still cold (see Chapter V), the colony must have done at a later date as sealed brood and young bees were left in the comb when it was abandoned. I subsequently recorded *florea* workers foraging at Sayq on *Clematis orientalis* and *Mentha longifolia* (28 and 29.vii.80 respectively) and Grahame Vivien then sent me specimens collected on flowers in the summer (17 August) of 1983. So whether these foragers were derived from the colony I had introduced to Sayq, from other resident wild colonies not located on previous visits or from colonies moving to this altitude in the summer, it was evident that *florea* colonies could occur at 2,000m. Nevertheless it seemed they were less abundant than in villages at lower altitudes.

Contrary to Williams (1979), *florea* does not occur naturally in Dhofar. However, J. Karpowicz (1980) reported that in September 1980 a colony remained alive after being carried overland by truck from northern Oman to Salalah on a packing case, but that it was subsequently destroyed.

When *florea* arrived in Oman is not known, but its widespread distribution and local comments that this species was the "Omani honeybee" whereas *jemenitica* is "foreign" indicate that it must have been present long before the 17th/18th Century when the latter were probably imported. If *florea* arrived without the help of man it is likely that they came across the present Strait of Hormuz area when it was dry land; this may have happened around 20,000 B.P., when sea-levels were thought to be at a minimum, before returning to near-present levels by 6,000 B.P. (Al-Asfour 1978; Brice 1978; Mandaville 1977).

However, as discussed in Chapter III, Pt IIB, until man provided numerous sources of water and more abundant forage by digging wells, constructing "aflaj" (water channels, see Wilkinson 1977) and irrigating crops, it is thought that *florea* would have been far more restricted in its numbers and distribution, assuming levels of rainfall in the past similar to those of today. Extended periods of drought might even have made survival of the species in Oman impossible. Archaeological evidence has indicated that in the Third Millenium B.C. Oman was a land of prosperous villages; irrigation based on wells and "gabarband" (a system of wadi-water retention, also used in Baluchistan) allowed the cultivation of cereals like wheat, barley and sorghum, and possibly pulses, by 2500 B.C. and probably earlier (Hastings *et al* 1975; Tosi 1975; Frifelt 1976; Berthoud & Cleuziou 1980). Then at the beginning of the Second Millenium B.C. there was an abandonment of this sedentary, urban life, possibly due to the development of nomadism based on the camel, but early in the First Millenium B.C. a new civilization developed in Oman, linked to that of southern Iran and the first "falaj" were constructed perhaps in the 7th or 8th Century B.C. (Wilkinson 1980).

Therefore conditions suited to *florea* must have existed in present-day northern Oman for much of the last 4,500 - 5,000 years and, if the bees were not already established prior to this, it is possible that man might have introduced them, deliberately or accidentally by boat, from Persia. However, according to the preliminary investigations of Professor F. Ruttner (pers. comm.) the Oman *florea* are closer biometrically to the *florea* of Pakistan, perhaps indicating old trade connections between these two regions. Yet parts of western Pakistan are closer to Oman's Musandam peninsula (a likely point of *florea* immigration) than are places like Dezful in south-west Iran and if Ruttner's Iranian *florea* samples were from this latter region and not from sites such as Bandar Abbas (across the Strait of Hormuz from the Musandam) the apparent biometrical differences between Omani and Iranian *florea* would be explained ie the Omani *florea* would be close to the *florea* in SE Iran/W Pakistan but less so to those in SW Iran. Until there is more archaeological, historical or biometrical evidence, the arrival of *florea* in Oman and the role of man, if any, must remain the subject of speculation. Comparison with the origins of other constituents of the Oman fauna and flora is of little help because of the paucity of information. The most detailed study has been on butterflies (Larsen 1984). It indicates that there has been only weak penetration of the oriental fauna into Arabia, but mostly into northern Oman; this still leaves the origins of *florea* wide open as Larsen's findings are consistent with both natural spread of *florea* and introduction by man.

CHAPTER II

NEST SITE SELECTION BY *APIS FLOREA*

A. INTRODUCTION

1. Review of nest site selection by *Apis* species outside Oman

Natural nest sites of *Apis mellifera* in temperate regions have been studied in detail only recently, by Seeley & Morse (1976) and Avitabile *et al* (1978). Most nests that they examined were in tree cavities 30 - 60 litres in volume with a small entrance of 10 to $140cm^2$ at the bottom; Avitabile *et al* found that the bees preferred SW-facing entrances. Experimental investigations on nest selection by *mellifera* swarms using paired nestboxes gave similar results, and also showed that swarms preferred south rather than north-facing entrances (Seeley & Morse 1978). Seeley & Heinrich (1981) considered that the selection of small, south-facing entrances near the base of cavities apparently facilitated nest thermoregulation in cooler latitudes of the northern hemisphere. Similar nestbox experiments by Rinderer *et al* (1982) have shown that there was a general tendency for colonies of Africanized *mellifera* in Venezuela (hybrids of the African *Apis mellifera scutellata* and European races of *A. mellifera*) to occupy larger cavities and to accept a wider range of cavity sizes than European swarms in Louisiana, USA. Winston *et al* (1983), however, report that the feral European colonies studied by Seeley & Morse in the USA are considerably larger than those of Africanized colonies in Peru, which have an average cavity volume of 22 litres and comb area of $8,000cm^2$ ($23,400cm^2$ for feral European colonies); the Africanized colonies they measured in Venezuela also had small comb areas, average $11,300cm^2$. This evidence is somewhat contradictory; maybe African and Africanized *mellifera* often occupy smaller cavities than *mellifera* of

European origin, but overall the cavity size range is greater (including open sites) for the tropical races and the size of the nests within the cavities may be relatively small. Rinderer *et al* thought the function of cavity-nesting for tropical honeybees might be rather different from that of bees in temperate climates, which have to survive through cold winters; they suggested that a large cavity with an insulating air space around the nest may precondition a colony in a warm climate to coolness, which would be important with nest entrances restricted as a defensive measure against smaller predators.

At the time this study in Oman started, most of the descriptions of the nest sites of *Apis florea* and of the other 2 Asian species of honeybee, *Apis cerana* and *Apis dorsata*,were either incidental or based on only a few observations and often not backed up with data. For instance in India, Douglas (1886) noted that *florea* nests that were built on thin branches were very small (about the size of a man's hand) but those in buildings might attain combs of several square feet in diameter. In Batavia (Java), Franssen (1932) reported that *florea* combs were always built on a twig of diameter 1 to 1.5cm, usually not higher than 4m above the ground and mostly in dense vegetation near the soil. In India, Ghatge (1949) found *florea* colonies in thick bushes or shady places at "low heights", some so low that they could be worked at while squatting on the ground. Also in India, Thakar & Tonapi (1962) stated that *florea* usually nested on the branches or twigs of trees, bushes and thorny creepers that provided protection and partial shade, but less frequently on rocks, building walls or roofs. The nests were not as high and inaccessible as those of *dorsata* and were exposed to sun, air and rains and though usually protected from the direct impact of violent wind blasts, were never enclosed in the dark. Pandey (1974) working in Uttar Pradesh (India) says that *dorsata* and *florea* nest in "open, bushy shades" whereas *cerana* nests in "dark places". Lindauer (1957) also described the nesting habits of the 3 Asian *Apis* spp. and Kshirsagar *et al* (1980) that of *florea*, but none of the above-mentioned papers lists quantitative information on the nest sites of *florea*.

Tirgari *et al* (1969) had 3 colonies under observation "outdoors" at Ahwaz, Kuzistan, Iran and found that they migrated in late autumn to new sites 5 to 100m away where they received maximum sunshine; in spring they again migrated locally into the dense foliage of trees where the combs were protected from direct sunshine. Tirgari (1971) reported further that most colonies which were observed in late autumn, winter and early spring were facing south (the edges east-west), but the colonies in summer locations were built in a north-south direction and the sides of the combs faced east-west. The bees always built combs in locations such that the sky was visible from the top of the nests. No data on the nest sites was presented, but Tirgari concluded that the migration was to provide a site with a favourable range of daily temperatures for brood rearing.

Akratanakul (1977) was the first to record systematically the nest sites of *florea* in any detail giving height, nest substrate, nest direction and shading of 30 colonies. Examination of the data indicates that most nests were in trees or bushes (one on a window frame) below 7m height, in a wide range of situations from being heavily shaded and almost inconspicuous to poorly shaded and very conspicuous. It was not clear whether the nest direction recorded referred to the angle at which the colony "pointed" or the direction in which the most exposed side of the comb faced. If the latter, most colonies faced between NW and NE, but no explanation was given for the selection (if any) of nest sites with this or any of the other attributes. Absconding was attributed to lack of food and disturbance/predation, not to unfavourable microclimatic conditions developing at certain types of nest site.

Free (1981) considered that diminution in the supply of forage was probably the main factor that caused absconding, but that temperature changes were also important in inducing changes of nest site, and presumably that temperature factors were involved in nest site selection too. However, these conclusions are based mainly on the same incidental reports in the literature that have been quoted above. Without systematic studies as to the factors determining nest site selection and absconding by *florea*, such conclusions can only be tentative.

Like *mellifera, cerana* nearly always nests in cavities such as tree trunks, and can also be kept in hives ranging from hollowed-out logs to modern types with movable frames (Watt 1966; Muttoo 1956). The nesting behaviour of *dorsata*,however, is the closest to that of *florea* in that the bees usually build their nests in the open, attached to the branch of a tree, overhanging rock or building (Watt 1966; Venkata Rau 1946; Muttoo 1956; Lindauer 1957). Deodikar *et al* (1977) examined attributes of 1861 *dorsata* nests; one conclusion was that branches with a north-south axis were preferred, but the data analysis was not clear and tree-sector occupied was not considered. It was suggested that wind and sun might determine such an orientation but no detailed explanation was offered.

The nesting habits of *dorsata*, however, do not always appear to be constant as in some areas aggregations of nests in a single tree may occur eg 92 nests in one tree in Ceylon (Lindauer 1957), while in the Philippines Morse & Laigo (1969) found no such aggregations, nor did they find nests on man-made structures (though this may have been due to their destruction by the local people). In contrast, *florea* nest aggregations have never been recorded and they do not usually nest as high as many *dorsata* colonies (Thakar & Tonapi 1962); *dorsata* nests have been recorded at heights of 20m, though they are sometimes found close (1m) to the ground as well (Morse & Laigo 1969). Lindauer (1957) did not make detailed comparisons of the nest sites of *florea* and *dorsata* but his descriptions indicated that, while good views of the sky could be attained from the nests of both species, *florea* nested in less exposed positions such as a "lightly-leaved bush" while *dorsata* bee-trees "always towered above the surrounding foliage, and had few leaves when colonized." On the other hand all the *dorsata* nests that Morse & Laigo (1969) observed in the Philippines were constructed where there was some overgrowth.

Thus, despite these various studies there was no consensus as to the functional significance of the nest sites being selected by the three Asian species of *Apis*, particularly *florea* and *dorsata*. Some observations indicated that *florea* needed a nest chosen to give a view of the sky and absconded when this was not available. Other observations suggested that absconding and selection of a new nest site were due to food shortage or predation or unfavourable microclimatic conditions at the old site. So, other than the survey of Deodikar *et al* (1977) for *dorsata*, no systematic investigation of nest site selection by *florea*, *dorsata* or *cerana* had been conducted before 1977 when this study was undertaken, though Seeley & Morse (1976) had published a list, mostly qualitative, of various nest characters of *florea* and *dorsata* that they had gleaned from the literature. However, a knowledge of the types of nest site sought by *florea* was of interest and importance for two reasons: (a) to determine the requirements that would have to be met in the design of a hive for *florea* and the most appropriate sitings for such hives and other colonies under management, (b) to understand the ecology and evolution of *florea*, and other *Apis* species, and the environmental pressures which have shaped them. It subsequently transpired that a comparative study along these lines had been carried out on wild *cerana*, *dorsata* and *florea* in Thailand (Seeley *et al* 1982; Seeley 1983) at the same time as these investigations on nest site selection etc by *florea* were being performed in Oman.

Seeley *et al* (1982) documented the nesting behaviour of these 3 honeybee species far more systematically than had been done before, and their paper should be referred to for detailed descriptions of *Apis* spp. nest sites in south-east Asia. In this major paper they concluded that predation was "a pervasive and powerful force in the evolution of these tropical bee societies" with *florea* focusing its defences on the detection stage of the predation sequence "detection - approach - consumption." They considered that *florea* colonies, being built low on the branches of dense, shrubby vegetation, were probably difficult for many of their predators to find, but that once detected the colonies were easily approached and overpowered because the nests were accessible and the stings of the small workers relatively painless. Though appreciating that the protective curtain of *florea* workers around the comb contributed to brood nest thermoregulation, Seeley *et al* suspected that defense was its basic function and that "nest invasions were a greater problem than fluctuations in brood nest temperature."

They also concluded that *florea* colonies would abandon exposed nest sites to conceal their nests from predators, but they did not eliminate the possibility that excess insolation might also stimulate colony movement, nor did they consider the light (sun, sky etc) requirements of *florea* for communication dances. They interpreted the selection of nest sites by *cerana* and *dorsata* in Thailand, and other features of their behaviour, in terms of defensive strategies rather than in terms of nest thermoregulation, food shortage or communication dance requirements.
On the other hand Seeley (1983) considered that winter survival was the main ecological challenge facing *mellifera* colonies in cold temperate regions of the world, and that success in meeting this challenge required

the selection of a well-sheltered tree cavity that tightly enclosed the bees and sufficient honey-filled combs, so that a warm micro-environment could be maintained.

Since the only thorough investigation of nest site selection by *A. florea* is that of Seeley *et al* (1982), the present results from Oman will be compared primarily with their results, rather than the other papers mentioned as most did not even document nest attributes such as height and substrate branch diameter. However, the Thailand study of Seeley *et al* was performed in one dry season only and if *A. florea* displays some seasonal variation in nest site choice, there might be some bias in its results as is explained further in the next section.

2. Prior knowledge of *Apis florea* nest sites in Oman

When first investigated in Oman (Dutton & Simpson 1977) wild *florea* were found nesting in mountain caves or rock niches which was unusual, for elsewhere in its range *florea* was known to nest primarily in trees, as has already been outlined in the previous section. The bee-keepers of the Dhahira region of interior Oman claimed that in winter the colonies were most likely to be found in east-facing caves, where they would benefit from insolation in the morning, but as the summer heat increased they would migrate to south-facing caves. Only the mid-day sun shone directly into such caves and was too high in the sky to penetrate deeply; apparently west-facing caves were not used because of the prevailing west wind in this region.

Later studies (Dutton & Free 1979; Williams 1979) revealed that *florea* also nested in trees in Oman; according to their informant some of the colonies stayed throughout the year in trees or bushes, usually on their south side where they were warmed by winter sun but shaded in summer when the sun was directly overhead. Other colonies apparently returned to the mountains at the end of the summer. Some colonies in mountain caves apparently moved further back, away from the cave entrance when the summer heat developed again, while others migrated to cultivated areas.

The use of nest sites as described was based on hearsay and was thus not altogether clear, but to some extent appeared to be seasonal. Studies based on recorded observations were therefore required to clarify and establish the verity of this interesting and plausible local information on *florea*. It is hoped that, in conjunction with other chapters, especially Chapter V on temperature regulation, Chapter VI which considers absconding and Chapters III and IV on Omani bee-keeping practices, that this chapter will help to identify some of the factors that influence *florea*'s choice of nest site and the overall role of nest site selection in the ecological strategy of the species for survival and reproduction. It should be borne in mind, however, that though some of these factors may be of significance throughout the range of *florea*, their relative importance may not be the same in different regions depending on climatic conditions, predation pressure etc; so nest site selection in Oman, an arid area with high summer temperatures but cool winter nights, may differ somewhat from that in say Thailand, which has a north-east monsoon producing a dry season and a south-west monsoon producing a rainy season. Seeley *et al* (1982) carried out their field-work in Thailand for 7 months in the dry season, so may not have recorded the whole picture of *florea* nest site selection if it varies seasonally; in Oman, my observations were made over a period of nearly 2¾ years and all seasons were covered.

B. METHODS

1. Finding wild colonies

From December 1977 to August 1980 details of the nest sites of as many wild *florea* colonies as could be located were obtained. More colonies were recorded from Khabura than any other district, but most regions and habitats within northern Oman are represented. Nests of *florea* were usually well concealed so were not easy to trace; the few colonies I discovered by myself were spotted either by chance or after several hours of searching.

The best way found to locate nests in bushes and trees in cultivated areas was to ask farmers if they had any *florea* colonies on their land and, if so, would they allow them to be examined. Most farms/gardens were less than 2 hectares in area (Dutton & Letts 1982) and, being intensely cultivated, it appeared that many farmers noticed new colonies of *florea* within a few weeks of their arrival, while irrigating and tending their crops. Some farmers were naturally reluctant to disclose the whereabouts of such nests as this might draw their presence to the attention of other people, including children, who might then disturb them or even take the honey for themselves. In some cases a colony might be pointed out to me, but on returning to examine it in more detail at a later date I would find it had disappeared as the owner, or someone else, had decided to take any honey before it was exposed to my examination or before another person was tempted to take the honey. Nevertheless, farmers were generally co-operative and at Khabura the presence of many colonies was volunteered to me by local people.

To record colonies in uncultivated areas (in trees in the mountains and "sayḥ", semi-desert gravel plains, and in caves) I accompanied Omanis who were accomplished in finding such nests; it was really a form of honey-hunting they practised on these expeditions, but most were specialist *florea* keepers who attempted to re-instate any colony they found after taking the honey. I was usually shown nests whose whereabouts were already known, but some of the "hunters" claimed they were able to find such nests by following the flight line of bees returning to their nest from a site where they had been gathering water (cf "Bee-lining", Seeley *et al* 1982) and by the presence of yellow drops of honeybee excreta on the rocks in the vicinity of a nest (cf Chapter III, P.121-2). Local names for these dried specks, with rather unreliable transliterations, were:- "qatra" (literally, drop), "ʿakus", "kuth", "rāyṭa", "aṭabā", "ʾakfaʿ".

A number of wild colonies were also recorded in buildings and other man-made structures, or close to them (often in ornamental plants) and these were brought to my attention by the householders (Omani and expatriate) who sometimes wanted them removed.

Thus colonies from a range of habitats were investigated and the 176 nest sites that were noted (156 in trees, bushes etc and 20 in caves, wells etc) must cover nearly the complete spectrum of types likely to be used by *florea* in Oman.

2. Nest site details recorded

When possible, the following details were recorded for each nest:-

(i) Location. Type of tree, cave, building, artefact used.

(ii) Height above (or below) ground of branch or other substrate to which the colony was attached. In most cases a tape measure was used, but on occasions and especially with high colonies out of reach, an estimate with respect to objects of known height had to be made.

(iii) Diameter of branch, twig or other substrate to which the colony was attached. If the colony had been removed from the branch, several measurements were sometimes made and a mean taken.

(iv) Orientation of the colony, with a compass (maps indicated that True and Magnetic North were within 1° of each other in Oman). This was usually the direction in which the distal end of the supporting twig pointed. From this, the orientation of the 2 broad surfaces of the brood comb could be determined. In certain cases, eg if the colony was on a branch close to a wall, the colony was considered to face in the direction of the more exposed surface (in this example the colony faces in the same direction as the colony surface away from the wall). The compass sector of the tree (eg N,NE, E and so on) in which the colony was located, usually the same as the direction "pointed" by the supporting twig, was also noted for a number of colonies. In a few cases, when a compass was not to hand, the orientation had to be estimated from the position of the sun and known landmarks. These measurements gave data in the form of circular distributions and their statistical analysis was based on Batschelet (1965).

(v) Shade/Exposure. This was the most difficult nest site attribute to quantify. At any site partially exposed to the sun, the shade experienced will change during the course of a single day, and also during the course of a year as the sun's arc moves. The shade from foliage received by nests in trees will also change as leaf fall occurs; most trees in Oman were evergreen, but the density of their foliage did appear to vary seasonally. To measure accurately the total sunlight received at one nest, continuous recordings from several light-meters pointing in different directions during the course of a year would be needed. "Spot" recordings at different nests for comparative purposes would be of little value; even if readings taken at two colonies within the space of a week and each at 09.00h were the same, the readings might be completely different at 15.00h. Variations in cloud cover would also make such "spot" comparisons difficult.

Instead, a brief visual description of the amount of shade covering each colony had to suffice initially eg for a colony in a cave, 100% shade/protection from directly above the colony might be recorded, along with a note that sunlight entered the cave early in the morning, striking most of the nest. Later during the course of these investigations, the visual description was supplemented with a shade/cover index on a 0 - 4 point scale, partly taking into account the value of cover from different directions ie cover from the south being more critical than from the north. This scale often proved too small in practice to discriminate between colonies that received visibly different amounts of shade and such colonies were given intermediate values eg 2/3, 3/4. Therefore, after all these records were gathered, a more discriminating 0 to 6 point scale was created (see below). The descriptions, shade indices and photographs for each colony were then examined and a value on the scale allocated. This allocation was performed "at one sitting" to ensure maximum consistency of the results.

Index Value	Percentage Shade	Index Value	Percentage Shade
0	0 - 10%	4	60 - 75%
1	10 - 30	5	75 - 90
2	30 - 45	6	90 - 100
3	45 - 60		

Though this assessment was far from ideal it gave an adequate measure of nest exposure that was similar to the "nest visibility" estimated by Seeley *et al* (1982) for honeybees in Thailand, and was a simple method appropriate for the circumstances.

(vi) In case there was evidence to suggest *florea* selected different types of nest site at different seasons, the owner was asked when he had first seen the colony and if he knew how old it was. From this information, an inspection of the state of the colony (brood, honey, stores etc) and knowledge of the seasons when many colonies swarmed (Chapter VI), an assessment was made as to the date the colony had arrived in the site. In many cases this was little more than a guess, not necessarily even accurate to within a month. For instance, a weak colony first seen at the end of September might be derived from one that had absconded just 3 weeks earlier after its nest had been robbed. Alternatively it might have been a swarm that had arisen after the end of the *Acacia tortilis* honey flow (Chapter VII) and had then been present, unobserved, since June.

(vii) Photographs were taken of some of the more accessible nests; these provided some of the above information directly and allowed other details to be confirmed. When a ruler was not in the photograph dimensions were measured with respect to the length of an adult *florea* worker (c. 10.25mm) or several worker cells (each 3.25mm diam.).

Apart from the location, it was sometimes not possible to record all the details cited above, because of various prevailing circumstances. For instance, after first seeing a colony, I might return a few days later to make a proper inspection to find that the honey had been taken and the bees had absconded. Other colonies were located out of reach in the top of dense thorny trees such as *Acacia nilotica* and *Ziziphus spina-christi*. In some such cases estimates were made of certain measurements; these estimates are only included in figures and tables when they were considered sufficiently accurate to fall within one of the stated ranges. Reliable informants provided a few of the records some of which were confirmed later, eg by traces of wax still on a tree branch or the roof of a cave.

Measurements from colonies which proved to be queenless were not included, in case this condition had influenced their choice of nest site.

Some of the nest attributes measured corresponded exactly to those measured by Seeley *et al* (1982) eg nest height and substrate branch diameter. Their 0 to 6 nest visibility scale may be loosely comparable (inversely) to my 0 to 6 shade scale; however, it is probable that many colonies in their 0 visibility category were not completely shaded and would fall into category 5 on my scale. Thus figures on their scale, which was intended primarily to indicate visibility to predators, if interpreted as indicating shade (for comparison with results here) would overestimate the proportion of colonies in very shady positions.

Nest habitat was not described in detail, as was done by Seeley *et al* (1982), but the colonies were put into broad habitat categories, Batina Gardens, Interior Gardens etc; the numbers of colonies in each category reflect the time spent on surveys there as well as the relative density of colonies.

C. RESULTS AND DISCUSSION

1. Location of *Apis florea* nests according to tree type occupied

1.1 Khabura and other Batina records

(i) Introduction

Table 2.2 shows the number and percentages of *A. florea* colonies found in different species of tree, bush etc in the old, cultivated areas (with their associated scrub) at Khabura along with a few records from other villages on the Batina. In order to determine whether the colonies were selecting any particular type of tree for their nests it was necessary to compare these figures with the relative numbers of different trees available. In an agricultural survey of a representative strip of the Khabura gardens, Dutton & Letts (1982) had already made accurate counts of the numbers of mature and young date palms and of *Citrus* trees (mostly limes) and measured the area of land that was devoted to these and other fruit trees and the areas of deserted land and that with scrub/trees. At least 20% of the Khabura colonies recorded fell directly into Dutton's survey area, while field observations and aerial photographs indicated that the areas in which the other Khabura colonies occurred were broadly similar in terms of tree composition.

(ii) Calculation of percentages of different tree types at Khabura

Dutton & Letts (1982) did not present data for the old gardens as relative numbers or percentages of different tree types (as required for this analysis) but it was possible, by rather involved computations, to derive these figures from several of their tables and figures as follows.

Dutton & Letts' Table 5.7.4 gave mean crop areas per hectare in the old Khabura gardens from which % area occupied by each crop was calculated (Table 2.1a). These figures, though, are different from relative tree numbers as they do not take into account planting density and exclude some of the intercropped trees ie limes and fruit trees.

However, Dutton & Letts' Table 5.5.1 gave numbers of discrete *Citrus* (489) and of *Citrus* interplanted with date palms (585) for old and new gardens at Khabura. Dutton suggested that the overall planting

Table 2.1 Relative abundance of different crops and trees in old gardens at Khabura, Oman. Derived from data in Dutton & Letts (1982); see text for assumptions and details of calculations.

(a) Percentage area occupied by discretely-planted, main crops and intercropped palms; based on Dutton & Letts' Table 5.7.4 which gives mean crop areas per hectare for the old, Khabura gardens.

	% Area
Discrete Palms	58.0
Intercropped Palms	7.7
Nothing/Scrub	23.8
Discrete Limes (*Citrus*)	2.9
Alfalfa	6.2
Discrete Fruit Trees	1.2
Bananas	0.1
Onions	.01

(b) Percentage area occupied by different tree types (with areas of intercropping being included twice, once for each constituent crop, giving a total of greater than 100%), numbers of different tree types and their percentage of total tree number in c. 105ha of garden at Khabura.

	% Area		Nos. of Trees		% Total Trees
Date Palms (Discrete)	58.0	65.7	7,739	← Old →	50.5
Date Palms (Intercropped)	7.7		4,970	← Young →	32.4
Nothing/Scrub	23.8		1,160		7.6
Discrete Limes (*Citrus*)	2.9	6.4	936		6.1
Intercropped Limes	3.5				
Alfalfa	6.2				
Discrete Fruit Trees (including bananas)	1.3	5.3	515		3.4
Intercropped Fruit Trees	4.0				
Intercropped Other	.2				
TOTAL	107.6		15,320		100

density of *Citrus* was similar whether discrete or intercropped, therefore the area of discrete *Citrus* compared to interplanted *Citrus* will be at a ratio of 489 : 585 (this assumes that the ratio of discrete : intercropped *Citrus* for old gardens is approximately the same as that for new gardens; this may be true, but in any case only a small proportion, 138 out of 1074 trees, of the *Citrus* sample came from the new gardens). Therefore with 2.9% of the crop area being discrete *Citrus* trees, 2.9 x 585/489 = 3.5% of the crop area is of *Citrus* interplanted with date palms. The total area of *Citrus* is 2.9 + 3.5 = 6.4%.

With 7.7% of the area of the old gardens being date palms intercropped with other trees and crops (from Table 5.7.4) but knowing that 3.5% of the area is of intercropped date palm and *Citrus*, it can be calculated that 7.7 - 3.5 = 4.2% of the area is of palms interplanted with crops other than *Citrus*. From field observations and Dutton & Letts' report this means approximately 4% fruit trees and 0.2% crops such as onions.

Thus, adding these percentage areas of intercropping to the percentage areas of discrete crops already derived from Dutton & Letts' Table 5.7.4, gives the overall percentage areas of the various trees and crops (Table 2.1b) - with a total of more than 100% because of the inter-cropping.

Having calculated the percentage area of the various crops, the corresponding numbers of trees needs to be found. From Dutton & Letts' Table 5.3.2 it can be calculated that the total numbers of palms (discrete, intercropped and edge) in the area of old gardens concerned were :- Mature, 7,739 and Young, 4,970. Dutton's designation of"young" palms corresponded broadly to my own (less than c. 3m high) for *A. florea* nests that were found close to the ground on their lower fronds.

From Dutton & Letts' Figure 5.5.1 it can be calculated that there were 936 *Citrus* trees (occurring in 22 of the old gardens) in the area to which the percentages in Table 2.1b refer. Thus 936 *Citrus* trees occupy 6.4% of the crop area. If the fruit trees, which occupy 5.3% of the crop area, are at the same density as the *Citrus* there would be 936 x 5.3/6.4 = 775 of them. However, most of the fruit trees eg Mango, Indian Almond, are larger than the *Citrus* and it is estimated that 1½ *Citrus* trees are equivalent to 1 fruit tree in terms of area. Thus it is calculated that approximately 775 x 2/3 = 515 fruit trees occupy this 5.3% of the crop area.

Aerial photographs and field observations indicated that approximately half of the "nothing/scrub" category was empty but half was occupied by trees and shrubs (*Acacia nilotica, Ziziphus spina-christi* etc) at approximately the same density as the fruit trees. Thus 515 x 11.9/5.3 ≃ 1160 trees and shrubs occupy 11.9% (half of 23.8) of this area.

These derived figures for numbers of trees in Dutton's Khabura survey area are presented in the second column of Table 2.1b. From these figures the percentage of the total number of trees was calculated for each tree category; these percentages are given in the third column of Table 2.1b and in Table 2.2 for comparison with the numbers of *A. florea* colonies in each category.

From Dutton & Letts' Figure 5.7.3 it was calculated that these 15,320 trees were in c. 105 hectares of gardens (97ha old, including "empty/scrub", and 8ha no longer cultivated) at an overall density of 145.4 trees/ha.

According to my own field observations, the primary components of Dutton's "scrub" category were *Acacia nilotica, Ziziphus spina-christi* and the other species listed under scrub/non-fruit trees in Table 2.2;

these are mostly native and naturalized species that were sometimes encouraged as shade, timber, ornamental etc trees. *Mangifera indica* (mango) and others listed in Table 2.2 were the main species in the fruit tree category. Dutton (pers. comm.) confirmed that this categorization corresponded with his. The trees within each category have been listed in what was thought to be their approximate order of abundance at Khabura. These final figures for relative numbers and percentages of each tree type are the result of rather involved calculations, based on Dutton & Letts' data, and a small degree of estimation. However, they are almost certainly accurate enough to fall within the range of variation that existed in different parts of the old Khabura gardens, where most of the *florea* colonies were found, and are suitable for use in the statistical analysis of nest site selection by these bees.

(iii) Analyses

Expected numbers of *florea* colonies in each tree category were calculated (Table 2.2) according to the frequency of trees in each category, on the assumption that the colonies selected the trees at random. From these expected numbers and the observed numbers, χ^2 - values were calculated to determine whether or not *florea* were selecting particular types of tree for nest sites.

Based on Hunter (1962), Selection Ratios for each tree type were calculated as follows:-

$$\frac{\%\ \textit{florea}\ \text{nests in tree type x}}{\%\ \text{tree type x in habitat}}$$

Values < 1 indicate rejection or avoidance of the tree type

Values > 1 indicate positive selection of the tree type

Table 2.2 Selection of trees for nest sites by *Apis florea* at Khabura and other sites on the Batina coast of Oman. Unbracketed figures :- percentage different tree types (derived from Dutton & Letts 1982), expected & observed numbers and observed percentages of *A. florea* colonies in different trees in old gardens at Khabura. Figures in brackets include a few colonies from similar gardens elswhere on the Batina coast. Selection ratios indicate selection/avoidance of tree types by *A. florea* colonies for nest sites. See text for further details.

		% Total Trees	No. of *A. florea* Colonies		% *A. florea* Colonies Observed	Selection Ratios
			Expected	Observed		
	Phoenix dactylifera (Mature)	50.5	33.8(38.4)	7	10.4 (9.2)	.206 (.182)
	Phoenix dactylifera (Young)	32.4	21.7(24.6)	4	6.0 (5.3)	.185 (.164)
Scrub/ Non-Fruit Trees	*Acacia nilotica*			6(12)	9.0(15.8)	
	Ziziphus spina-christi			10(11)	14.9(14.5)	
	Prosopis cineraria			4	6.0 (5.3)	
	Sesbania sesban			1	1.5 (1.3)	
	Azadirachta indica			3	4.5 (3.9)	
	Euphorbia sp. indet. RPW 792			1	1.5 (1.3)	
	Acacia tortilis			1	1.5 (1.3)	
	Tamarindus indica			1	1.5 (1.3)	
	Sub-Total	7.6	5.1 (5.8)	27(34)	40.3(44.7)	5.3 (5.88)
	Citrus spp.	6.1	4.1 (4.6)	16(17)	23.9(22.4)	3.92 (3.67)
Fruit Trees	*Mangifera indica*			4 (5)	6.0 (6.6)	
	Terminalia catappa			3	4.5 (3.9)	
	Cordia myxa			3	4.5 (3.9)	
	Morus sp.			2	3.0 (2.6)	
	Punica granatum			1	1.5 (1.3)	
	Psidium guajava			0	0 (0)	
	Ficus carica			0	0 (0)	
	Sub-Total	3.4	2.3 (2.6)	13(14)	19.4(18.4)	5.7 (5.41)
	Totals	100%	67 (76)	67(76)	100%	

Combining "Fruit Trees" (Expected values <5) with *Citrus* and testing whether or not there is selection overall for different tree types:-

Khabura: $\chi^2_3 = 209.5$; Sig. $p < .001$

Batina : $\chi^2_3 = 258.7$; Sig. $p < .001$

(iv) Interpretation of Results

There is little difference in the percentages of colonies in different tree types whether or not the extra Bātina colonies are added to those at Khabura. The percentage of colonies in *Acacia nilotica* trees did increase from 9.0 to 15.8% with their inclusion but this **was a result of a more intensive search in** an area of abandoned date gardens close to the sea, where these trees were more numerous than elsewhere. Bearing this in mind, the results from Khabura and the Bātina will be considered together. The statistical analyses (χ^2- values, Table 2.2) show very strongly that *florea* colonies are not selecting at random the trees in which they nest. The selection ratios indicate that they are avoiding both mature (.206, Khabura) and young (.185, Khabura) date palms, but favouring the Scrub/Non-Fruit Trees (5.3, Khabura), *Citrus* (3.92, Khabura) and Fruit Trees (5.7, Khabura).

If date palms, being avoided, are excluded from the figures, rather fewer colonies than might be expected occur in *Citrus* trees and rather more in the Scrub and Fruit Trees (combined), but the differences are not significant (Table 2.3). The small differences could easily be explained by slight errors in the estimates of relative tree numbers, the tree counts having been made in only a portion of the area in which *florea* colonies were found, and by colonies in some trees being missed. The avoidance of date palms cannot be attributed to such errors; they were clearly the most abundant tree (>80%) of the cultivated Batina strip, yet contained only 14.5% of the *florea* colonies. It was usually easy to see their nests attached to the base of frond mid-ribs and exposure, especially lack of shade, is thought to be the main reason why *florea* did not often nest in date palms. In fact of the 4 colonies recorded in young date palms, 2 were in shady positions close to the ground enveloped by lucerne (*Medicago sativa*) which was being grown around the trees.

Table 2.3 Comparison of *Apis florea* **nest frequency in** *Citrus* **versus** Other Trees, excluding date palms, at Khabura - unbracketed figures. Figures in brackets include a few colonies from similar gardens elsewhere on the Batina Coast.

	No. of Colonies	
	Observed	Expected
Citrus	16(17)	20(23)
Scrub and Fruit Trees	40(48)	36(42)
Totals	56(65)	56(65)

Testing selection by *A. florea* for Scrub and Fruit Trees versus *Citrus*:-

Khabura: $\chi^2_1 = 1.24$ NS

Batina : $\chi^2_1 = 2.42$ NS

1.2 Gardens/Oases in the Interior of Oman

(i) Calculation of percentages of different tree types

Table 2.4 shows the numbers and percentages of *florea* colonies found in different species of trees in oases of the Interior of Oman. Dutton & Letts (1982) made accurate counts of relative numbers of palms, *Citrus* and other fruit trees in two such oases, Ibri and Arāqi, in the Dhahira region. Though the frequencies of *Citrus* trees and young date palms were rather higher in Ibri than Arāqi, and the frequency of mature palms rather lower, an average of the tree frequencies found in the 2 oases is likely to be representative of relative tree numbers in most Omani oases (13 out of 44 of these *florea* colonies were in fact recorded from Ibri). The figures in Dutton & Letts' (1982) Table 5.3.3 (Ibri) and 5.3.5 (Arāqi) were therefore combined as percentages and are presented in Table 2.4. The trees/bushes listed as "others" were not counted by Dutton & Letts, only fruit trees, and therefore I have estimated from my own observations that they typically constitute about 3% of the total trees; to balance this addition I have deducted 2% from the figure for mature date palms and 1% from the figure for young palms (these being the two most abundant categories). Therefore, though each colony will not have selected its nest site from trees/bushes in these exact proportions, the figures should correspond well to overall nest site availability for the 44 wild *florea* colonies investigated in these Interior oases. Expected numbers of *florea* colonies were calculated according to the relative proportions of the different trees, <u>excluding</u> bananas (*Musa* spp.) as these were not considered to provide potential nest sites because of their structure (mostly leaf with no suitable branch or twig for attachment). Indeed, I never saw any *florea* nests on banana plants in Oman and only one was reported to me.

Table 2.4 Selection of trees for nest sites by *Apis florea* in gardens/oases of the interior of Oman. Percentages of different trees available (derived from Dutton & Letts 1982 - details in text), expected and observed numbers, and observed percentages of *A. florea* colonies in these trees. Selection ratios indicate selection/avoidance of trees by *A. florea* colonies for nest sites (see section 1.1 (iii) for details).

		% Total Trees	No. of *A. florea* Colonies Expected		No. of *A. florea* Colonies Observed	% *A. florea* Colonies Observed	Selection Ratios
	Phoenix dactylifera (Mature)	46.2	22.2		5	11.4	.25
	Phoenix dactylifera (Young)	24.8	11.9		4	9.1	.37
	Citrus spp.	13.1	6.3		25	56.8	4.3
	Musa sp.	8.5	0		0	0	0
Fruit Trees	*Psidium guajava*	2.6	1.3		0	0	0
	Mangifera indica	0.9	0.9	3	2	4.5	3.8
	Carica papaya	0.3			0	0	
	Ficus carica	0.3			1	2.3	
	Morus sp.	0.3			0	0	
Others	*Ziziphus spina-christi*	3.0	1.4	7	2	4.5	5.3
	Prosopis cineraria				2	4.5	
	Jasminum sp.				1	2.3	
	Salsola sp.				1	2.3	
	Ornamental indet.				1	2.3	
	Totals	100	44		44	100	

Combining "Fruit Trees" and "Others" (Expected values<5) with *Citrus* spp. and investigating whether or not there is selection by *A. florea* for different tree types, by testing versus mature and young date palms.

$\chi^2_2 = 82.2$; Sig. $p < .001$

(ii) Interpretation of results

The χ^2- value of 82.2, Table 2.4, shows there is very clear selection among the tree-types by *florea* for nest-sites in Interior gardens, as with the colonies found at Khabura and elsewhere on the Batina coast. The selection ratios show that once more both mature (.25) and young (.37) date palms were avoided, the ratios being a little higher but of the same order as those from the Bātina. Over-exposure to the sun is also the reason advanced for this avoidance of date palms. Two out of the 4 colonies on young date palms were in fact well-shaded by dense ground vegetation, like the two amidst lucerne at Khabura.

When date palms, bananas and "Others" (for which tree numbers were only estimated) are excluded, and observed and expected numbers of *florea* colonies in *Citrus* and Fruit Trees are compared (Table 2.5a), the figures indicate that there may be some preference for *Citrus*, but that selection is not statistically significant. At Khabura, when scrub and fruit trees were combined, they contained proportionately more *florea* than the *Citrus* trees, though the difference was not significant (Table 2.3). On the assumption that *florea* were selecting sites with adequate shade, as suggested by the avoidance of date palms, this apparent preference for *Citrus* is most likely explained in terms of avoidance of guave trees, *Psidium guajava*. This species was the most abundant of the fruit trees, at least in Ibri and Arāqi where there were more than the other fruit trees combined, but no nests were found in them; its foliage is not as dense as that of others such as mango, *Mangifera indica*. Likewise, pawpaw, *Carica papaya*, is superficially similar to the date palm in shape and would provide little in the way of shade or a suitable nest support. When these trees are excluded (Table 2.5b), the observed and expected values correspond almost exactly; though the χ^2 test is not strictly valid, as one expected value is less than 5, no significant selection is indicated.

Table 2.5 Comparisons of *Apis florea* nest frequency in
(a) *Citrus* versus "Fruit Trees" (excluding date palms, bananas and "others") and
(b) *Citrus* versus Mango and Fig and Mulberry
in gardens/oases of the interior of Oman.

(a)

	No. of Colonies	
	Observed	Expected
Citrus	25	20.96
Fruit Trees	3	7.04
Totals	28	28

$\chi^2_1 = 3.097$ $.05 < p < .1$ NS

(b)

	No. of Colonies	
	Observed	Expected
Citrus	25	25.12
Mango, Fig, Mulberry	3	2.88
Totals	28	28

$\chi^2_1 = 0.006$ NS

The selection ratio for "Other" trees (5.3, Table 2.4) is the same as that for Scrub/Non-Fruit trees at Khabura (Table 2.2) which, with some of the trees being the same, eg *Ziziphus* and *Prosopis*, adds support to the consistency of the selection by *florea* for such trees and to the accuracy of the surveys of nests and vegetation, even though the samples were small. The slightly higher selection ratio for *Citrus* in the Interior (4.3) than at Khabura (3.92) could just be due to sampling error; however, it could also be due to the fact that up to 25% of the *Citrus* trees in the Interior oases were of varieties or species other than limes, *Citrus aurantifolia*, whereas the *Citrus* on the Batina were almost entirely limes (Dutton & Letts 1982). The non-lime *Citrus* were often larger trees, which perhaps provided more shade; indeed on one visit to a region of gardens in Ibri of 10 *florea* colonies found in *Citrus* trees only 3 were in trees I identified as limes, but 7 in "non-limes". Though the ratio of limes : non-limes was not counted, the siting of these 10 colonies did suggest that non-limes were particularly favoured, giving a higher selection ratio for all *Citrus* in the Interior, than on the Batina.

1.3 Wild habitats

Frequencies of *florea* nests in wild habitats, ie uncultivated by man but some used as rangeland for goats and sheep by pastoralists, in northern Oman are given in Table 2.6. The numbers of colonies involved are too small for statistical analysis. Also, accurate figures were not available for relative frequencies of the tree species in the different habitats, so expected numbers of *florea* nests in each (assuming selection at random) could not be calculated.

However, with *Acacia tortilis* being the dominant tree of the plains and *Ziziphus spina-christi* that of the wadis, and with them con-

Table 2.6 Frequency of *Apis florea* nests in different species of tree/bush in wild habitats of northern Oman.

Plant Most Frequent In:			No. of colonies found Plains	Wadis	Mountains	Totals
Plains	Acacia tortilis	(tree)	7	0	1	8
Plains	Salvadora persica	(bush)	1	0	/	1
Plains and Wadis	Prosopis cineraria	(tree)	2	0	/	2
Wadis	Ziziphus spina-christi	(tree)	0	4	0	4
Mountains	Commiphora sp. (prob. myrrha)	(bush)	/	/	1	1
	Total no. of colonies		10	4	2	16

taining 7 out of 8 and 4 out of 4 of the colonies in these habitats, respectively, it is probable that, of the plants available, they can provide satisfactory nest sites and are not completely avoided. The same applies to *Prosopis cineraria*. Other species of tree are scarce and though bushes are abundant in places, most are low and presumably will only be used, as with the myrrh bush (*Commiphora*) and *Salvadora persica*, when other suitable nest sites are absent nearby.

All the species mentioned can have fairly dense foliage, though this is less so for *Acacia tortilis*. However, without extra si~~t~~ghtings it can only be concluded that when *florea* do nest in these wild habitats, they will tend to use trees that offer a certain amount of shade, rather than exposed bushes.

1.4 New and ornamental gardens

Little time was spent searching for *florea* colonies in the "new gardens" on the Batina that were brought into cultivation mostly in the 1970s (described by Dutton & Letts 1982), as they did not offer so many good nest sites as the "old gardens", having larger areas of vegetables and fodder crops and fewer trees, mostly immature. Two colonies were found in these new gardens, both in aubergine plants (*Solanum melongena*), and they have been included with the colonies found in shrubs and trees in "ornamental" gardens, most of them surrounding new houses in the capital area of Oman (Medinat Qaboos, Mīna al Fahal, Seeb and so on). The number of nests found in each species of plant are listed in Table 2.7.

After seeing several of such colonies it became apparent that a number of them were quite close (within 1m) to the buildings and walls enclosing the gardens, and that these might have been providing some shade. The presence or absence of such structures was therefore recorded

Table 2.7 Nest sites of *Apis florea* in "new" and ornamental gardens and proximity of nests to walls and buildings that might offer shade and protection.

Nest Site	Number of *A. florea* Colonies			
	Walls in vicinity absent	Wall present nearby ~ 1-10m	Wall very close < ~ 1m	Total
Bougainvillea glabra		1	6	7
Trees, shrubs indet.	1	3	1	5
Lantana camara		2		2
Solanum melongena	2			2
Ipomoea pes-caprae			1	1
Datura sp.			1	1
Phoenix dactylifera			1	1
Nerium mascatense		1		1
Total	3	7	10	20

as well (Table 2.7). The close proximity of 10 out of 20 of the colonies to the walls may in part be due to the fact that many of the garden shrubs, particularly the *Bougainvillea*, were grown close to these structures and not further away in the open. Unfortunately no actual data on the distribution and abundance of these plants in ornamental gardens was gathered.

However, the shrubs were not usually restricted to walls of any particular aspect and the colonies would have had a choice of walls against which they could site their nest; the aspect and position (bearing) with respect to the colonies of the closest walls was measured in several cases (Table 2.8). With all 6 of the colonies where this information was recorded, they were adjacent to walls facing between ESE and S. The mean bearing of the walls from the colonies was 319^o (ie to the NW); the Rayleigh test (Batschelet 1965) shows that this distribution is not random but that there is a preferred bearing ($Z = 3.745$, Sig. $p < .05$).

The sample is too small for statistical analysis by the χ^2 test, but if these 6 colonies were selecting sites against these walls at random, the expected number adjacent to different walls would be as follows:-

	East to South Quadrant	:	3 Quadrants from South, through North to East
Expected	1½	:	4½
Observed	6	:	0

With this arrangement, it can be seen that the probability of a colony being adjacent to a wall in the East to South quadrant is 1/4 and against the remaining walls is 3/4, if there is no selection by the bees. Thus, analysed as a binomial, the probability of all 6 colonies being in the

Table 2.8 Position/bearing with respect to nest, and aspect of walls close (<~1m.) to which 6 *Apis florea* colonies had selected nest sites in ornamental gardens.

Mean angle calculated according to Batschelet (1965) - see section 2.4.

	Bearing of wall from colony	Approx. aspect of wall
Bougainvillea glabra	330°	SSE
" "	340°	SSE
" "	360°	S
Ipomoea pes-caprae	315°	SE
Datura sp.	290°	ESE
Phoenix dactylifera	320° (also 230°)	SE (also NE)
Mean	*319°	SE/SSE
95% Confidence Limits	293° - 345°	

* Therefore mean colony exposure is to the SE (139°), 95% confidence limits 113° - 165°.

one quadrant is $\frac{1}{4^6} = 2.44 \times 10^{-4}$. This is highly significant and indicates strongly that *florea* colonies nesting against walls favoured those with an East to South aspect.

Indeed, after the departure of colonies from 2 of these sites at Khabura, other colonies landed in virtually the same positions that had been adopted by the previous incumbents. One "new" colony, absconding from an experimental hive (No. 9) on 14.xii.79, attached its comb to the lower edge of a portakabin overgrown by a creeper, *Ipomoea pes-caprae*, on which an earlier colony, a swarm of unknown origin, had started to build its comb just a few cm away on 14.vi.79. (This colony was removed to a hive, 5, and on 14.vi.79 a queenless swarm from another hive, 13, settled and built comb on the edge of the portakabin exactly where the absconding colony later settled.) At the second site, a *Bougainvillea* growing against the SSE facing wall of a small courtyard garden, a colony, FD, had been present for nearly a year before absconding when its comb collapsed at the end of May 1980 (see Table 6.3 and associated comments, Chapter VI). Yet after I left Oman, R.W. Dutton (pers. comm.) reported another colony settled at nearly the same site. Some Omanis, for instance Nāsr Ahmad al-Ghaythi of Zāhib (Chapter IV), also reported that colonies sometimes "returned" to old nest sites in trees and caves (probably different colonies in reality), so such "returning" behaviour may not be due to chance, but to certain sites being particularly suitable.

Whether there is some pheromonal attraction of the new colony to the remnants of wax comb at such a site, or whether the site is selected on its physical characteristics alone, is not known. However, the above information does strongly suggest that *florea* colonies near buildings in Oman favour walls with a SE/SSE aspect where they are likely to receive more insolation in the morning but less in the afternoon;

and if there is adequate shade from foliage and from the honeycomb above, direct insolation at mid-day on the brood comb should be minimal. It appeared that NW facing walls were avoided; colonies would not benefit from warming insolation in the cooler hours of the morning in such sites. A similar tendency, but not statistically significant, was recorded for the *florea* kept in wall recesses by Nāsr Ahmad al-Ghaythi (Chapter IV), and the implications are discussed further in section 4 of this chapter with the results on nest orientation and tree sector occupied.

2. Location of *Apis florea* nests in bushes and trees : height distribution

Height distributions of *florea* colonies in trees and bushes, from all habitats, are given in Figures 2.1a and b. The mean height 3.28m (n = 126) is very close to that recorded by Seeley *et al* (1982) for *florea* in Thailand, but the pattern of distribution is different. The modal height in Thailand was between 1.5 and 2.0m, but in Oman the distribution was distinctly bi-modal with the primary mode between 0 and 1.0m and a secondary one between 3.0 and 4.0m, with relatively few colonies between 1.0 and 2.0m. There are 4 possible reasons for this "dip" in the distribution:-

(i) Unrepresentative sampling of *florea* colonies. This is not likely as those colonies between 1.0 and 2.0m are closest to eye level and should have been the easiest to locate.

(ii) Greater predation, particularly by man, of *florea* colonies between 1.0 and 2.0m. This is plausible as such colonies would be amongst the easiest to locate and remove. However, most colonies that I recorded were reported to me by the main "predators" themselves, the garden owners, and it is unlikely that they would omit to

Figure 2.1 Nest height distributions for *Apis florea* in trees in Oman.

a. For 93 colonies measured accurately enough to fall within 0.5m limits.

b. For the above 93 colonies, plus another 33 colonies allocated to the same 0.5m categories, but whose height was measured or estimated less accurately (to within *circa* 1m).

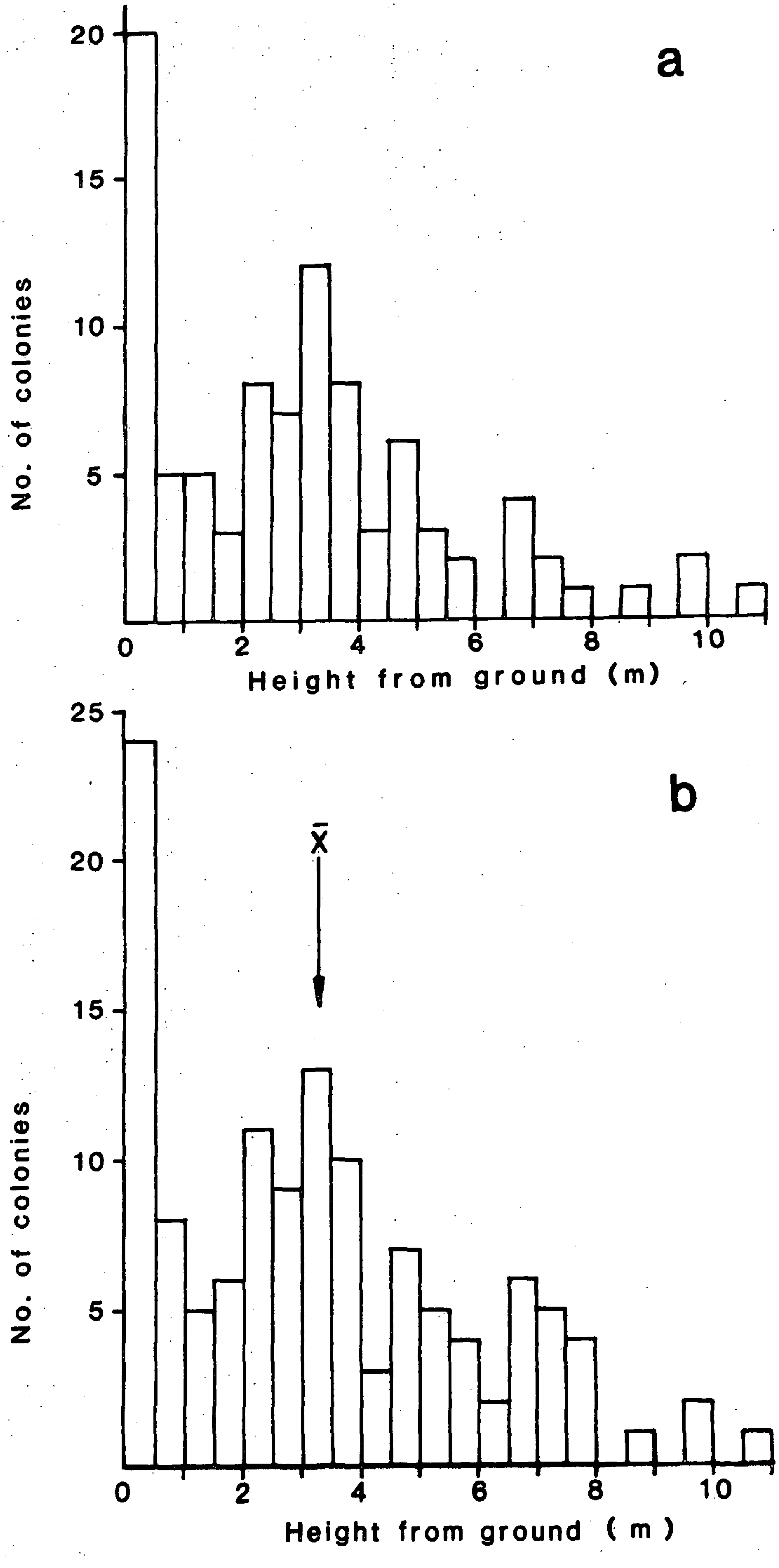
Mean height (taking mid-point of each 0.5m class x no. in that class) = 3.28m

n = 126, Range 0.2 - c. 10.7m

Median = 3.0m (end of 2.5 - 3.0m class)

Primary Modal Class = 0 - 0.5m

Secondary Modal Class = 3.0 - 3.5m


a
No. of colonies
20
15
10
5
0
2
4
6
8
10
Height from ground (m)
b
x̄
No. of colonies
25
20
15
10
5
0
2
4
6
8
10
Height from ground (m)

tell me of colonies at this height, but point out ones that were lower and higher.

(iii) Selection, by *florea*, of lower and higher nest sites would also seem plausible to avoid the greater chance of detection by man at intermediate heights. However, there was no evidence to suggest there were two sub-populations of *florea* selecting different nest sites and with as many (11) nests between 1.0 and 2.0m as, say, between 4.0 and 5.0m (10 nests) there was not complete avoidance of this height.

(iv) Nest site availability between 1.0 and 2.0m might be low.

To consider this last possibility a breakdown of the nest heights of colonies was made (Figure 2.2 and Tables 2.9 and 2.10), broadly corresponding to the different tree/bush types set out in the previous section (Tables 2.2 and 2.4). Though the limits of the vegetation strata above and below *florea* nests were not recorded, as by Seeley *et al* (1982), a knowledge of the typical structure of the different tree and shrub species that were occupied by the colonies permits interpretation of the Oman data (the plant species used for nests were not identified by Seeley *et al* in Thailand).

Date palms were by and large either short, with fronds arising from the trunk close to the ground, or comparatively tall with the first fronds emerging usually well over 3m from the ground (the lower ones having been removed). The height distribution of *florea* nests in this species (Figure 2.2a) matches this pattern closely.

Colonies in native and naturalised shrubs and trees (Figure 2.2b) have a pattern of height distribution similar to the overall pattern (Figure 2.1). However, further breakdown according to plant species suggests, though the samples become small, that *florea* are not avoiding particular nest heights, but occupy sites at any height less than c. 8m when the structure of the plant makes this possible. For instance,

Figure 2.2 Nest height distributions of *Apis florea* colonies in trees and bushes in Oman. Breakdown of data in Figure 2.1b into different tree categories as follows:-

a. Date palms
b. Native and naturalised shrubs and trees; for further breakdown see Table 2.9.
c. Shrubs and trees in "new" Batina gardens and in ornamental gardens; for further breakdown see Table 2.10.
d. Cultivated fruit trees other than *Citrus* spp.
e. *Citrus* spp.

Characteristic shapes of some of the trees and shrubs are illustrated.

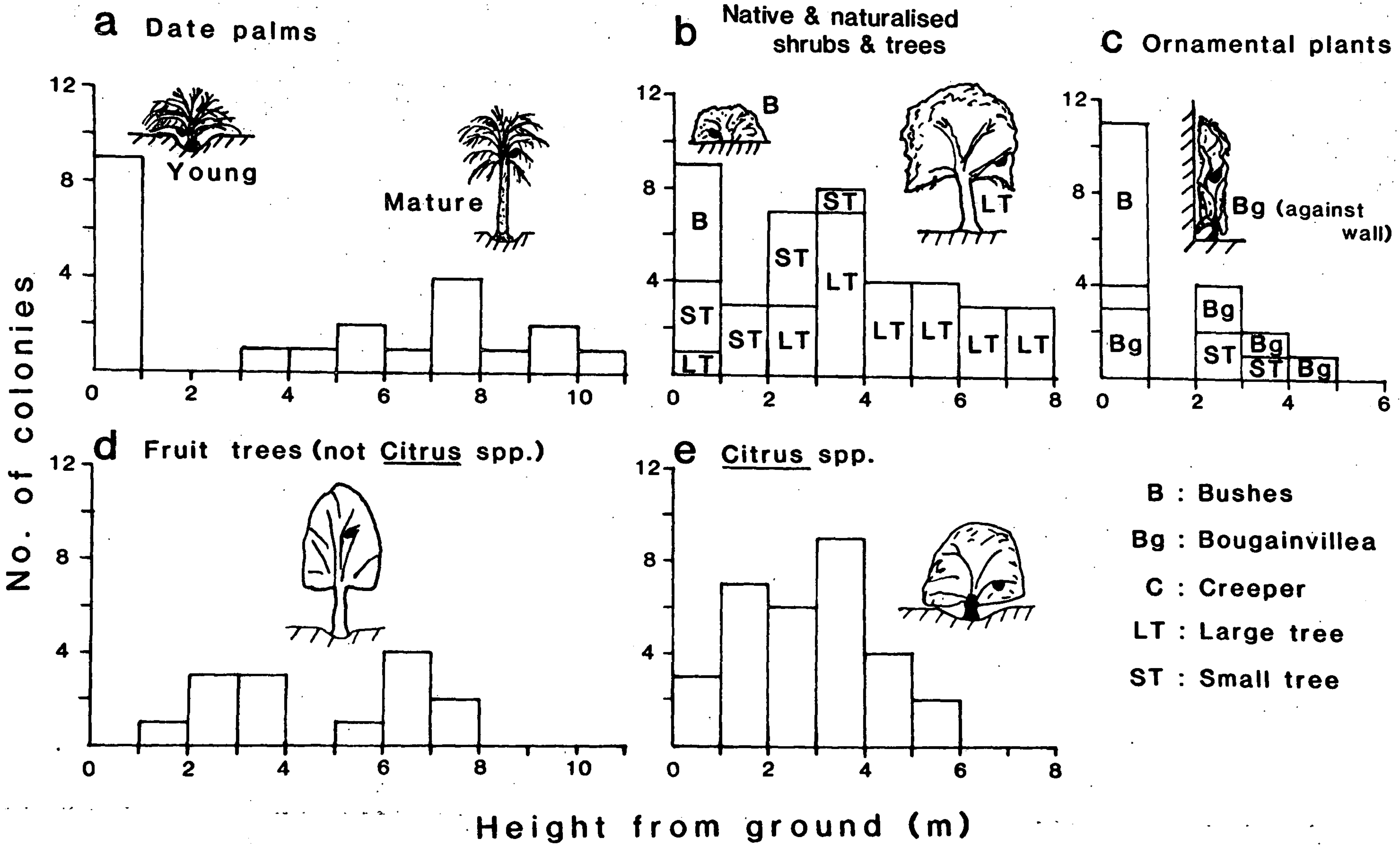

a Date palms
Young
Mature
b Native & naturalised shrubs & trees
C Ornamental plants
Bg (against wall)
d Fruit trees (not Citrus spp.)
e Citrus spp.
B
ST
LT
Bg
No. of colonies
Height from ground (m)
0
2
4
6
8
10
12
B : Bushes
Bg : Bougainvillea
C : Creeper
LT : Large tree
ST : Small tree

Table 2.9 Nest height distribution of *Apis florea* in naturalised and native shrubs and trees, in old gardens and wild habitats in Oman. Breakdown of Fig. 2.2b according to plant species and structure.

		No. of colonies per height class							
	Height (m)	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8
Bushes	Commiphora sp.	1							
	Jasminum sp.	1							
	Salsola sp.	1							
Small Trees	Acacia tortilis	2	3	2	1				
	Euphorbia sp.			1					
	Sesbania sesban			1					
Bush to Large Tree	Prosopis cineraria	3			1			1	
Large Trees	Ziziphus spina-christi			3	4	2	1		1
	Acacia nilotica	1			2	1	2	1	2
	Azadirachta indica					1		1	
	Indet.						1		

Table 2.10 Nest height distribution of *Apis florea* in plants in "new" Batina gardens and in ornamental gardens in Oman. Breakdown of Fig. 2.2c according to plant species and structure.

		No. of colonies per height class				
	Height (m)	0–1	1–2	2–3	3–4	4–5
Bushes	Lantana camara	2				
	Datura sp.	1				
	Solanum melongena	2				
	Nerium mascatense	1				
	Bush indet.	1				
Creeper	Ipomoea pes-caprae	1				
Climber	Bougainvillea glabra	3		2	1	1
Trees	Indet.			2	1	

Acacia tortilis is usually a small tree which, particularly when young, may have branches and foliage fairly close to the ground and Table 2.9 shows that colonies are found at all heights. However, the larger trees such as *Ziziphus spina-christi* and *Acacia nilotica* do not often have many branches or foliage within 2m of the ground (perhaps from browsing and cutting), so *florea* colonies can only nest higher in the trees. As young plants, these trees are spindly in habit with little shade or support suitable for *florea.* In contrast, most bushes and shrubs in Oman, in habitats where *florea* were found, appeared to be fairly compact and less than 1 - 2m high. Thus unless *florea* were to nest in exposed sites at the tops of the bushes, their nests would need to be below 1m in height to obtain adequate shade.

Similarly, in the mainly ornamental gardens (Figure 2.2c and Table 2.10) small bushes were usually dominant, with just a few trees and only *Bougainvillea* bridging the height gap, so that most colonies were low down in the bushes but a few higher up, in trees which did not have low branches. Colonies in *Bougainvillea* between 1 and 2m might be expected, but this absence may be due to the small sample size.

Fruit trees, such as the mango, did not often have branches close to the ground either (probably from pruning) and it can be seen that the height of *florea* colonies is distributed fairly evenly above 2m (Figure 2.2d). However, *Citrus* trees and especially limes, *C. aurantifolia*, often have an almost hemispherical structure with the branches and foliage extending close to the ground, so that nest sites are usually available from almost ground level to the top of the tree. Figure 2.2e shows there is no "dip" in the number of nests between 1 and 2m, but that they are distributed fairly evenly between 0 and 6m, in a pattern similar to the overall height distribution recorded by Seeley *et al* (1982).

Therefore, it appears that the bimodal distribution of *florea* nest heights is primarily a function of nest height availability, with bushes below 1 to 2m and taller trees without lower branches predominating. The two species of tree, *Acacia tortilis* and *Citrus aurantifolia*, which sometimes do have branches right down to ground level are therefore the exceptions in the vegetation which "prove the rule" that *florea* colonies select any available nest site between 0 and 8m (occasionally to 11m) around a mean of about 3m; despite the comparatively small number of nests between 1 and 2m there is probably no avoidance of any particular height below 8m.

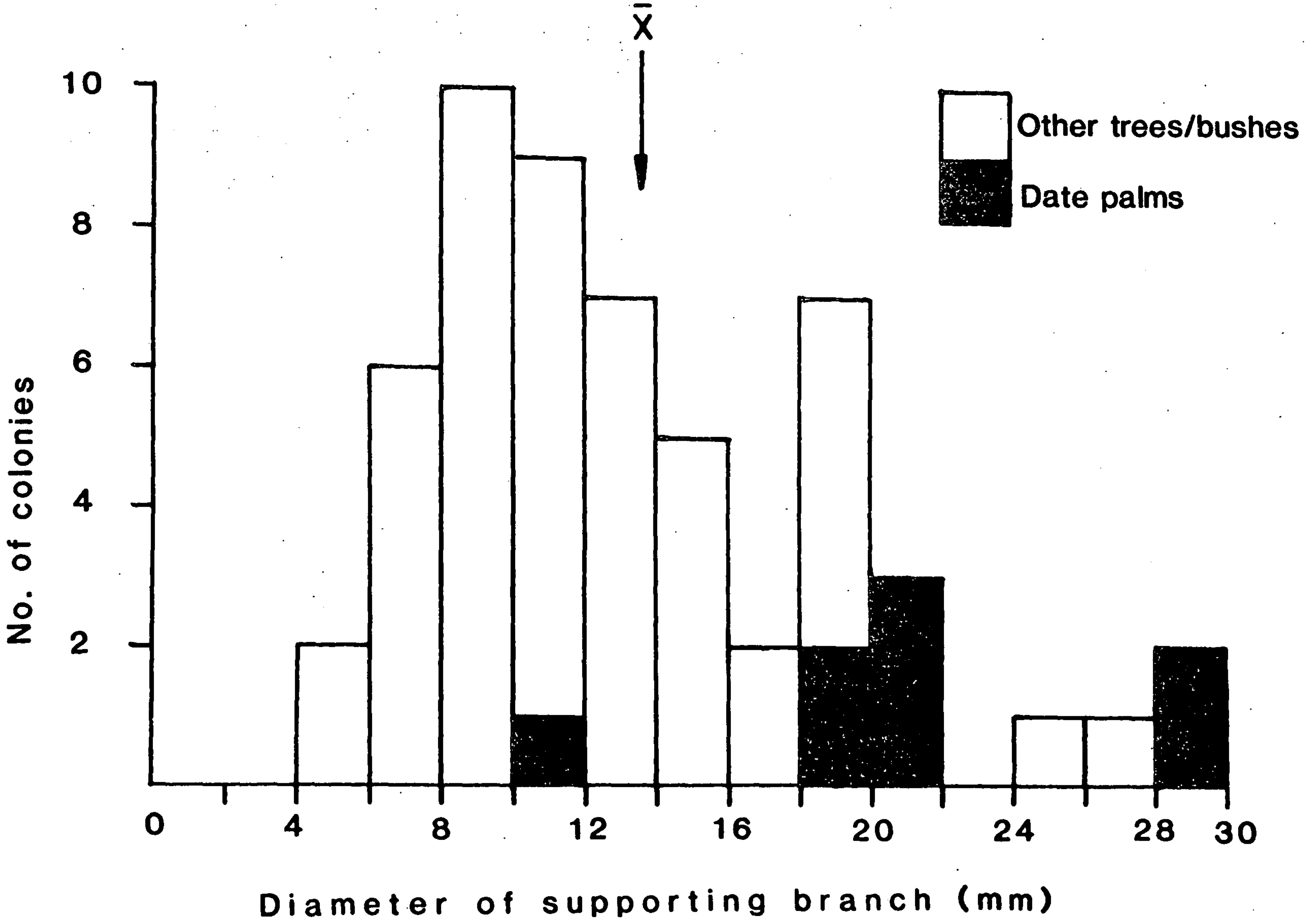
3. Location of *Apis florea* nests in bushes and trees : size of supporting branch

The distribution of the diameters of the nest support branches used by *florea* in Oman are given in Figure 2.3. The mean of 13.6mm is close to the 12mm recorded by Seeley *et al* (1982) for *florea* in Thailand. In trees, the combs of colonies did encircle supports as large as 30mm in mean diameter (40mm wide by 20mm high in this case of a date palm frond mid-rib) and one colony, not included here but in section 6 on cavities, was attached to a piece of timber 48 x 67mm (mean 57.5mm) in cross-section, the honeycomb encircling it at one end. Therefore, even though colonies will attach their combs to very large structures and the roofs of caves, not encircling a supporting branch at all, it is evident that *florea* favoured branches or twigs between about 6 and 20mm in diameter.

The hatched area in Figure 2.3 indicates that the support diameter for nests on palm fronds is rather higher (mean 21.25, S.E. 2.05mm, $n = 8$) than for nests on other trees (mean 12.3, S.E. 0.71mm, $n = 47$) and this difference is significant, $t = 4.69$, $p < .001$.

Figure 2.3 Distribution of support branch diameters for *Apis florea* nests in trees in Oman. Hatched areas are for colonies in date palms.

Mean diameter : 13.6mm ($\frac{1}{n}$ Σ mid-point of each class x frequency). Range : 5 - 30mm. Modal Class : 8 - 10mm. Median : 12mm. n = 55.


X̄
Other trees/bushes
Date palms
No. of colonies
10
8
6
4
2
0
4
8
12
16
20
24
28
30
Diameter of supporting branch (mm)

Most of the *florea* nests on date palm fronds were close to the trunk where the frond mid-rib is at its thickest. The colonies could, however, have selected sites closer to the distal end of the frond if a smaller support had been the priority; but if they had chosen such a position they would have received less shade and been liable to greater movement in the wind. So the fact that they did select a position where the frond was significantly thicker than the diameter of supports used in other trees, adds further credence to the hypothesis that *florea* colonies select sites with some shelter (ie nearer the trunk), even if other features (here substrate branch diameter) are not optimal. That colonies have to nest on such a broad support to obtain what may be only a bare minimum of shade from the relatively sparse foliage of the date palm, may be another reason why *florea* avoid these trees for nesting sites.

Many of the trees eg *Acacia tortilis*, *Acacia nilotica*, *Prosopis cineraria* and *Ziziphus spina-christi* in Oman had large spines and thorns on their branches and twigs but this did not seem to deter *florea* from building nests in them. Some nests were situated on branches with one or more side shoots and frequently twigs and thorns other than those from the supporting twig were embedded in the brood comb and honeycomb. For instance one colony in an *Acacia tortilis* tree had twigs of diameter 2mm and 3.5mm protruding into the honeycomb, with thorns from 3 to 15mm long completely enveloped in the wax; 17mm of a larger thorn, total length 23mm, was also embedded in the wax. Another colony of *florea* in an *Acacia tortilis* tree similarly had thorny twigs of 1.5mm and 3-4mm diameter in its honeycomb; in some cases a cell wall would follow the edge of the thorn, in others the thorn would go straight through the cell walls. These thorns, rather than being a problem, may therefore even strengthen the bonding of the comb to the tree and in addition should provide some protection from larger predators such as man.

4. Location of *Apis florea* nests in bushes and trees : orientation of nests and compass sector of tree occupied

The orientation of colonies in trees is shown in Figure 2.4a, with the colonies grouped according to 8 sectors of the compass. The figure indicates the bearings at which the colonies and their supporting branches (distal end) point, ie away from the centre of the tree. The same number of colonies would be expected in each sector if the nests were orientated at random (uniform distribution), but the significant ($p < .01$) χ^2_7 value of 21.96 shows random orientation is not the case, and Figure 2.4a indicates how the branches pointing from west through to north-east were avoided, while those pointing from east through to south were preferred.

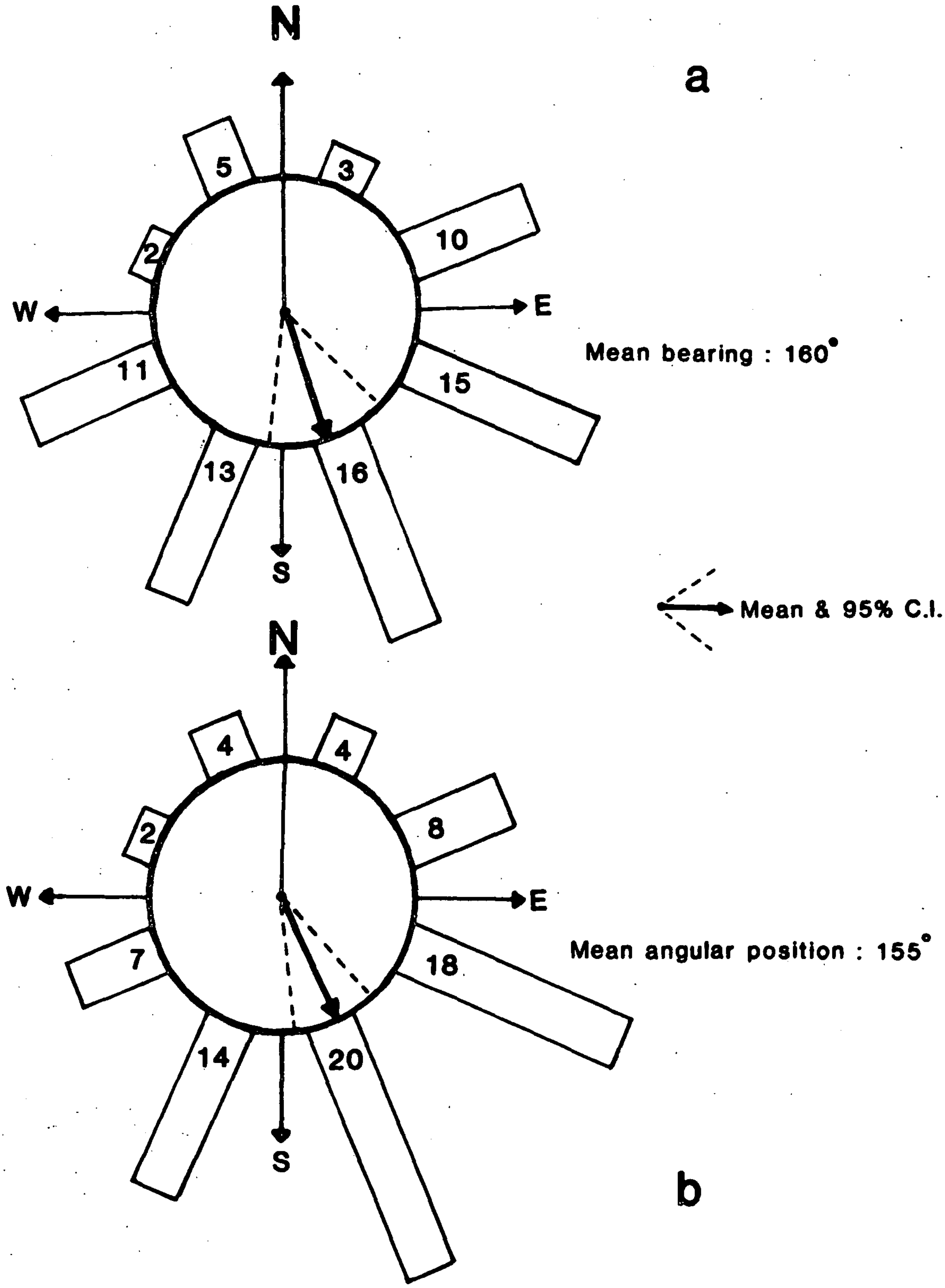
Angles of $0^\circ - 360^\circ$ cannot be treated as linear dimensions for the calculation of mean bearings, standard errors etc; instead, valid measures of mean direction and dispersion were calculated according to methods detailed by Batschelet (1965). Using each colony measurement ($n = 75$), not the grouped data, the <u>mean direction</u> or mean angle of orientation was 160.2° (approx. SSE) and the mean angular deviation (a measure of dispersion similar to the standard deviation) was 64.7°. The 95% confidence interval for the mean angle was $133.9^\circ - 186.5^\circ$ ($160.2^\circ \pm 26.3^\circ$). The Rayleigh test confirmed the earlier chi-squared test that the population did not have a uniform distribution, $Z = 9.80$, sig. $p < .01$.

Of the 25 colonies for which the region (eg NE sector, SSW sector etc) of tree occupied by the nest was also recorded, the tree compass sector (angle) for 21 of the colonies matched closely the

Figure 2.4a Orientation of 75 *Apis florea* colonies in bushes and trees in Oman, grouped according to 8 sectors of the compass:- $1^\circ - 45^\circ$, $46^\circ - 90^\circ$ etc. Orientation was measured as the bearing at which the distal end of a colony pointed ie the end pointing away from the centre of the tree. Mean bearing 160.2°; mean angular deviation 64.7°; 95% confidence interval for the mean angle $133.9^\circ - 186.5^\circ$. Rayleigh test statistic $Z = 9.80$, sig. $p < .01$. Comparing observed and expected values, $\chi^2_7 = 21.96$ sig. $p < .01$. Both tests indicate a non-random distribution.

Figure 2.4b Compass sectors of bushes and trees occupied by 77 *Apis florea* colonies in Oman as measured by colony orientation (Figure 2.4a) with certain colonies transferred to more appropriate sectors because of their proximity to walls etc. See text for details of re-classification. The 8 sectors are $1^\circ - 45^\circ$, $46^\circ - 90^\circ$ etc. Mean angular position 155.0°; mean angular deviation 60.6°; 95% confidence interval for mean angle $136.7^\circ - 177.3^\circ$. Rayleigh test statistic $Z = 14.94$, sig. $p < .01$. Comparing observed and expected values, $\chi^2_7 = 34.06$ sig. $p < .001$. Both tests indicate a non-random distribution.

See text for derivation of statistics after Batschelet (1965).


N
a
5
3
10
2
W
E
Mean bearing : 160°
11
15
13
16
S
Mean & 95% C.I.
N
4
4
2
8
W
E
Mean angular position : 155°
7
18
14
20
S
b

corresponding colony orientation (bearing at which the colony and supporting branch pointed). This would be expected as, in general, branches radiate out from the centre of a tree and within limits are approximately straight. In the case of colonies in date palms, of which the fronds are straight and arranged actinomorphically (ie radially symmetrical), the orientation of a colony and the frond to which it is attached is exactly the same as the compass sector or region of the palm tree which it occupies. Of the 4 colonies for which the position in the tree did not correspond to their orientation, 2 were near the centre of the trees, a third was on a twig which pointed at 270° (W) but was in fact in the NE part of the tree, and the fourth was attached almost perpendicularly to, rather than along, a twig pointing at 50° in the SE (140°) sector of its tree. Therefore for most colonies, orientation was a satisfactory measure of the compass sector of tree occupied.

Figure 2.4b shows the data on colony orientation being used in this way, as a measure of the tree sector occupied by *florea* nests, after a re-classification of some of the data as follows:- (a) the 2 colonies at the centre of trees were excluded (b) the 2 other colonies mentioned above were transferred to their appropriate tree sectors (c) the 6 colonies in plants adjacent to walls were transferred to sectors corresponding to the aspect of the wall (d) 4 extra colonies were included for which the sector of tree occupied was measured, but not orientation. Thus Figure 2.4b should only contain a very small number of incorrectly represented colonies ie those colonies for which tree compass sector was <u>not</u> measured <u>and</u> in which the compass sector did not match the colony orientation.

Comparing the observed values in each of the 8 sectors with those expected on the assumption of the null hypothesis, namely a uniform distribution of colonies around the centre of trees, a strong selection by *florea* for the east to south compass sector or aspect of trees and walls is indicated ($\chi^2_7 = 34.06$, $p < .001$, $n = 77$). The mean compass sector was 155.0°, the mean angular deviation 60.6°, and the 95% confidence interval for the mean sector was $136.7^\circ - 173.3^\circ$ ($155.0^\circ \pm 18.3^\circ$). The Rayleigh test statistic value, $Z = 14.94$, was significant ($p < .01$) providing confirmation of the χ^2 value, so the null hypothesis can be rejected.

Therefore, even though the compass sector occupied was not measured directly for 46 of the 77 colonies, but only as indicated by their orientation, Figure 2.4b and the statistics show that the inclusion of the "sector" and other data in the re-analysis of the orientation data (Figure 2.4a), results in an even more distinct distribution. More detailed information on the actual tree compass sector occupied by these 46 colonies is therefore likely to have enhanced this trend, not diminished it; this suggests that the positioning of the colony in a certain sector of a tree might be as or more important than its orientation.

In fact if the orientation with respect to the sun was of primary importance, and not the sector of the tree, a bi-modal distribution could be expected with, for example, half of the colonies "pointing" south and in the southern sector of trees, and the other half "pointing" north and in the northern sector. In this situation, the colonies in both categories would run along a north-south axis and both would be at identical angles with respect to the sun, throughout the day ie both at right angles early in the morning and so on. However, the actual distribution is uni-modal indicating that it is a particular sector of the trees or a position against a wall with a particular aspect, that the colonies are selecting. A branch which allows them to orientate their nest along a line running approximately from NNW to SSE may be advantageous too, but not if positioned in the northern half of a tree.

This evidence supports Humayd Sulayman al-Shimili's observation in the Dhahira region of interior Oman that some *florea* nest on the south side of trees throughout the year (Dutton & Free 1979) and substantiates the pattern of occupation that was recorded for *florea* kept by Nāsr Ahmad al-Ghaythi in recesses along 4 walls of his garden (Chapter IV, Tables 4.1 and 4.2). A greater occupation than expected was observed in the east facing wall and lower occupations in those facing north and west, though the samples recorded were not large enough for the differences to be statistically significant. Crane (1983a) recorded a similar preference (by beekeepers) for the construction of *mellifera* boles in Britain and Ireland with a south or south-east aspect.

The advantage to *florea* colonies of nesting in the south-east quadrant of a tree would appear to be thermoregulatory. They would be in a position to receive more insolation than in the north-western quadrant, especially early in the day when ambient temperatures are lowest and the brood would benefit from extra warmth (see Chapter V). Furthermore, the insolation should facilitate foraging activity by the workers earlier in the day. Avitabile *et al* (1978) and Seeley & Morse (1978) have found that *mellifera* in the northern hemisphere prefer cavities with south-west to south-facing entrances and Seeley & Heinrich (1981) also conclude that such selection facilitates nest thermoregulation.

This result may seem surprising in a country such as Oman with a hot climate, where colonies of *florea* might be expected to seek as shaded a site as possible in the NW quadrant of trees. However, maintaining the temperature of a single, small brood comb with a comparatively large surface area above 32°C could place a considerable energetic burden on a colony. The monthly means of daily mean ambient temperatures are below 30°C for 7 months of the year and the monthly means of daily minimum temperature are down to about 15°C for 4 months of the year (see Appendix II) and recordings of nest temperatures have shown that *florea* are not able to thermoregulate as well as *mellifera* at low ambient temperatures (Chapter V). Most colonies did occupy sites which provided substantial but not 100% shade (see next section) so presumably sufficient radiant energy filters through the foliage around a nest to help meet the bees' thermoregulatory requirements. Then when the temperatures are highest the sun will be nearly directly above the colony and the expanded honeycomb should provide some shade and insulation to the brood comb (and the bees do not appear to expend much energy in controlling the temperature of the exposed honeycomb itself - see Chapter V).

Of the 10 colonies that selected sites which were orientated between 270° (W) and 45° (NE), 4 had definitely arrived at these sites between the middle of May and the middle of June, the time of year with the highest temperatures (see Appendix II). Another 4 colonies had almost certainly arrived at these sites between the end of April and the beginning of September and it was likely that the remaining 2 colonies also arrived at their chosen nest sites in late spring or summer. Some of these 10 colonies were thought to be reproductive swarms but one at least had absconded from its previous site. In general it was difficult to estimate reliably the age of nests (length of time the colony had been established at a particular site) so further analysis to see if nest site selection by swarms varied with the time of year was not attempted, though such information would be valuable. Nevertheless, the few records above that were examined have revealed that at least 8 of the 10 colonies that nested in the potentially shadiest sectors of trees had selected these sites in the hottest months of the year and it was unlikely that any had selected such sites in the cooler winter months. This was further evidence that *florea* were selecting nest sites according to their suitability for colony thermoregulation.

It should however be pointed out that the primary swarming season occurs in late spring/early summer (see Figure 6.3a and Table 4.14) and judging from Figure 2.4a, many of the new colonies at this time of year must still nest in the SE quadrant of trees and would soon encounter the highest temperatures of summer. Therefore, it appears that most swarms and absconding colonies throughout the year will select nest sites in the 90° - 225° sector of trees, but there is a tendency for some colonies to establish nests in the 270° to 45° sector in summer (though rarely, if ever, in winter).

Could protection from the wind have been a factor inducing colonies to select nest sites in particular tree quadrants? With the two predominant airflows in Oman coming from almost opposite directions in two distinct periods, from the north-west or north between November and mid-April and from the south-west between late June and mid-September (Pedgley 1970; Horn & Nielsen 1977a) this seemed unlikely. Furthermore, due to various factors eg deflection by mountain ranges, there is regional and altitudinal variation in the prevailing wind direction in Oman (Pedgley 1970) and this would tend to obscure any local relationship between nest orientation and wind direction that might have existed, as nest sites were recorded from several regions of the country. On the Batina coast where most *florea* nest records were obtained, winds from the north-east were overall the most prevalent in 1980 according to monthly "wind roses" from Seeb (Oman National Meteorological Service, unpublished), so SE quadrant nests and orientations would appear to have little advantage here. At higher altitudes in the mountains of the Jabal Akhdār the prevailing wind is from the north, but at lower altitudes there is an increasing south-west component in summer (Horn *et al* 1977; Gallagher & Woodcock 1980). In the Dhahīra region a local man claimed the prevailing wind was from the west and colonies nesting in the mountains therefore avoided caves with this aspect (Dutton & Simpson 1977), but I did not record any wild colonies in caves there so was not able to check this statement.

Seeley *et al.* (1982) and Seeley (1983) considered that in Thailand nest site selection by *florea*, and the two other south-east Asian species of *Apis*, was particularly important as a defense strategy but placed less emphasis on its role in aiding colony thermoregulation. However, whether *florea* build their nests to the NW or SE of walls or in particular sectors of trees should not make any difference to the likelihood of their detection by predators. Therefore, the results here indicate that the selection of at least one nest site attribute in Oman is being determined by the thermoregulatory requirements of *florea* colonies and not by predation pressure.

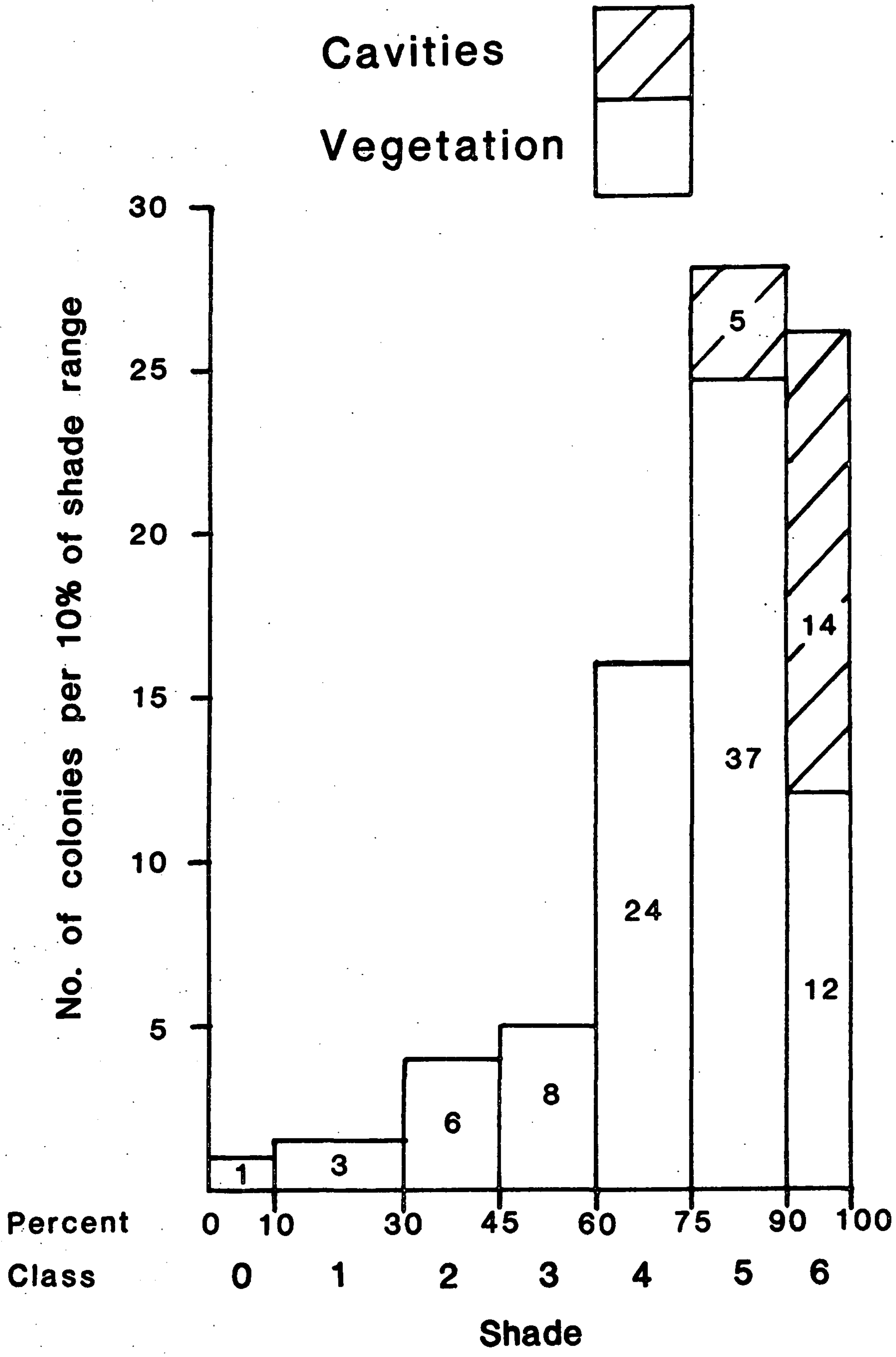
How do *florea* identify the tree sector and comb orientation required? This should present little problem to a member of the genus *Apis* whose abilities to use the sun for orientation purposes are well known (von Frisch 1967). Memory of a previously used comb direction, with the earth's magnetic field as a reference, may also/alternatively influence the orientation of a new comb (or selection of a branch along which to build a new comb in the case of *florea*) as has been demonstrated for *mellifera* (De Jong 1982).

5. Location of *Apis florea* nests in bushes and trees : shade

Despite the inadequacy of the method of visual estimation of the shade experienced by each *florea* colony, Figure 2.5 shows a clear pattern. With a mean shade value of 71.7% as determined by this method and the modal frequency being 75 - 90%, it appears that most colonies in trees are selecting sites which offer a substantial amount of shade,

Figure 2.5 Shade covering naturally established nests of *Apis florea* in cavities, bushes and trees in Oman. See text (Methods 2. v) for details of estimation. The hatched areas indicate colonies in cavities (see Results section 6.4) and the unhatched areas colonies in bushes and trees. The 7 classes (0 - 6), indicating percentage shade, are of unequal width so nest frequencies are marked on the histogram, not on the ordinate.
Mean shade values ($\frac{1}{n} \Sigma$ mid-point of each class x frequency):-

Colonies in bushes and trees : 71.7%, n = 91
Colonies in cavities : 91.7%, n = 19
All colonies : 75.1%, n = 110


Cavities
Vegetation
30
25
20
15
10
5
No. of colonies per 10% of shade range
1
3
6
8
24
37
5
12
14
Percent
0
10
30
45
60
75
90
100
Class
0
1
2
3
4
5
6
Shade

but not usually sites that are completely shaded. This concurs well with the findings on nest orientation in the previous section where colonies were shown to be selecting sites in the SE sector of trees; if it had been completely shaded sites that were being sought, most colonies would have been expected in the NW sector of trees and to the NW of walls. To benefit from warming insolation some radiant energy would need to penetrate to the nest through the foliage, but not so much that overheating ensued. 25% exposure should therefore permit adequate, but not excessive, heating and particularly for "SSE" colonies which would receive the heat when most needed, early in the morning.

Even for colonies in categories where the shade value was less than 60%, the expanded honeycomb above the brood should provide extra shade and insulation from the strong mid-day sun. The single colony which was estimated to have no more than 10% shade was in a *Ziziphus spina-christi* tree that had lost most of its leaves due to drought, and only bare twigs were above the nest. It was likely that the colony had selected this site when the foliage was more dense and was now finding it most unsuitable. No brood was present when it was examined in July, many bees were "fanning" and it looked as though it would soon abscond.

If concealment from predators was the primary factor determining choice of nest sites by *florea* in Oman, as Seeley *et al* (1982) suggested was the case in Thailand, more tree colonies would certainly have been expected in category 6 (90 - 100% shade) since such shaded sites would presumably provide better cover. The shade/exposure of colonies in cavities is discussed in section 6.4.

Another reason for *florea* not selecting totally concealed sites concerns their communication dances. Von Frisch (1967) showed that when *mellifera* foragers were using the plane of vibration of polarized light as a reference when indicating the position of a food source, it was necessary for them to have a view of blue sky and to perform their dances on a horizontal platform - not on a vertical surface. Similarly, *florea* in Ceylon have been shown by Lindauer (1957) to use polarized light and the sun for reference when they point directly at the food sources during their dances on the horizontal honeycomb platform; dances were disoriented unless the dancing bees had a clear view of the sky from the honeycomb.

Koeniger *et al* (1982) confirmed Lindauer's behavioural descriptions and noted that there was a correlation between the location of the dance on the honeycomb platform and the direction of the dance eg a dance pointing NE would be performed on the north to east sector of the honeycomb. Unlike Lindauer, Koeniger *et al* concluded that when dancing *florea* could not see the sky they related the direction of the food source to something they could perceive (other than the sun or sky) when in the experimental room as well as when outside. Nevertheless these colonies without a view of the sky showed a strong tendency to abscond. Tirgari (1971) in Iran also noted that in 3 cases when colonies of *florea* were deprived of blue sky they moved to another location in two days.

Lindauer, though, also demonstrated that the dances were disoriented if the bees were forced to perform them on vertical parts of the comb and it was therefore supposed that *florea* could not transform information on the position of the food source to a vertical plane (as do *mellifera* dancers which use gravity to indicate the position of the sun in the darkness of their hives). Akratanakul (1977) in Thailand also found that *florea* bees dancing on a vertical comb performed an irregular dance from which recruits were unable to obtain information concerning the direction and distance of food. However, in Oman where *florea* nest in caves, Free & Williams (1979) have since observed workers of this species performing apparently normal dances on the vertical comb face; but it is not known if such dances are effective or accurate. If the dances are effective, Omani *florea* dancers (like those of *mellifera*) can presumably equate gravity with the position of the sun, but at times when this is not visible cannot equate gravity with the plane of polarized light; and their dances then surely have to be performed on a horizontal surface.

However, even though *florea* may be capable of performing dances, not necessarily accurate, on a vertical surface when the sun or sky is visible (as do *dorsata*), a horizontal dance platform is normally used by colonies in trees (Lindauer 1957; my own observations). Therefore a horizontal surface is probably the preferred and most accurate dance floor for *florea* and to be effective should provide a view either of the sun or of some blue sky (for polarized light). Completely covered nest sites might eliminate this use of polarized light (on the assumption that *florea*, like *mellifera*, cannot transform directional information that is based on polarized light to a vertical dance surface).

Polarized light is valuable for foragers at times when the sun is obscured by clouds, mountains etc and the inability to use it would necessitate dances with respect to some other feature or on a vertical surface. These might be less accurate or not favoured and, in the latter case, only possible when the sun is visible during foraging flights.

However, there is increasing evidence that *mellifera* bees contain ferromagnetic material, can perceive the earth's magnetic field and may use it for orientation (Martin & Lindauer 1981; De Jong 1982; Kuterbach *et al* 1982; Crane 1983b). Also that they can memorise the sun's course in relation to landmarks visible on previous sunny days, such as a line of trees, and use these to locate a food source on overcast days (Dyer & Gould 1981). *Florea* bees may be able to use such cues too and it is manifest that more research is needed to understand better their dancing behaviour. Nevertheless it seems clear that partially exposed nest sites should facilitate their dances and therefore be favoured during the nest selection process.

6. Natural *A. florea* nests in caves and similar structures

6.1 Introduction and overall site classification

20 naturally established colonies were recorded in sites other than bushes and trees; these have been allocated to a "cave" category, though most were in equivalent man-made structures and only 3 in natural caves (Figs. 2.6 & 3.4; Table 2.11). 12 of the colonies were recorded from places along the Batina Coast, including the capital region, and 8 (including those in natural caves) from places in the interior of Oman. The nest sites included a packing-case turned on its side, a coil of telephone cable against a wall, the inside of a house along the bottom edge of an inward-opening window, a vertical metal pipe 9cm in diameter 4.4m down the centre of a well and another 1.9m down a well on a vertical

Table 2.11 Nest sites of *Apis florea* in Oman, other than in bushes and trees - "cave" category

Type of Nest Site	No. of Colonies Recorded	Typical Position of Nest
Window, Building etc	9	Above ground level
Natural Cave	3	At ground level
Vertical Shaft (especially wells)	4)	Below ground level
"Tunnel" (for access to falaj, well etc)	4)	

Figure 2.6 Nest sites of *Apis florea* in various man-made "cavities", all at Khabura, northern Oman.

a. Colony which had absconded from an experimental hive (2), only 2½ days after being installed, to an empty packing case 25m away on 4.ii.80. The open side of the case faced nearly SW (220°) and the comb faced approximately S (170°); this was nearly the same orientation as in the hive, where it faced due south. The photograph, taken on 6.ii.70, shows the direct attachment of the comb to the horizontal wooden substrate (ie no dance platform) and that nectar and pollen are already being stored in extended cells at the top, while eggs have been laid in the comb below (the curtain of bees had been brushed aside).

b. Colony attached to a vertical pipe carrying water from a well. The colony was 4.4m below ground level and 2.4m above the water; it was thought to have settled there in the first half of April and contained approximately 290gm of honey and was rearing brood when the photograph was taken (19.vi.80).

c. and d. General view of location (c) and close-up (d) of colony nesting in a barred "window", blocked-off from the inside, in the ESE facing wall of a house. Though exposed and visible to the front and likely to receive insolation in the morning, the colony was very difficult to detect. It was thought to have arrived at this site in the cooler months (November 77 - February 78) and was a large colony, rearing drone brood, when the photograph was taken (27.iv.78).

a

b

c

d

plastic hose 2cm in diameter that returned the cooling water from the well's diesel pump. This shows the diversity of structures and sites which *florea* would use in Oman.

It was difficult to take comparable measurements of certain nest site attributes with this diversity eg diameter of support when the substrate was the under-side of a packing case or a vertical rather than horizontal pipe; nevertheless some useful information was gained on other attributes, though the sample sizes were rather small.

The caves themselves, including those adopted by *florea* bee-keepers (Chapter III, Sections B and C), were frequently little more than deep hollows under over-hanging rocks (Figure 3.4, Chapter III). The caves usually extended back no more than about 3m with heights typically less than 1m ie not the sort which an upright man could enter. The entrances were broad, not restricted, so in most cases with the colonies only 0.5m to 2.0m back from the cave entrance a man could reach the colony by kneeling or lying down and inserting his head and shoulders into the cave. Therefore, these caves and other sites are different from the cavities selected by *mellifera* (Seeley & Morse 1976, 1978; Avitable *et al* 1978) and *cerana* (Seeley *et al* 1982; Seeley 1983) which have entrance openings usually no bigger than 140cm^2 that can exclude the larger predators. Also *florea* colonies, which are comparatively small, would not be able to control the microclimate within the relatively large cavities recorded here as do the other 2 *Apis* spp. in their selected cavities.

One *florea* colony which was included in the tree category might alternatively have been included in this section as it was in a large hole, just above a side branch, in the trunk of a *Prosopis cineraria* tree; but this too was not like the cavities selected by the two hole-nesting *Apis* spp. since the opening was almost as large as the cavity itself and the whole comb could be removed intact, without the need to enlarge the entrance.

6.2 Height distribution

The distance from ground level of 15 colonies was measured and in Table 2.12 these have been split into the 3 categories used in Table 2.11. The distances given do not refer to the nearest solid structure below the nest, which for example might be a window sill, but to the ground. With the colonies in caves the heights were measured from the attachment at the top centre of the comb; in fact two of the colonies were attached to sloping roofs and in one of them the height from the cave floor of the comb attachment ranged from .12m to .27m and the bottom of the comb almost touched the cave floor in places. On the other hand, 3 colonies in "tunnels" at the edge of "falaj" inspection holes were 1.8m below ground level, yet there was still a further 1.8m below them to the floor of the tunnel, and the colony 4.4m down a well was still 2.4m above the water at the bottom. Therefore the values in the table indicate only typical nest heights, but do not convey in detail their distance from other structures which may or may not have influenced the colonies in selecting their sites.

Table 2.12 Distances, above and below ground, of 15 *Apis florea* colonies naturally established in caves and similar structures in Oman. For further details see text.

Type of Nest Site	Distance from Ground Level, m		
	Mean	Range	n
Window, Building etc	+3.48	.16 to 12	7
Natural Cave	+ .23	.2 to .25	3
Vertical Shaft, "Tunnel"	-2.34	-4.4 to -1.8	5
Overall	+0.89	-4.4 to +12	15

Therefore, as was also concluded from the height distribution of colonies in trees (Results, Section 2), apart from avoiding very high structures, *florea* do not appear to have a particularly favoured nest height and will even nest below ground level. They presumably select sites on the basis of other characteristics. If predation by large predators such as man was a serious problem it might be expected that low nest sites such as those in caves, which were particularly accessible, would be avoided but this did not appear to be the case.

6.3 Aspect of cavities and orientation of nests

The orientations (aspects) of the entrances of 10 of the cavities or nest site structures are given in Table 2.13; the entrances to the colonies underground were vertical, with no particular orientation so could not be included. Though the Rayleigh test indicates there is no preferred aspect (that is statistically significant), the sample size is small. The mean aspect is 132.9^{o} (approx. SE) which is consistent with the findings in section 4 of this chapter, that *florea* usually select nest sites in the east to south-west sector of trees. The observed number (6) of cavities used by *florea* with this aspect is greater than that (3.75) which would be expected if there was no selection for caves with a particular aspect; but the sample is also too small for analysis by the chi-squared test.

Exactly the same interpretation can be put on the data for orientation of the colonies within the caves (Table 2.13). The mean angle at which the most exposed surface faces is 138.0^{o} (approx. SE) and more colonies than would be expected occur in the corresponding E to SW sector, but the sample is also too small to be statistically significant. Once a colony has selected a particular cave the aspect of its own most exposed surface is obviously limited, but it was interesting

Table 2.13 Aspect of 10 cavity entrances and orientation of the *Apis florea* colonies using them in Oman. Cavity includes those types of site detailed in Results 6.1 (p. 56) and colony orientation is the direction in which the most exposed side of the comb faces as described in Methods 2 (iv) (p. 26). The numbers of cavities and colonies in each of 8 sectors are given and have then been put in two groups; those in the 3 sectors facing E to SW and the rest. The expected numbers in each group assuming a random (even) distribution are in brackets below the observed numbers. Statistical analyses after Batschelet (1965).

Aspect/Orientation	No. of Cavities			No. of Colonies		
1°- 45°		0			1	
46°- 90°		1			1	
91°- 135°		3			2	
136°- 180°	4 (6.25)	1	6 (3.75)	4 (6.25)	2	6 (3.75)
181°- 225°		2			2	
226°- 270°		0			0	
271°- 315°		1			1	
316°- 360°		2			1	

Mean aspect of cavity entrances : 132.9° (approx. SE), Mean angular deviation : 69.6°. Rayleigh statistic Z = 0.693, NS

Mean orientation of colonies : 138.0° (approx. SE), Mean angular deviation : 69.6°. Rayleigh statistic Z = 0.691, NS to note that of these 10 colonies in cavities, 8 faced very nearly the same way as the cavity entrance (ie one side of the comb faced out of the cavity and the other faced inside so was hidden from view) while only one colony was perpendicular to the entrance (ie its comb ran from the front, back into the cave). The other (tenth) colony was at an angle to the entrance of its cavity, a packing case, but slightly closer to the perpendicular position; as a result it was facing at 170°.

Therefore it appears that once *florea* colonies have selected a cave or other cavity they usually build their comb so that one side faces out of the entrance. This may be the most suitable position for the landing and dances of returning foragers, but may also be the most effective for thermoregulation. If, as appears to be the case, *florea* are selecting caves facing SE into which there may be some direct sunlight, the insolation will strike a greater surface area of comb if it is positioned "broadside on" at the entrance, rather than "end on". The warming effect would then be greater and is presumably beneficial to the colony early in the morning, especially in winter. The exact position of the comb will of course also be determined to some extent by the texture and contours of the "cave" roof and its floor.

6.4 Shade/exposure

The amount of shade experienced at the nest was estimated for 19 of the colonies (Table 2.14). As might be expected, colonies in cavities were generally in rather shadier sites than those in trees (Figure 2.5) with mean shade values of 91.7% and 71.7% respectively, the overall mean being 75.1%. Most colonies were found in trees and bushes, but it should not necessarily be concluded that *florea* colonies were selecting such sites in preference to cavities because the trees offered greater exposure. It may have been that colonies were using

Table 2.14 Shade experienced at the nests of 19 colonies in cavities in Oman. Cavities include those types of site detailed in 6.1 of the Results. See text (Methods 2.(v) p. 26) for details of estimation. The final two columns indicate whether or not a colony was <u>thought</u> to receive direct insolation sometimes (not 100% reliable as the sun was not always in the appropriate position when each colony was examined). Mean shade value 91.7% ($\frac{1}{n}$ Σ mid-point of each class x frequency).

Class	Percent Shade	No. of Colonies	With Direct Sun	No Direct Sun
0 to 4	0 - 75%	0	0	0
5	75 - 90%	5	5	0
6	90 - 100%	14	6	8

trees because there were not enough cavities available. However, as is also considered in the final discussion of this chapter, with village buildings near to and in the gardens and with many caves in the hills, there did not appear to be a shortage. Nevertheless, the temperature measurements in caves (see the following section 6.5) did indicate that not all had a suitable microclimate. Alternatively, some colonies may have been deliberately selecting shady cavities just in the hotter months (see section 6.7); but cavities are probably not better than trees for avoiding predators (see D, Final Discussion).

Furthermore, visibility to predators and shade may not be the only factors involved in the selection as it is not known how effective the foragers' communication dances are, on the vertical surfaces that would have to be their dance platform in these cavities (Lindauer 1957; Free & Williams 1979; Free 1981). The problems that a colony, in a tree and completely shaded from the sky, would face with its communication dances have already been discussed (Section C. 5) and a colony in a cave, even if the sky is visible from inside, is effectively in a similar situation as it only has a vertical dance floor.

Florea dancers almost certainly cannot use the plane of vibration of polarized light as a reference for dances on such a vertical surface (Von Frisch (1967) found that *mellifera* dancers can only use polarized light when dancing on a horizontal surface), so the dancers would be dependent on the ability to transform forage information, based on the sun's position, to a vertical surface. Such vertical dances are not normally performed by colonies with a flat surface available, so may not be as accurate or satisfactory.

Thus colonies in caves, being in virtually the same situation as completely covered tree-colonies, as far as communication dances are concerned (ie both would have to use vertical surfaces, but for different reasons) may partly explain why the shade values for colonies in caves are greater than those in trees. That is they are able to select a very sheltered/shaded position (if desired) and need not consider whether sufficient sky is visible for horizontal communication dances. Tree colonies on the other hand need to select sites with a view of the sun or some sky if they are to make good use of their horizontal dance platforms.

6.5 Cave temperatures

In order to see if microclimatic differences from ambient temperatures existed which might explain the selection or rejection of caves by *florea* colonies, temperature measurements were made inside

2 natural rock caves off the Wadi Hawasina, in the foothills of the Hajar mountains. The first cave recorded (No.4, Fig.2.7a) contained a colony which had flown there of its own accord and the second (No.5, Figs. 2.7b and 3.6) a colony which had been brought there by a bee-keeper (Khalifa); from wax cell remains on the roof, the latter cave must have previously contained colonies of *florea*, either put there by the beekeeper and/or of natural origin. There were a number of "sidr" (*Ziziphus spina-christi*) and "samur" (*Acacia tortilis*) trees in the wadis dissecting the area and various other caves so it did not appear that the wild colony had been forced to choose a sub-optimal site because of limited nest site availability, but the bee-keeper might not necessarily have selected the best cave for the other colony.

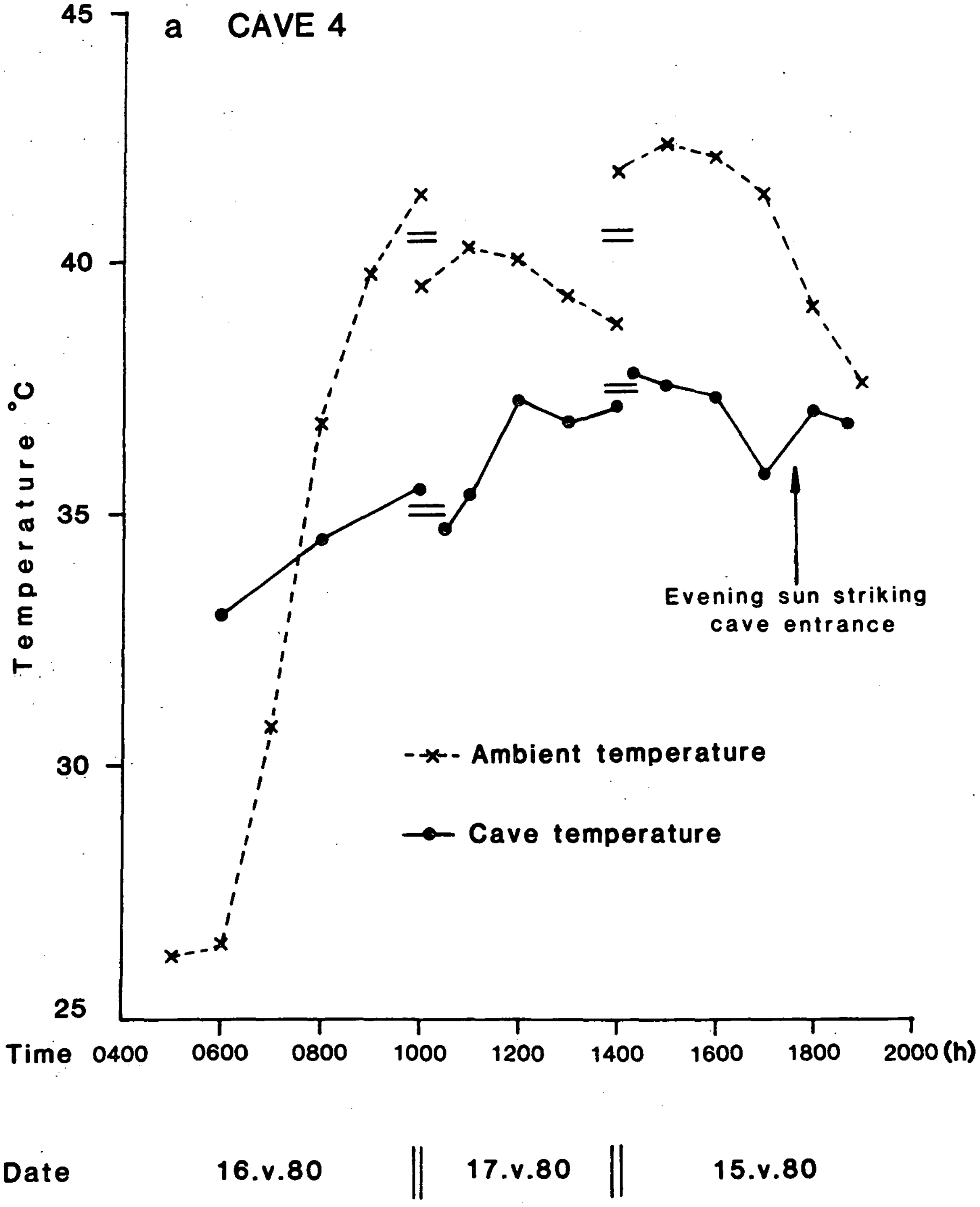
The temperatures in May 1980 (the first really hot month of the year) of cave No. 4 facing NW (310^{o}) were considerably more stable than the outside shade temperatures measured under a tree, varying from 33^{o}C just after dawn to 37.7^{o}C in the afternoon, while the latter ranged from 26.3^{o}C to 42.3^{o}C over the same period (Fig. 2.7a). Though both sets of temperature conditions might stress a colony, there would be less temperature stress in the daytime on a colony in the cave than on one in a tree. At night, the cooler temperatures outside the cave might be preferable to a colony, but not sufficiently advantageous to make it worthwhile for the colony to endure the daytime temperature stress; the night-time ambient temperature might even be a little below the optimum and the warmer cave rather better.

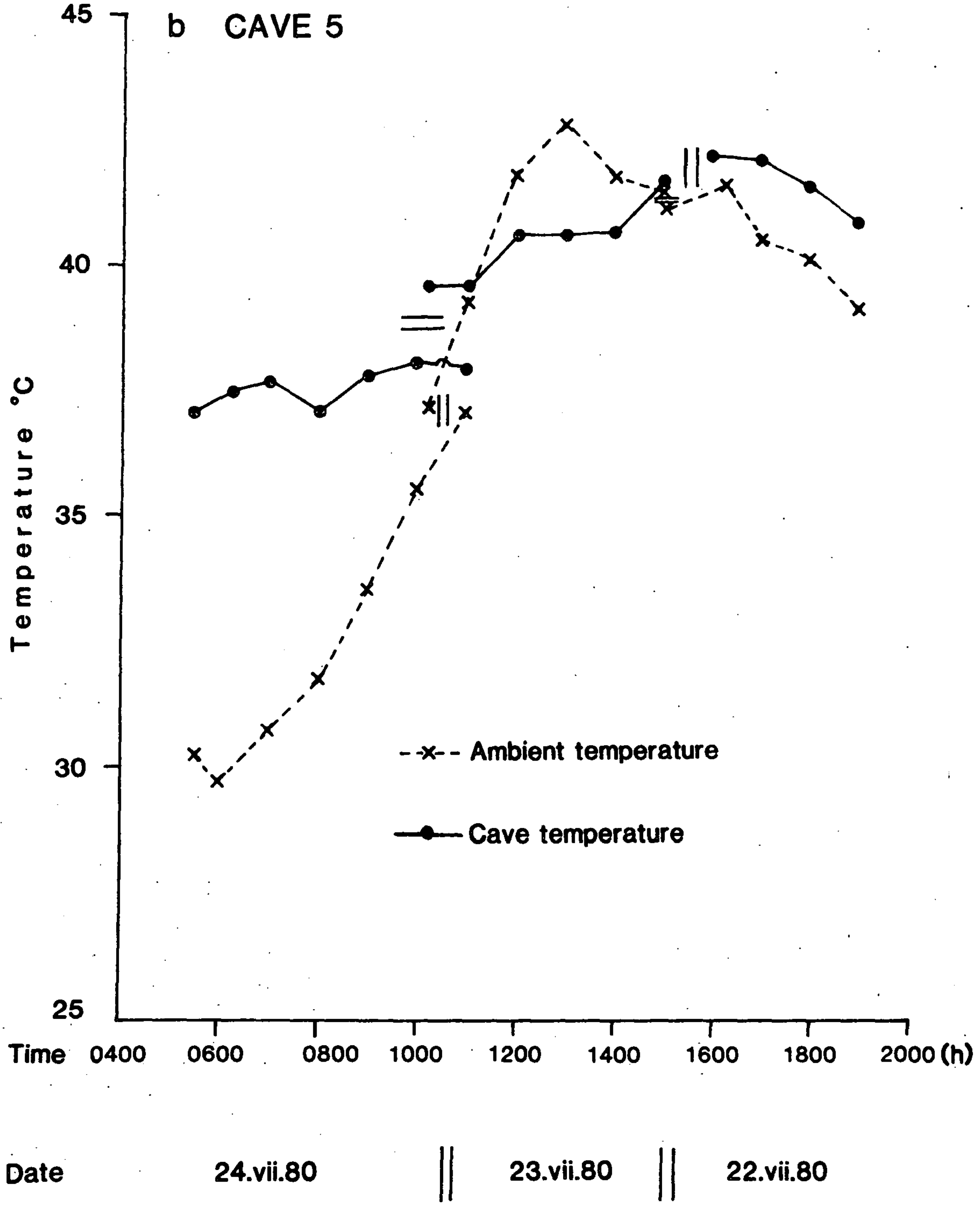
The temperature readings (Fig. 2.7b) made later in the summer, at the end of July 1980 in the other cave (No. 5) facing nearly due north (350^{o}), tell a different story. Though the temperature in the cave (37^{o} - 42.1^{o}C) is still less variable than the ambient temperature (29.7^{o} - 42.7^{o}C) and does not reach quite such a high peak, inspection

Figure 2.7 Air temperatures inside two small caves and under a tree (shade) to the side of the Wadi Tifli (near to the Wadi Hawasina) in the foothills of the Hajar mountains in northern Oman, altitude c. 300m. Measurements were made with mercury thermometers. Parallel lines separate recordings from different days.

(a) Cave No. 4, facing at a bearing of 310°, to which a colony of *Apis florea* had absconded around the beginning of April (see text). Measurements were made on 15, 16, 17.v.80.

(b) Cave No. 5, facing at a bearing of 350°; a bee-keeper had put a colony of *Apis florea* in this cave at some time in April or possibly early May. Measurements were made on 22, 23, 24.vii.80. The cave is illustrated in Figure 3.6.


a CAVE 4
45
40
35
30
25
Temperature °C
Evening sun striking cave entrance
Ambient temperature
Cave temperature
Time 0400 0600 0800 1000 1200 1400 1600 1800 2000 (h)
Date 16.v.80 17.v.80 15.v.80

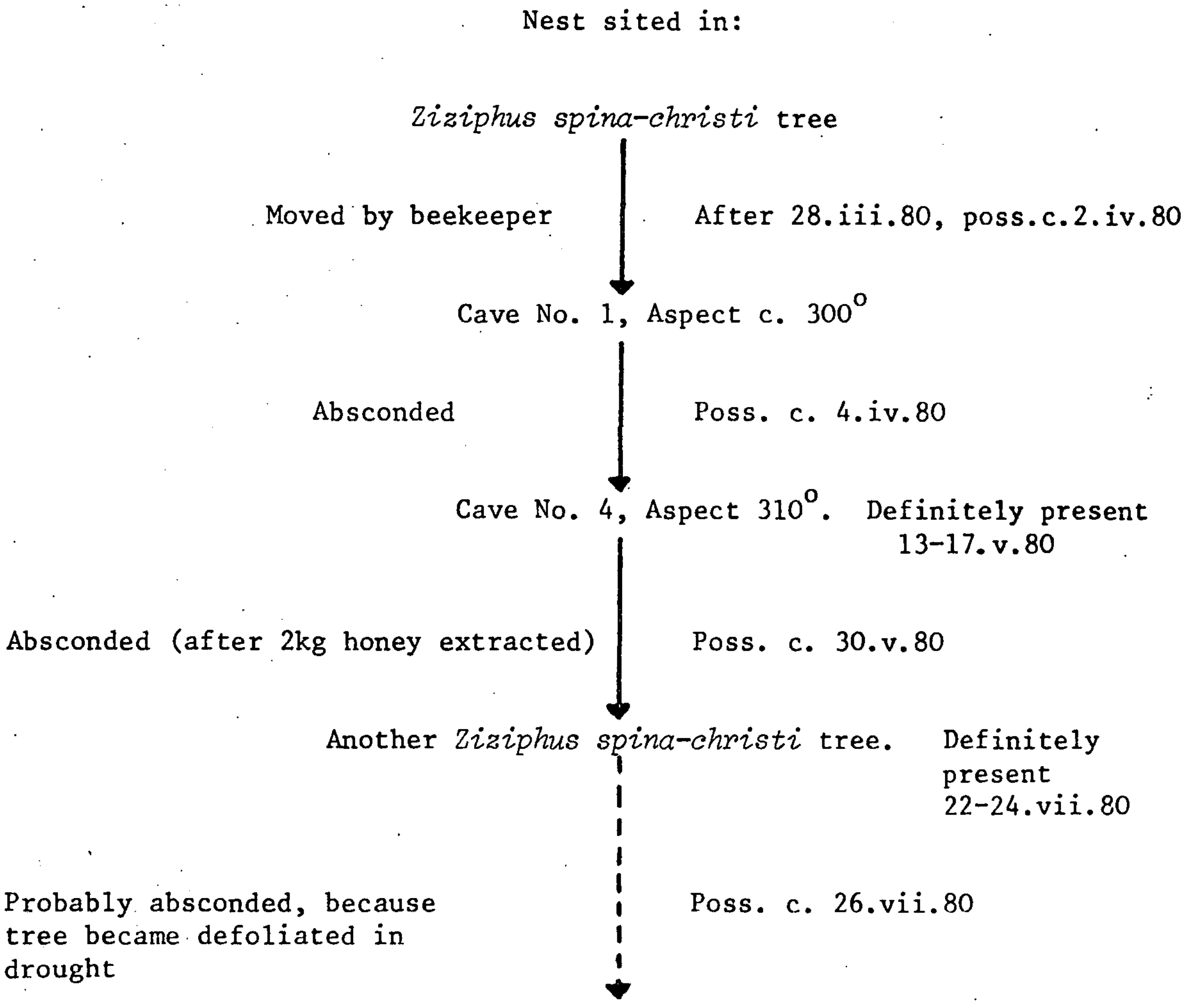

b CAVE 5
45
40
35
30
25
Temperature °C
Time 0400 0600 0800 1000 1200 1400 1600 1800 2000 (h)
- -x- - Ambient temperature
—●— Cave temperature
Date 24.vii.80 || 23.vii.80 || 22.vii.80

of the graphs shows that overall in the daytime it is hotter in the cave. The same must also be true at night, so a colony in this cave at this time of year may experience considerable stress with temperatures almost permanently above 35°C, while outside in a tree it might be rather better with temperatures between 30°C and 35°C for some of the day and night.

Thus the recordings from these 2 caves show that even without direct sunshine (just a little in cave No. 4 in the evening) cave microclimate can be very different from that in normal shade, eg in a tree, and may offer opportunities and disadvantages to *florea* colonies accordint to the time of year.

6.6 History of colonies occupying the caves in which temperatures were recorded

The natural responses of the colonies (without disturbance) to the conditions that existed in these 2 caves, in terms of absconding or remaining, would have been informative, but the histories of the colonies were not known with absolute certainty and they suffered disturbance when the beekeeper took honey from them. As far as I could ascertain from the beekeeper, who first showed me the colony in cave No. 4 on 13.v.80, and from my own observations of his various colonies on 28.iii. 80, 13.v. 80, 15-17. v. 80 and 22-24. vii. 80,its putative history was as follows (overleaf):-



It appeared that the beekeeper had found the colony in a "sidr" tree in spring and moved the colony to cave No. 1. He either took the honeycomb from the colony at the time he moved it or some days afterwards, but this disturbance and/or unsuitable conditions in cave No. 1 induced the bees to abscond to cave No. 4, probably at the beginning of April. Cave No. 4 was only approximately 150m from cave No. 1, faced in a similar direction (310°), was relatively deep and the colony had attached itself near the back of the cave, approximately between 1.0 and 1.5m from the entrance.

Thus the cave was selected when the temperature was beginning to rise in late spring and, as has already been discussed, probably provided a suitable microclimate (Figure 2.7a) for the colony; the bee-keeper said he later harvested approximately 2kg of honey from the nest. After this it absconded to a "sidr" tree about 100m away, probably at the end of May - beginning of June. It may have absconded because of the disturbance of honey-harvesting and/or because the microclimate at its chosen nest site had become very hot - as did cave No. 5 in July (Figure 2.7b) - and the "sidr" tree was cooler.

The colony actually in cave No. 5 had been brought there in the "samur" (*Acacia tortilis*) flowering season, ie in April or early May, and had subsequently yielded c. 0.5kg of honey in this site - probably towards the end of May. The disturbance of honey-harvesting was presumably not sufficient to make the bees abscond at the time and the cave microclimate was satisfactory. However, when the temperature recordings were made at the end of July no brood was present in the colony, no pollen was visible, sealed honey cells occupied only 5% of the total comb and unsealed honey cells less than 5%. This was indicative that absconding might soon occur, though there was very little foraging activity and virtually no forage available in the vicinity that would have stimulated brood rearing. No more visits were made to the colony after 24.vii.80, but another colony that had been put in a similar cave, No. 7, in the same rock face about 30m away was, on 22.vii.80, in much the same state as the colony under study and it absconded on 23.vii.80. On this basis I deduced that the colony in cave No. 5 would also have absconded before the end of July and the reasons for both (5 and 7) colonies absconding was not disturbance, but the hot microclimate that existed in the caves in July, exacerbated by lack of forage in the vicinity.

Firm conclusions cannot be drawn from these few observations. Would the temperatures inside cave No. 4 have become higher as the season progressed and followed the same pattern as the temperature in cave No. 5 at the end of July, or did cave No. 4 have different physical characteristics? For instance cave No. 7 from which the other colony of bees was known to have absconded on 23.vii.80 was just below the top of a plateau with only approximately 0.5m of rock above it and the bottom surface of this rock (ie the cave roof) was fairly hot to the touch. Therefore, as the summer temperatures build up and the rocks absorb heat, even north-facing caves like this can develop intolerable microclimates; cave No. 5 had a thicker roof (exact thickness of rock above not recorded) than cave No. 7, but nevertheless in summer the rock obviously retained heat and re-radiated it when outside temperatures were lower.

6.7 Discussion

So each cave or other cavity may have its own peculiar temperature characteristics dependent on factors such as its size, shape, rock type and aspect that may result in it being warmer or cooler than the outside atmosphere according to the time of year; there are probably temperature gradients within the cavities too, making certain sites of attachment for *florea* better than others. To what extent *florea* can assess the characteristics of such cavities before making a selection is not clear, but the data on orientation of colonies in trees (section 4) and the similar data on cavities in section 6.3 suggests that they do make some selection on the basis of aspect. However, the cave temperature data also suggests that some sites may not be suitable the whole year round - at least for weak colonies - and a change of nest site to another cave or a tree may be necessary.

To consider the possibility of seasonal variation in the type of cavities selected by *florea*, the time of year at which colonies arrived at cavities of different orientations was checked. Of the 3 colonies which arrived in cavities facing from west to north, 2 were known to have arrived in April at the beginning of the hottest period and the 3rd was thought to have arrived in September, towards the end of this hot period. The dates of arrival of 2 of the colonies in wells were also known reasonably accurately; one definitely arrived on 30.v.79, the other was first seen on 14.vi.80 and was said to have arrived in April. These colonies, being in very shaded positions, can be considered equivalent to those in N facing caves.

Of the 7 colonies in cavities facing from NE to SW all were known or deduced to have arrived in the autumn-winter-spring months, from October through to the middle of March at the latest. These few observations are consistent with a hypothesis that orientations and sites are selected appropriate to the prevailing temperature conditions ie caves facing south in winter etc. The data on colonies in trees, however, indicated that some *florea* colonies arrived in SE sectors throughout the year, even in summer, but that of the small number of colonies in NW tree sectors, most arrived in summer (Results, section 4). Therefore there appears to be some seasonal variation in nest site selection, but the pattern is in need of further elucidation.

However, those colonies which do stay in one site for several months may sooner or later encounter less favourable temperature conditions and I speculate that in these circumstances 3 options are open to the bees:-

(i) Strong colonies (populous with good food reserves) that are able to thermoregulate satisfactorily under the more adverse conditions would remain in the original site selected, maybe rearing brood at a reduced level according to forage availability and reserves.

(ii) Some weak colonies, less able to cope with the temperature extremes would cease brood rearing and become relatively inactive; equivalent to hibernation and aestivation in winter and summer respectively, the nest temperature tending to fluctuate, between limits, with ambient.

(iii) Other weak colonies would abscond, selecting a more suitable site that facilitated thermoregulation and brood rearing.

The option followed would depend on the strength of the colony, how extreme the temperatures experienced were, the extent (if any) of disturbance or predation at the existing nest site and the availability of alternative sites. Therefore once a site has been selected and a colony has started to develop, various factors come into play, which determine the length of time spent there and which induce absconding; these are discussed further in Chapter VI but the sort of consequences to colonies of their nest site selection must at least be illustrated and considered briefly here. These proposed "options" and the principles involved apply equally well to colonies which have selected nest sites in trees, but are discussed in relation to colonies in caves because they provide some good examples.

Example (a) The third colony (Figure 3.4, Chapter III) to have selected a NNW (340^o) facing cavity (mentioned above) was thought by the bee-keeper to have arrived there in September, and its size when I first saw it on 28.xii.79 suggested he was correct. The temperatures in September are high (Appendix II) and a north-facing cave at that time would almost certainly be preferable to one facing south. However, with low temperatures 3 months later in December the reverse would be the case and a south-facing cave might be better, providing some insolation to aid with thermoregulation. Nevertheless, in this case the colony had grown strong during the "sidr" (*Ziziphus spina-christi*) flowering season in late autumn and on 28.xii.79 had a large area of brood, much stored honey and foragers were seen to be gathering at least 2 kinds of pollen and probably nectar. It was therefore a case of option (i), a strong colony staying in the site selected in an earlier season and devoting its energy to maintaining the temperature of its large brood "investment" - rather than letting brood rearing run down so it could abscond/migrate to a warmer site.

Example (b) However, the bee-keeper then proceeded to upset the balance by removing all the honey from this wild colony. He put the brood comb back in the cave very clumsily (Chapter III, Figure 3.5) and though the bees re-clustered, he said they absconded 2 days later - presumably after some of the sealed brood had been able to emerge. Later, he pointed out to me the rocky mountain in which he subsequently found the colony (about 0.8 to 1km from its original site) and though I did not visit the cave the aspect of the mountain face was approximately south. Therefore, though this large colony had originally adopted option (i), predation by man had altered the situation and the maintenance with food and warmth of a large area of brood with no honey stores would have been difficult, so the colony absconded to what must have been a better (warmer) site for that cold time of year - option (iii).

Example (c) The strong colony in cave No. 4, discussed earlier, also appeared to be a case of option (i), until it was predated when, being the hot season, it absconded to a site in a tree that was potentially cooler - option (iii).

Examples (d) and (e) The colonies in caves No. 5 (on the likely assumption that it did soon abscond) and No. 7 would also be cases of option (iii), weak colonies absconding to presumably more suitable sites as the summer temperatures in their caves became too extreme.

It is all too apparent from this speculation that the data on the seasonal nature of cave nest site selection is very sparse. More measurements are needed at different times of year of the diurnal temperature fluctuations in caves (used and abandoned by bees) of different conformation and aspect. At the same time, the selection of these caves by *florea* and how the colonies develop should be followed, and the nature of the sites to which any abscond compared with those they have deserted and others available.

It might then be determined whether the colonies in the mountains are occupying caves at certain times of year because (a) they provide the best sites, with suitable temperature characteristics that trees cannot offer or (b) because certain trees eg with dense foliage in fact provide the best sites but, unlike in cultivated areas, there are insufficient of them available and colonies are therefore forced to use caves as second best, with their possible disadvantages for forage communication dances.

Whatever the complete picture, it can be tentatively concluded that cave orientation and internal temperature characteristics are important factors in determining nest site selection. Also that there appears to be some seasonal variation with the final selection to some extent dependent on the ambient temperature conditions at the time. A site offering the best opportunity for growth and reproduction in the short term may sometimes be chosen and if the colony thrives it may then be able to survive subsequent adverse conditions; if it does not thrive or is predated it may abscond.

The data on tree sector occupied, however, with most colonies selecting SE sectors, did suggest that there can be optimal sites likely to be suitable for the year as a whole. Such sites may not be the best at any one point in time, but should overall be the most satisfactory with less extreme microclimatic pressures, which would thus obviate the need to abscond. The ability to move nest site relatively easily (abscond) must be a useful asset, but at a cost in terms of energy and the gap in brood rearing, so mainly for use in emergencies. Thus colonies that can waste less time and energy by selecting sites where they can grow and reproduce for much of the year should usually be more successful than those which select sites that necessitate a move after only a few months.

Finally, it should be remembered that some of these colonies which have settled in sites that prove to be suitable only for a few months may not have deliberately selected a short-term site, but only did so because they were not able to assess the sites' characteristics adequately eg the colony which absconded from cave No. 4 to the *Ziziphus spina-christi* tree that lost its leaves under drought conditions. There is bound to be some variation in the nest sites selected and not all sites will be optimal or even well chosen, particularly in areas where the availability of suitable ones is limited.

D. FINAL DISCUSSION

Overall selection of habitat, trees and cavities by *Apis florea* for nest sites

Though habitat and vegetation structure in Oman were not described quantitatively in this study, as in Thailand by Seeley *et al* (1982), it was apparent that little of the area occupied by *florea* was even superficially comparable to Thai primary rain forest. Perhaps just a few densely vegetated parts of the intensively cultivated date gardens of the interior oases might have been structurally similar to Seeley *et al*'s tropical rain forest category as these gardens have relatively high average tree densities (438 Palms + Fruit Trees/ha at Arāqi, 573/ha at Ibri; Dutton & Letts 1982) that are greater than those of the Bātina gardens (145 trees/ha, including uncultivated patches; see Results 1.1 (ii) in this chapter). However, in general, interior date gardens would correspond to the areas Seeley *et al* described as "secondary growth", as would the old Batina gardens. The new Batina gardens, ornamental ones and the "wild" plains and mountains, all with relatively sparse tree cover, probably correspond in structure to the "cleared areas" described for Thailand.

It can be seen from the totals in Table 2.15 that if the four general habitats are grouped into 2 categories, equivalent to "secondary growth" and "cleared areas" as above, that most colonies (125; 71%) in Oman were recorded in "secondary growth" (cultivated date gardens) and fewer (51; 29%) in "cleared areas" (wild habitats and new gardens). On the other hand in Thailand, most (61.6%) of the *florea* colonies were in the cleared areas and only 34.1% in the secondary growth and 4.3% in the primary rain forest, which suggests they were selecting rather more exposed habitats in Thailand than in Oman.

Though the larger number of colonies recorded from cultivated areas in Oman in part reflects the greater search effort there by myself and informants, and though the distinction between date gardens and new gardens was not always clear cut (eg there were cleared areas within the old gardens and some of the new ones were developing quite dense vegetation), it was nevertheless apparent that a greater density of colonies occurred in the "secondary growth" oases than the "cleared" wild habitats. This in turn may have primarily been due to the seasonal scarcity of forage and absence of water in certain wild areas, but it may also have reflected the greater availability and suitability of nest sites in the more densely vegetated areas.

Table 2.15 Overall numbers of naturally established *Apis florea* colonies recorded in different nest sites (including colonies attached to physical substrates) in Oman, divided according to four broad habitat categories. Percentages of the colonies in the different habitat categories are given and also the percentages nesting in cavities, as opposed to trees.

	Number of nests in different general habitats				
Plant Used	Khabura and other Batina Gardens	Interior Oases	Wild Habitats	New and Ornamental Gardens	Total
Phoenix dactylifera (mature)	7	5	/	0	12
Phoenix dactylifera (young)	4	4	/	1	9
Citrus spp.	17	25	/	0	42
Mangifera indica	5	2	/	0	7
Acacia nilotica	12	0	/	0	12
Ziziphus spina-christi	11	2	4 (Wadis)	0	17
Azadirachta indica	3	0	/	0	3
Sesbania sesban	1	0	/	0	1
Terminalia catappa	3	0	/	0	3
Cordia myxa	3	0	/	0	3
Prosopis cineraria	4	2	2 (Plains)	0	8
Morus sp.	2	0	/	0	2
Punica granatum	1	0	/	0	1
Ficus carica	0	1	/	0	1
Euphorbia sp.	1	/	/	0	1
Tamarindus indica	1	0	/	0	1
Acacia tortilis	1	0	8 (7 Plains 1 Jabal)	0	9
Jasminum sp.	0	1	/	0	1
Solanum melongena	0	0	/	2	2
Bougainvillea glabra	/	0	/	7	7
Lantana camara	/	0	/	2	2
Nerium mascatense	/	0	0	1	1
Datura sp.	/	0	/	1	1
Ipomoea pes-caprae	/	0	/	1	1
Commiphora sp.	/	/	1 (Jabal)	/	1
Salsola sp.	/	1	0	/	1
Salvadora persica	/	/	1 (Plains)	/	1
Ornamentals indet. (incl. Leguminosae)	/	1	/	5	6
Sub-totals	76	44	16	20	156
Cavities (caves, wells, etc.)	4	1	6	9	20
TOTALS (PERCENTAGES)	80 (45.5%)	45 (25.6%)	22 (12.5%)	29 (16.5%)	176
% Total in Cavities	5%	2.2%	27.3%	31.0%	11.4%

Therefore in Oman, where the predation pressure is apparently less than in Thailand (Chapter IX and Appendix I), most *florea* colonies were occupying a quite densely vegetated habitat where the opportunities for concealment were presumably high, but in Thailand, with the greater predation pressure, the colonies were in more open habitats. If predation was the major factor determining nest site selection by *florea* in Thailand and concealment was the main strategy for avoiding it (Seeley *et al* 1982) it is not altogether clear to me why the *florea* colonies did not occupy "secondary growth" and "primary rain forest" habitats where concealment would presumably be the greatest. Seeley *et al*'s visibility figures indicate that most *florea* colonies were well concealed in the "cleared areas"; but I suggest that the concealment was not maximum apropos insolation and the colonies might have been avoiding the most densely vegetated primary forest areas, despite better concealment opportunities from predators, because insufficient sunshine penetrated for communication dances and particularly thermoregulation. This interpretation might be based on misconceptions of the Thai environment, but I believe should be considered in view of the apparently different findings in Oman.

My experience in Oman indicated that *florea* nests were not easy to find whatever the habitat and degree of exposure, and I can well believe that 63% of Seeley *et al*'s colonies were not "immediately visible" from any of 4 sides, above or below, to an observer 5m away. I felt it was often the small size, particularly when viewed from end-on or below, of *florea* colonies and their shape and dark colour amongst the branches which made their detection by sight difficult, not just the degree of concealment of the nest site. Both well-concealed and relatively exposed colonies might be equally difficult to spot from 5 or 10m - until one knew where they were! (eg see Fig. 2.6 c→d).

Visibility, like shade, is not an easy attribute to measure and the human visibility scale used by Seeley *et al* is probably inapplicable to other predators which may use other visual or completely different sensory cues to detect a colony of bees. I found the most effective searching technique was to peer into bushes and trees from close to or within, as did Omani *florea* "hunters" - not to gaze at possible sites from a distance of 5m or more. So, though *florea* colonies clearly select more concealed sites than *dorsata*, Seeley *et al*'s visibility scale may not be entirely appropriate, even for man as a predator, in describing a nest site. Because of their large size, most *dorsata* colonies would probably be visible in sites where *florea* colonies would be considered "invisible". In fact, once located, I found some previously "invisible" *florea* colonies could be spotted from greater than 5m and I suggest that Seeley *et al*'s visibility scale did not indicate adequately the full range and extent of colony exposure to solar radiation.

Thus colonies in Oman and Thailand may have been selecting partly exposed sites suitable primarily for thermoregulation and communication dances, but it happened that the appropriate conditions for these (circa 75% shade, 25% exposure) nearly always provided adequate concealment from various predators; this concealment value may therefore have been of only secondary importance. The finding in Oman that *florea* show a preference for the SE quadrant of trees strongly supports the hypothesis that thermoregulatory requirements are of prime importance in nest site selection by *florea*.

Whether or not *florea* were nesting in shadier sites in the Omani date gardens than in the Thai cleared areas, because of higher summer temperatures in the former regions, cannot be ascertained as Seeley *et al* did not directly measure shade. However, they do cite a case of a mixed orchard where 4 *florea* colonies were found nesting in 23 leafy mango trees (*Mangifera indica*) but none in 321 custard apple trees (*Anona squamosa*) which had lost most of their leaves. The number (4) of *florea* colonies recorded was too small for the chi-squared test that they applied in their statistical analysis to be valid, but nevertheless a highly significant association between *florea* colonies and leafy mango trees is still shown if the more appropriate Fisher exact probability test (Siegel 1956) is used, $p = 3.09 \times 10^{-5}$. Relatively low light levels were recorded next to the nests and it was concluded that *florea* selected nest sites surrounded by dense foliage, but these observations do not indicate whether such selection is for thermoregulation or against predation.

Similarly either interpretation could be put on their observation that colonies which become more exposed at the beginning of the dry season showed a greater tendency to abscond than those whose visibility had not increased. Trials that Seeley *et al* conducted, exposing 3 colonies but keeping them shaded by leaving vegetation overhead, while leaving 3 controls shaded and concealed, showed that the former, exposed colonies abscond more rapidly. This did suggest colonies might be abandoning their nests because of exposure to predators, but they did add the caveat that excess insolation might also stimulate colony movement. I too would guess that it was quite possible that the shade they left above these colonies was not adequate and was contributory to their absconding.

Table 2.15 also shows that the percentages of the total number of colonies in wild habitats (27.3%) and new gardens (31%) that were found in cavities were greater than the percentages found in cavities in the Batina (5%) and Interior (2.2%) date gardens. Assuming these figures reflect the true proportions of cavity nesting colonies in these areas and they are not the result of inadequate searching, there are 2 possible explanations for this difference in nest site distribution between the habitats.

(a) Compared to the gardens there are more cavities available in the mountains, and relatively few trees that provide the correct shade/exposure, so more bees have to make use of the sub-optimal cave nest sites.

(b) There are differences in the meteorological conditions between densely vegetated gardens and the more open wild habitats, and certain caves offer a better microclimate than trees in these circumstances.

Without detailed measures of nest site availability and more measurements of cavity temperatures, the relative importance of the 2 explanations cannot be determined but I suspect there is some truth in each. When one considers the buildings, wells etc that offer potential nest sites in oases there may be as many per unit area as there are caves in the hills, but the density of trees in wild habitats is obviously lower than in date gardens. Perhaps most cavities are not very suitable eg cave No. 5, Figure 2.7b, and are not usually selected in oases, but have to be used more often from necessity in the mountains where trees are scarce.

On the other hand the temperatures in cave No. 4, Figure 2.7a, were better (cooler) than nearby tree temperatures in May; also south-facing caves might retain the heat better in winter and therefore some cavities may be actively selected in favour of trees at certain times of year. The 2 colonies in wells at Khabura arrived there just before and during the hottest period of the year (section 6.7), again suggesting that in some months there is a greater tendency to favour such sites because they are cooler, to sites in trees.

It is not likely that caves are selected to avoid predation as the colonies are not well hidden inside them and are only difficult to find if there are a lot of caves to search. Once found, colonies would be particularly susceptible to predation by invertebrates and vertebrates, as they are close to the ground and not in thorny trees. Colonies in windows, on buildings and in wells were also easier to spot than those in trees, but these positions sometimes made the nests more inaccessible.

Similarly, the greater number of *florea* colonies found in cultivated areas (almost certainly reflecting a higher density as well as a greater search effort) did not suggest that predation was a major factor involved in determining the distribution of colonies between these and wild areas. Predation pressure from man must have been greater in the areas he cultivated and also from other predators such as ants, hornets and bee-eaters that benefited from the water and food that man's activities provided. Yet the bees were not deterred from nesting in such areas; the floral rewards of man's crops and weeds and the shelter - but not complete shade - from the vegetation presumably outweighed such predation problems.

Three other minor points on nest sites can be mentioned here, 2 in relation to remarks in the literature. Dutton & Free (1979), Williams (1979) and Free (1981) report an Omani bee-keeper's comment that some *florea* colonies move further back into caves in the heat of the summer. I never encountered or heard reports of colonies actually shifting the position of their whole comb such a short distance within one cave; it is more likely they would move to a completely different site (cave or tree) that would offer a more significant change in microclimate.

Free (1981) reported that the comb of *florea* colonies is often attached to a palm leaf; this study has shown that, though colonies will nest on date-palm leaves, they are usually avoided and it is only because palms are by far the most abundant tree in Omani gardens that a number of colonies have been recorded in this species.

As for the overall numbers of *florea* colonies in different tree species in Oman, most were found in *Citrus* trees (Table 2.15). Though larger samples would be needed to consider the relative selection for scarcer trees such as mangoes, indian almond and others, a person searching for *florea* colonies would probably do well to pay most attention to gardens with *Citrus* trees, particularly if planted evenly in rows allowing easy inspection, and to concentrate on the SE quadrant of the trees.

To reiterate the main conclusions, it appears that in Oman most *florea* colonies were selecting quite well-hidden nest sites, often in dense patches of vegetation, but they were situated so as to receive a small amount of insolation. The south-east quadrants of trees and cavities and walls with east to south aspects were particularly favoured and such sites should facilitate colony thermoregulation and forage communication dances. In the hotter months there was a greater tendency for some of the colonies to choose more sheltered sites such as wells and the northern parts of trees. Predation pressure on *florea* was probably less than in Thailand (Appendix I) and did not appear to be of such major importance in determining nest site selection in Oman, as Seeley *et al* (1982) concluded it was in Thailand.

CHAPTER III

SITING OF *APIS FLOREA* COLONIES BY BEE-KEEPERS AND OTHER ASPECTS OF TRADITIONAL HONEYBEE MANAGEMENT IN OMAN

General Introduction

Having considered in the previous chapter the nest sites selected by wild colonies of *Apis florea* it is pertinent to consider next the types of nest sites chosen for *florea* by Omani bee-keepers. The satisfactory siting of colonies is a critical facet of the overall management of this species and is treated in detail in Part I; the positioning of colonies in trees, in natural caves and in man-made cavities will each be examined separately and information is tabulated where possible.

However, the enumeration of the prevalence of various practices was not easy as there proved to be almost as many methods of keeping *florea* as there were bee-keepers, each bee-keeper or bee-keeping family having their own favoured techniques and folklore. The techniques were usually variations on a theme that involved the "zoora", a mid-rib of a date palm frond split down the middle to hold the comb, and the methods practised by Humayd Sulayman al-Shimili of al-Ghubbi as described by Dutton & Simpson (1977), Dutton & Free (1979) and Williams (1979) appeared to be typical of that theme. Therefore, in Part II of the chapter details of Omani *florea* management will be described which differ from Humayd's methods, and which have not been mentioned in the first part of the chapter, especially those of practical interest.

Details of "honey-hunting" expeditions to the "jabal" (mountains), an important activity for some *florea* specialists, will also be related and the survival of *florea* in these remote areas considered. Unless specifically stated, details of the colonies kept by and the bee-keeping practices of Nāsr Ahmad al-Ghaythi at Zāhib, who had the most advanced *florea* management system that I encountered, have not been included in this chapter. A separate chapter (IV) is devoted to him and his bees. Thus in this thesis it is hoped that nearly the full range of management techniques to which *florea* is subjected in Oman will be covered; though various examples which were alike have not been described in detail, selected ones are given throughout this chapter to illustrate certain points. For brevity, in certain tables bee-keepers have been given designatory letters, a, b, c, d, e etc so that cross-references can be made between tables and between tables and text.

PART I SELECTION OF NEST SITES FOR *APIS FLOREA* BY OMANI BEE-KEEPERS

A. SITING OF *APIS FLOREA* COLONIES IN TREES AND BUSHES

1. Introduction

Although early studies on *florea* management in Oman primarily described techniques of keeping colonies in caves, both natural and artificial (Dutton & Simpson 1977; Dutton & Free 1979; Williams 1979), many colonies are also sited in trees. The trees used may either be in the gardens or in uncultivated areas where pastoralists and garden-owners, for instance Nāsr Ahmad al-Ghaythi (Chapter IV), might put their colonies. The types of trees and bushes used and other site characteristics are described here and compared with naturally selected tree sites.

The data on sites selected by wild colonies was being collected concurrently with information on practical bee-keeping and was not analysed till later, so I did not appreciate that the exact position in which a bee-keeper put a colony in a tree was necessarily of much significance, particuarly as the sites the bee-keepers chose seemed to be mainly for their own benefit ie in easily accessible positions in trees close to their houses. Therefore, though convenience was certainly an important criterion, I may have underestimated the extent to which some bee-keepers took into account other factors, such as colony orientation, in determining the final choice of site and as a result did not always measure these attributes.

Mainly for this reason, but also because I did not want to disturb colonies that were not mine, the sample sizes for some nest-site attributes are small, some of the measurements having been estimated.

2. Type of bush or tree

The plant species in which the various colonies in trees were kept are listed in Table 3.1. *Citrus* trees were clearly the most frequently used, even though there were more young palms available (Tables 2.2 and 2.4) and must therefore be preferred by most bee-keepers. This distribution closely reflects the selection pattern exhibited by wild colonies of *florea* whereby the most abundant date-palm was avoided in favour of plants with denser foliage, such as *Citrus* spp. (Chapter II, C.1). It appeared that the taller trees such as *Ziziphus spina-christi, Mangifera indica* (mango) and *Terminalia catappa* (Indian almond) were also not often used in the date-gardens, presumably because they have few branches at the base and it would have been necessary to climb them to find a suitable shady site. Nearly all the trees used offered sites accessible from the ground.

Apart from the many trees and bushes used by Nāsr Ahmad al-Ghaythi for siting his *florea* colonies in the "sayḥ" or gravel plains (Chapter IV) the only record of *florea* being kept in trees outside

Table 3.1 Types of bush/tree used by 13 bee-keepers in Oman for siting colonies of *Apis florea* under their management. The number of colonies kept in each species and the number of bee-keepers recorded using each species are given.

Nest Site	No. of Colonies	No. of Bee-keepers
Citrus spp.	18	10
Phoenix dactylifera (young)	2	2
Vitis vinifera	2	2
Mangifera indica	1	1
Punica granatum	1	1
Jasminum sp.	1	1
Tecoma stans	1	1
Ziziphus spina-christi	1	1
TOTALS 8 species	27	13*

* This figure is 13 not 19 because some bee-keepers used more than one species of plant; in fact Humayd Sulayman al-Shimili and members of his family had colonies in 5 different species.

the cultivated areas was of one pastoralist, Said Ali (bee-keeper d), on the Bātina plain keeping a colony in a *Ziziphus spina-christi* tree in November 1979. He said he had found the colony about 1 month previously (end of September, beginning of October) and initially had put it in one of his ESE facing caves at the side of a wadi where he kept colonies during the winter (5 had been recorded in these caves in December 1977). However, ambient temperatures can still be high in autumn and he had considered the colony was getting too hot in its cave, so had moved it to a shadier position in the ESE part of the *Ziziphus spina-christi* tree less than 100m away, in the wadi. He said it was usual for him to move colonies from his ESE facing caves to tree sites where there was better shade in the heat of the summer. It so happened that a wild colony of *florea* had settled in the same tree, within a few metres of the first but further round towards the NE, apparently soon after the kept colony had been sited there; this event supported the bee-keeper's choice of nest site.

Though this man and Nāsr were the only 2 *florea* keepers actually recorded keeping colonies in trees outside cultivated areas, there were probably others who did the same. However, it did appear that most bee-keepers with access to gardens kept their colonies there in summer (in trees or cavities) while the pastoralists in the plains and mountains, on the whole, used caves throughout the year.

3. Height of nest site

The mean height at which *florea* colonies were sited in trees by Omani bee-keepers was 1.84m (Table 3.2) which is lower than the mean of 3.28m for natural nests (Chapter II, Figs.2.1a and b). With 11 out

Table 3.2 Nest height distribution of *Apis florea* colonies sited in trees and bushes by bee-keepers in Oman

Nest Height, m	No. of Colonies
0 - 0.49	3
0.5 - 0.99	4
1.0 - 1.49	2
1.5 - 1.99	2
2.0 - 2.99	1
3.0 - 3.99	1
>4.0	2

Mean Height : 1.84m
Standard Error : 0.50m
Range : 0.34 - 7.0m
n : 15

of 15 colonies at or lower than 2m (which is just over head height), this indicates that most colonies are put at a height convenient for access by the bee-keeper from the ground. The low height distribution also reflects the fact that the *Citrus* trees which were favoured are not as tall as most other trees available - though one reason that *Citrus* trees were favoured may have been their low height with branches near the ground!

The highest colony, 7m, was in a mango tree and was kept there, by a less experienced bee-keeper, as this was the site at which he had found the colony. The next highest colony, c. 5m, was that mentioned in the previous section being kept in a *Ziziphus spina-christi* tree by the pastoralist, Said Ali. It would have been difficult for him to have put the colony at head height in this or nearby trees as they did not have suitable low branches. The other 2 colonies above 2m belonged to a man on the Batina who was not a specialist *florea* keeper; one had been returned, in a split date frond mid-rib, to its original natural site after its honey was removed and both were probably put at this height to keep them out of reach of children/neighbours.

4. Type of colony support

The ways in which managed colonies were supported were recorded and are summarized in Table 3.3. All but one of the beekeepers used a "zoora" pl. "zoor ", the mid-rib of a date palm frond; it would be split longitudinally down the middle to within a few cm of one end, the comb wedged in the middle and the split pieces at the other end, then tied together. The "zoora" and comb would usually be rested on and/or tied to two adjacent radiating branches in a tree, so that the "zoora" was at a tangent (forming the third side of a triangle with the trunk of the tree as the apex). The typical way in which a "zoora" is utilized for supporting combs has been described for Humayd Sulayman al-Shimili of al-Ghubbi by Dutton & Free (1979) and Williams (1979) and similarly for Nāsr Ahmad al-Ghaythi of Zahib in this thesis, Chapter IV.

Table 3.3 Types of support used for 27 colonies of *Apis florea* kept in trees by 13 bee-keepers in Oman. Their use is explained further in the text.

Type of Support	No. of Colonies	No. of Bee-keepers
"Zoora" (mid-rib of date palm frond)	22	12
On original supporting stick	2 (one later moved to "zoora")	2
Tied to branch	2	1
Box	1	1

Two colonies were recorded that had been moved from their natural nest sites with their combs still attached to the twig they had themselves selected. In fact several of the colonies recorded may initially have been brought by a bee-keeper to a new site on their original twig, and later transferred to a "zoora" when the honey was removed; I found this was definitely the case with a colony belonging to one bee-keeper after inspecting it on more than one occasion. This probably happened most often with small colonies that contained quantities of honey too small to be worth removing and which could be transported easily with little risk of the brood comb breaking away (as it was liable to do with colonies possessing a large brood comb).

One man, Sulayman Sayf al-Muskari of Murāni near Ibra (Sharqīya region), bee-keeper O, believed that a colony should, if possible after its honey has been taken, be re-attached to the same type of support and at the same site. When visited on 10.xii.79

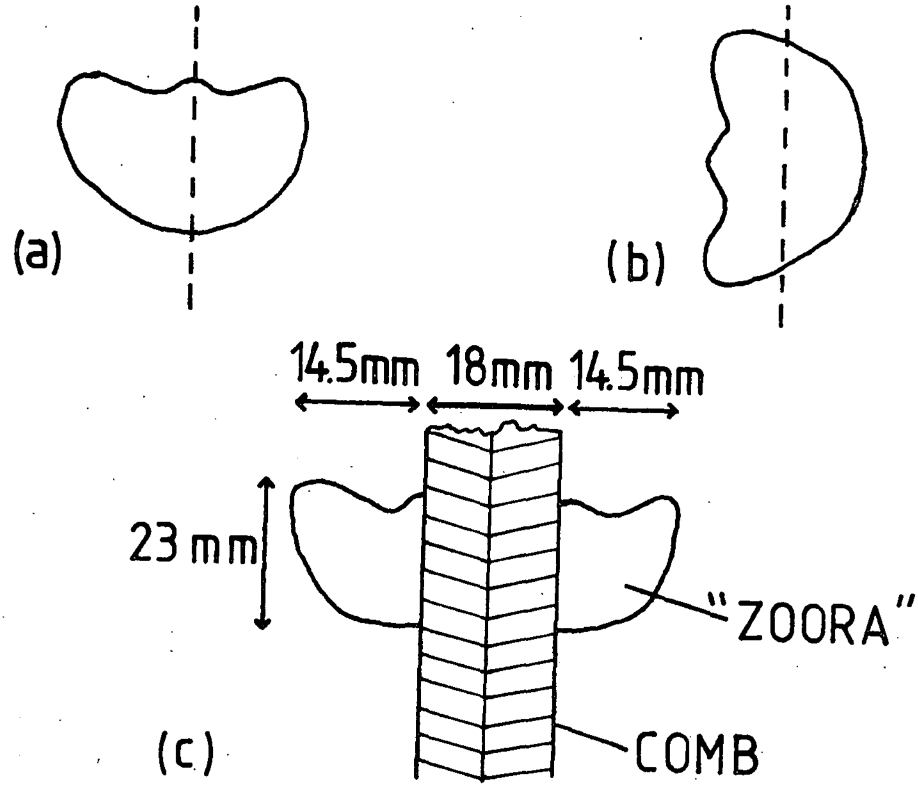
he had 2 colonies dealt with in this way, one tied along a branch in a lime tree (*Citrus aurantifolia*) and the other tied along the mid-rib of the frond of a young palm tree - apparently not the original, which must have been removed with honey still attached, but this was considered to be equivalent to it (Fig. 3.1). A third colony had been cut from another lime tree and had had much of its honeycomb removed, but in such a way that the brood comb was still attached to the original twig, which was then put back in the same lime tree.

So, rather than wedging a colony in a split stick, Sulayman preferred to keep it on the same supporting stick, if necessary by tying it, so the bees could build their comb again around their chosen support. This technique was attractive in principle, as some honey should be left to the bees and brood should not be lost as a result of being squashed between the split stick, but in practice may not have been satisfactory since these particular colonies were not in a very good state. Since much of a *florea* honeycomb is constructed below the top of its supporting twig it would be difficult to remove just a portion of it without either damaging the honeycomb itself, causing much honey to leak out, or weakening the attachment of the brood comb which might subsequently fall away. Tying a brood comb to a support is not simple either, for with my own hiving experiments I sometimes found the weight of the brood comb was sufficient to cause the string, leaflets etc holding the comb to cut through the soft wax, so that the brood comb fell away.

Finally, one colony was partly supported/enclosed by a wooden box (probably the sort used for packing oranges) in/under a lime tree, but unfortunately full details were not recorded. The bee-keeper (L) concerned usually kept his colonies on "zoor " in trees or cavities and this colony too I believe was attached to a "zoora" and the box, rather than being a deliberately constructed hive was just a convenient way of keeping and sheltering the colony at that particular site in the hot season.

Figure 3.1 Colony of *Apis florea* kept by Sulayman Sayf al-Muskari at Murāni near Ibra in the Sharqiya (Eastern) region of Oman, on 10.xii.79. He had taken the honey from this colony on 18.xi.79 and then tied the brood comb with 3 palm leaflets, along a frond mid-rib that was still growing on a young date palm. Most bee-keepers wedged colonies into "zoora" that had been detached from a palm and split down the middle, but Sulayman believed that tying the colony to its original or a similar branch was more natural. See text Section A.4, p. 85-86.

Figure 3.2 Cross-sectional views of "zoor" (date frond mid-ribs) used for supporting colonies of *Apis florea* in Oman. Showing (a) usual split along vertical axis (b) less usual split along horizontal axis with "zoora" then turned on its side (c) how a comb is wedged in the middle effectively making the support's diameter, around which the honeycomb must be built, larger. Dimensions are of a large "zoora" from al-Ghubbi described in the text (p. 87).


(a)
(b)
14.5mm
18mm
14.5mm
23 mm
"ZOORA"
(c)
COMB

5. Size of colony support

The dimensions of most of the "zoora" used were not measured, their length to some extent depending on the distance between the branches on which their ends were to rest. Those used by Nāsr Ahmad al-Ghāythi (Chapter IV Pt I, A.3) averaged .67m long and seemed fairly typical of those used by other *florea* keepers. Nāsr was, however, particularly consistent in the lengths he used as the "zoora" had to fit in his wall recesses, while other bee-keepers probably employed a greater range of sizes. For instance one *florea* "zoora" used by a neighbour of Humayd Sulayman (bee-keeper h) at al-Ghubbi was fairly robust, having been cut near the base of the frond, and measured 1.05m long while another used by bee-keeper m in the Batina gardens was even longer at 1.23m. At the opposite end of the scale, one employed in Diqāl, a village in the Bātina plain, was very slender and only 0.6m long.

The cross-sections ("diameter") of the "zoor " varied correspondingly and of course became much thicker once split and opened up for the comb to be wedged inside. At the proximal end, where the split started, the "zoora" from al-Ghubbi was 29mm "thick" (deep) and at the distal end where the split ends were bound together it was 27mm thick; at the same positions the height of the "zoora" was 23mm and 21mm respectively. For the very slender "zoora" from Diqāl, the corresponding measurements were 15 to 13mm thick (deep) and 9 to 8mm high.

The size of the split in the middle of the "zoora" depended on how tightly the *florea* comb was clamped inside, but would be approximately the thickness of the brood comb ie just under 20mm. Thus, once the comb was clamped in the "zoora", the cross-section of the support in the case of the large "zoora" from al-Ghubbi would have been as large as 29 + 18 = 47mm by 23mm (Figure 3.2). This is considerably larger than the 13.6mm mean diameter for naturally selected supporting twigs/branches (Chapter II, C.3), and nearly all other "zoora" used would be larger too. However, this factor did not appear to deter the bees or bee-keepers from using these "zoora" which have the advantage of being abundant, straight (unlike most twigs) and rigid, while the ends maintain a certain springiness once split that helps hold the comb when it is inserted.

The "zoora" were usually split along a vertical axis and rested in their natural, horizontal position but on at least one occasion a "zoora" was seen to have been split along a horizontal axis and then turned through a right angle from its natural position so it was resting on its side (Figure 3.2).

6. Tree Sector and Colony Orientation

The data on this aspect of siting *florea* colonies in trees is very limited, concerning only 13 colonies and 7 bee-keepers (Table 3.4). When I discussed such matters with them, *florea* keepers usually seemed to be more concerned whether a colony should be placed in a tree in a garden or in a cave/cavity at a particular season, rather than the exact positioning in a tree. However, with their concern that colonies should receive the correct amount of sun or shade when selecting an appropriate position for a colony in a tree, if bee-keepers were looking for a shady site they would be more likely to find this in the northern sector of a tree. Alternatively, if looking for a more sunny site they would be most likely to choose a position in the southern sector of the tree. There was some evidence of selection for the latter (though whether deliberate or by the "chance" method above was not clear),with 5 autumn-winter-spring colonies being in a sector from E to SW (Table 3.4a). A 6th colony, however, was in a S to SSW sector all year round; maybe once established it was strong enough to be able to cope here with the extremes

Table 3.4 Positioning of *Apis florea* colonies kept in trees and bushes in the Sultanate of Oman, according to season and owner. The letters d, f, h etc refer to different bee-keepers and the abbreviations in brackets to the seasons of the year in which the colonies were kept in the trees. Su: Summer, circa May to August. A: Autumn, circa September to mid-November. W: Winter, circa mid-November to mid-February. Sp: Spring circa mid-February to April.

(a) Sector of tree occupied by 10 colonies, belonging to 7 bee-keepers

Bearing (degrees)	Autumn - Winter - Spring	Summer
1° - 45°) 46° - 90°)	o (W) f** (Sp-	Su)
91° - 135°	d (A) m (Sp-	Su)
136° - 180°	∿o (W)	
181° - 225°	∿p* (A) o (W), ∿h (W-Sp), ∿q (A-W-Sp-	Su)
226° - 270°		
271° - 315°		
316° - 360°	q (A)	q (Su)

continued overleaf

Table 3.4 continued

(b) Direction in which most exposed side of colony faces; 9 colonies belonging to 6 bee-keepers

Aspect/Bearing (degrees)	Autumn - Winter - Spring	Summer
1° - 45°		
46° - 90°		
91° - 135°	h (W), o (W), m (Sp	Su)
136° - 180°	p* (Sp)	
181° - 225°	q (A-W-Sp	Su)
226° - 270°		
271° - 315°	p* (A), q (A)	q (Su)
316° - 360°	q (A) ∿f (Sp	Su) q (Su)

∿ : position approximate, estimated without a compass

* : positioned by a "casual" bee-keeper

** : sited in a *Citrus* tree against a cliff, so colony is classified according to the aspect of the cliff, not the actual tree sector. A photograph indicated the two approximately corresponded.

of both winter and summer. Two colonies in NE to SE sectors were present from spring through to summer and another colony was kept in a NW to N sector from summer till the end of autumn, but without knowing the different extents to which each was exposed to solar radiation during both hot and cool seasons, little comment can be made as to whether the sites were intended to be most suitable for spring, summer or autumn.

The data on the direction faced by kept colonies is no more conclusive (Table 3.4b); there is perhaps a tendency for bee-keepers to orientate colonies with the exposed side northwards if established in summer and south or eastwards if established at other times, but not for them to change the colony orientation as the seasons change. These orientation topics are worthy of further investigation in view of the findings that naturally established colonies in Oman overall favoured sites in the SE sector of trees, but with some colonies establishing themselves in summer, selecting sites in northerly sectors (Chapter II, C.4). The present siting practices of Omani bee-keepers and their degree of success should be considered more closely and the bee-keepers could be encouraged also to test for themselves whether siting colonies according to the natural orientation preferences of the bees reduces absconding, while facilitating foraging and brood rearing.

7. Shade

Despite the inadequate method of estimating shade, it is apparent from Table 3.5a and b that bee-keepers never put their *florea* colonies in sites that were excessively exposed to the sunshine; all the colonies, winter and summer, were judged to have greater than 75% shade/ cover. Warmth and cold were factors often referred to by bee-keepers with respect to the nest site requirements of their *florea*, and sites with insolation to warm the bees early in the morning were considered

Table 3.5a Shade experienced by 16 of the 27 *Apis florea* colonies that were recorded being kept in trees and bushes in northern Oman by 9 different bee-keepers. See Chapter II, B Methods 2 (v) for manner of estimating shade.

+ : direct sunlight, - : no direct sunlight hitting or thought to hit colony

? : exposed to direct light, but not certain whether direct sunlight would strike colony or not

* : colony in this site during spring and summer) therefore included twice
** : colony in this site all year)

Shade		Season during which colony was being kept					
		Autumn/Winter/Spring			Summer		
%	Category	+	?	-	+	?	-
<75	0 - 4	0	0	0	0	0	0
75- 90	5	$2+1^{*}+1^{**}$	$3+1^{*}$	0	$1+1^{**}$	1^{*}	0
90 - 100	6	1	$1+3^{*}+1^{**}$	0	2	$3^{*}+1^{**}$	0

Table 3.5b Summary of Table 3.5a, assuming all ? colonies receive at least a little direct sunlight and that the siting of colonies in the one place during spring and summer are two independent sitings ie those colonies marked * and ** are included twice.

Shade		Season during which colony was being kept	
		Autumn/Winter/Spring	Summer
%	Category	+	+
<75	0 - 4	0	0
75 - 90	5	8	3
90 - 100	6	6	6

by some to be particularly important in the cooler months. It seemed that most colonies were put in positions to receive at least some direct sunlight (Table 3.5a and b), but more careful observations, on the time of day and extent to which colonies were exposed to it at different seasons, are needed to determine how effectively the bee-keepers practise what they preach in this respect.

There was also some evidence to suggest that colonies in summer were put in rather shadier sites than during the winter, for 6 out of the 9 summer colonies (67%) were in the highest shade category (6), but only 6 out of the 14 autumn/winter/spring colonies (43%). However, it was obviously not always necessary for a colony to be moved to a different site as the seasons changed, since 4 colonies were kept successfully at their existing sites from spring through to summer - a time when there is a very marked temperature change. Two further colonies were kept in their respective sites the whole year round.

With gardens being small in Oman, observant and serious bee-keepers may become familiar with particular tree sites from which bees do not abscond as the seasons change and therefore may use them regularly. The general pattern though, with experienced bee-keepers, appeared to be one of favouring slightly different types of tree site according to the time of year; however, flourishing colonies might be left in the one position from spring to summer, while newly gathered ones would be put in a different site, chosen in part because of the shade requirements.

8. Discussion

The information presented in this section suggests that two general considerations determined the way in which *florea* bee-keepers used trees for siting colonies. One was the convenience of the site and the materials involved for the bee-keeper, the other was the suitability of the site, as perceived by the bee-keeper, for the bees. The height of the colony and type of support used (the "zoora") were usually for the convenience of the bee-keeper, while the amount of shade provided was for the benefit of the bees. The type of tree selected would appear to satisfy both parties, particularly where the *Citrus* tree was concerned. The positioning/orientation of the colony within the tree in some cases may have been for the supposed benefit of the bees, but in other cases will have been determined by the presence of convenient resting places for the "zoora" or other support. Overall the tree nest sites chosen by the bee-keepers were not that dissimilar to naturally selected sites and until a greater understanding of the precise nest requirements of *florea* for communication dances, thermoregulation etc is obtained, close adherence to such a practice is probably wise.

B. SITING OF *APIS FLOREA* COLONIES IN NATURAL CAVES

1. Introduction

This section considers the use, by *florea* "honey-hunters" and bee-keepers in the mountains of northern Oman, of natural caves of the type described in Chapter II. C.6.1. In some cases the bee-keepers had built up low barriers of stones across the front of the cave entrances which may have helped to conceal the colonies, but they would not have prevented entry by a determined predator; such walls would also serve as an "alāma", a sign which indicates that a colony is owned (Dutton & Simpson 1977).

Some of the caves were near a bee-keeper's home, for instance if his village or settlement was near or at the edge of a wadi which had suitable cavities in its banks, while others were several kilometres distant in steep rocky hillsides. The "honey-hunters" I accompanied on their expeditions to the hills in fact practised a form of management as they did not completely destroy a nest from which they had taken the honeycomb, but returned the brood comb to the cave by wedging it against the roof with sticks (this chapter, Pt II, A.2). It was highly likely that some of the colonies I observed already supported in this way by sticks had originally arrived in the caves of their own accord but nevertheless they have been put in the "kept" category only as it was a bee-keeper who was the last to install them there.

On the two occasions I was with "honey-hunters"/bee-keepers when they removed honey from colonies in caves, the combs were returned to the same cave rather than taken to another one. Whether such bee-keepers do ever move colonies at certain times of year to other nearby caves with a different aspect was not clear. One of those concerned, Khalifa (bee-keeper c) of the Wadi Hawasina, did move colonies from distant caves to ones nearer his abode, but I understood this was primarily for his own convenience rather than to provide a better site for his bees. He did however consider that *florea* needed the warmth of the sun in the winter and shade in the summer, so may have taken this into account when choosing the caves near his home. Humayd Sulayman al-Shimili similarly brought colonies of *florea* from caves in the mountains near Ibri to sites near his home (Dutton & Free 1979; Williams 1979) but it is not known either if he ever transferred them to other caves in the mountains.

Whether or not these colonies I observed had been moved to the caves or had initially flown there of their own accord, it was apparent from extensive traces of the hexagonal patterns of wax comb on the cave roofs that many of them had contained colonies of *florea* on prior occasions. In other words, they had been used, maybe regularly, by *florea* in the past with or without the help of bee-keepers (but there was no way of telling at what seasons these prior occupations had been). The "honey-hunters"/bee-keepers confirmed this; for instance, Khalifa (bee-keeper c, from the Wadi Hawasina), referring to the wild colony in a NNW facing cave from which he took the honey and returned the brood comb on 28.xii.79 (see Chapter II, C. 6.7), said that *florea* often came to this cave of their own accord, sometimes staying after he took their honey. On the other hand, on occasions when they absconded he told me another (or possibly the same?) colony might later occupy the cave.

Some caves empty of bees also had traces of wax on their roofs indicating past occupation but data on their orientations etc are not included in the analyses below. Of the occupied caves, only data on orientation and shade are presented as parameters on the position of colonies within the caves (ie height and depth) may have been selected by the bee-keeper for ease of access and inspection rather than for microclimatic reasons. The objective of measuring cave orientation was to establish to what extent bee-keepers practised the policy, expounded by some, of keeping colonies at different sites appropriate to the season. Orientation and shade were measured as described in Chapter II, p. 26 and 59-60.

2. Orientation of caves

The aspects of caves used by 7 *florea* bee-keepers are given in Table 3.6a, and the time of year they were kept there indicated. The bee-keepers, as far as I knew, were not related and were effectively independent in their practices, though 2 or 3 of them might at some stage have been in contact with each other. It can be seen that all 13 colonies in caves facing in the East to South quadrant were there over the cooler months of the year from October to March, and it was 6 different bee-keepers that were siting the colonies in this way. One of the bee-keepers (c) had a colony in a WNW facing cave in spring (March) and at the same time another colony in a SE facing cave. He was the bee-keeper who re-established a strong, wild colony in the same NNW facing cave in December having removed the honey from it (see Chapter II, C, 6.7). In summer he had 3 colonies in NW to NE facing caves, so he did <u>tend</u> to use caves with orientations appropriate to the season, but did not always strictly adhere to such a policy. Even though his 3 summer colonies were in N facing caves, 2 still absconded and the third looked as though it was on the point of absconding (it was in cave No. 5 which became very hot in July and which had temperature measurements made inside, Chapter II, Figure 2.7b). The 2 other natural caves being used in summer contained colonies belonging to a single bee-keeper (f) and both faced N to NE.

Therefore, of 20 colonies kept by 7 bee-keepers in natural caves, 18 kept by 6 of the bee-keepers were in positions consistent with a policy of using approximately north facing caves in summer, but south-east facing ones from autumn to spring. One bee-keeper was responsible for the 2 colonies which did not fit this pattern. Unfortunately, of the 18 "correctly" placed colonies, 13 were autumn to spring but only 5 were summer records and these latter belonged to just 2 bee-keepers, so the summer sample size was very small. Part of the reason for the small summer sample size was that bee-keepers and myself were reluctant to embark on honey-hunting expeditions in the very hot months of July and August when honey yields were likely to be low. Also, apart from the one bee-keeper who was less consistent with the orientation of the caves he used, the records of summer caves came from bee-keepers different to those providing the records of winter caves. It would have been valuable to have had detailed records of the caves used by each of 2 or 3 bee-keepers in both summer and winter.

Table 3.6a Orientation of 20 natural caves used by 7 bee-keepers/ "honey-hunters" for *Apis florea* colonies in Oman. The letters a,b,c,d etc refer to different bee-keepers and the abbreviations in brackets to the seasons of the year in which the colonies were kept in the caves (see Table 3.4 for details).

Aspect/Bearing (degrees)	Autumn - Winter - Spring	Summer
1° - 45°		c(Su),f(Su),f(Su
46° - 90°		
91° - 135°	d(A-W),d(A-W),d(A-w),d(A-W),d(A-W),e(A-W),e(A-W)	
136° - 180°	b(A-W),g(A-W),g(A-W),g(W),a(W),c(Sp)	
181° - 225°		
226° - 270°		
271° - 315°	c(Sp)	
316° - 360°	c(A-W)	c(Su),c(Su)

Table 3.6b Orientation of 19 of the *Apis florea* colonies within the above caves. The comb of the other colony, c(Su), in a cave facing N was removed after it absconded and before its orientation was measured.

F: One side of colony/comb faces out of the cave
A(F): Colony/comb at an angle to cave entrance, but closer to F
A(P): " " " " " but closer to P
P: Colony/comb runs along a line pointing directly out of the cave entrance

	F	A(F)	A(P)	P
Cooler Months (Autumn, Winter, Spring)	6	0	3	4
Hottest Months (Summer)	1	0	3	2
Total	7	0	6	6

Table 3.6c Shade experienced by 18 of the 20 above-mentioned colonies kept in natural caves. See Chapter II, Methods, p. 26-27 for manner of estimating these values.

+ : direct sunlight, - : no direct sunlight, hitting or thought to hit colony

Shade		Season during which colony was being kept			
		Autumn/Winter/Spring		Summer	
%	Category	+	-	+	-
<75	0 - 4	0	0	0	0
75-90	5	8	0	0	0
90-100	6	1	4	0	5

3. Orientation of colonies within caves

As explained in Chapter II, p. 59-60 for colonies in natural caves, the orientation of the colonies themselves within the caves was measured. Of the 13 winter colonies in caves with a south-east aspect, 6 faced out of the cave entrance, 4 were perpendicular to it and 3 were at an angle to the entrance (but closer to the perpendicular orientation). Of the 7 colonies in W to NE facing caves, one was not measured before it absconded and its comb was removed, one faced out of the cave entrance, 2 were perpendicular to it and 3 were at an angle (all closer to the perpendicular orientation). This spectrum of angles (Table 3.6b) suggests that the bee-keepers did not consider that the orientation of the comb within a cave was particularly important, only the aspect of the cave itself; the orientation of the combs within the caves I believe was primarily dependent on the position of convenient resting places eg see this chapter, p. 100 and p. 122.

4. Shade

Table 3.6c indicates the amount of shade and insolation experienced by the *florea* colonies in the positions at which they had been sited by the bee-keepers. All 5 colonies observed in summer were completely shaded, receiving no direct sunlight. Of the 13 colonies in the relatively cool autumn to spring season only 4 were completely shaded in this way. However, 2 of them had been put in these sites in the middle of March just before the hot season, so maybe the bee-keeper was anticipating the future requirements of the bees. The third colony, which has been mentioned before (p. 68-69, 93,94 and Figure 3.4) had selected its shady cave in autumn and was re-installed in it in December when the bee-keeper took the honey (Figure 3.5).

It absconded soon after and the complete shade, with no warming insolation, may have been a contributory factor to this desertion. The 4th colony had been put in a shady, but south-facing, cave during the winter which may or may not have been ideal. It had not absconded and when the bee-keepers took the small amount of honey in it in March, they returned the colony to the same position in the cave, which was then probably suitable for the approaching months with temperatures beginning to rise.

All of the more exposed colonies (8 in shade category 5 and 1 in category 6, but all experiencing some direct insolation) were in these sites in the cooler autumn to spring months and not in the summer. None were in very exposed positions, categories 0 - 4, as was the case with wild colonies nesting in cavities, all of which were in shade categories 5 and 6 too.

5. Discussion

From the above observations, it appeared that the bee-keepers, as well as using south-east facing caves in winter and north facing caves in summer, sited the colonies within caves in such a way that many of the winter colonies were exposed to some insolation. Colonies in north-facing caves obviously cannot be put in a position to receive any sunlight, but with south-facing caves the bee-keepers can put the colonies at different depths within the caves, as they consider appropriate, in order to attain different degrees of exposure.

Unfortunately, the distance into the cave at which the colonies were sited was not recorded; such measurements might have usefully supplemented the rather approximate data on degree of colony exposure. However, as the temperature recordings inside caves have already suggested (Chapter II, p. 62-64 and Figures 2.7a and b), different caves probably have their own individual temperature characteristics, and direct exposure of a colony to the sun will not be the only factor determining a cave's suitability for the bees. It is most unlikely that the bee-keepers ever measured a cave to make sure they had the best position for a colony of *florea* for a given time of year, but their observations on wild colonies and experiences of keeping them in various caves (eg length of time a colony spent in a cave, the month in which it absconded) must have taught them the types of cave and positionings in caves most likely to be successful.

Some bee-keepers, for instance c (p. 94), may have been less aware of a colony's nest requirements than others and consequently been less consistent in the sites they chose, but overall it appeared that the bee-keepers did pay some attention to the thermoregulatory problems of *florea* in the extreme climate prevailing in the mountains of northern Oman. They often talked in terms of certain nest sites being hot or cold but, having no knowledge of the communication dances of honeybees, did not appreciate that they might need a view of the sun or sky. Nevertheless, at least one bee-keeper did tell me that enclosed spaces such as boxes/hives were not suitable for *florea* (maybe from his own practical experience, finding that the bees absconded) but did not give any reason why this should be so.

C. SITING OF *APIS FLOREA* COLONIES IN ARTIFICIAL CAVES AND BUILDINGS

1. Introduction

Various man-made cavities used by bee-keepers as sites for their colonies of *florea* are now considered. Some of the cavities had been especially constructed for *florea* and include "artificial caves" like that described by Dutton & Free (1979). Others, such as the unglazed window-openings of houses, were obviously designed for other purposes but along with miscellaneous incidental sites, as occurred in ruined buildings, were deemed convenient and suitable by the bee-keepers. One such colony in a window is illustrated in Figure 3.3a.

All these sites were very close to the bee-keepers' dwellings, unlike some of the natural caves, and it was probable that most of the colonies had originally been brought to and installed in the sites and that the cavities had not been selected by colonies of their own accord in the past.

The wall recesses in which colonies were kept by Nāsr Ahmad al-Ghaythi are considered separately in Chapter IV, but 2 similar recesses or "bee boles" (Figure 3.3b) at Diqāl on the Batina plain are included here. Orientation and shade measurements were made as described in Chapter II (p. 26 and 59-60).

2. Orientation of cavities

Table 3.7a shows the orientation of 22 man-made cavities used by 7 bee-keepers for *florea* colonies. If the seasonal nature of the sites is disregarded the overall mean direction or angle is 151°, the mean angular deviation 44° and the confidence intervals $121^{\circ} - 181^{\circ}$ (95%) and $113^{\circ} - 189^{\circ}$ (99%); $n = 14$, having considered some of the cavities to be effectively one, according to notes 2 and 3. The Rayleigh Statistic $Z = 6.936$, significant $p < .01$ (see Batschelet 1965 for data analysis methods) indicates that bee-keepers were not selecting cavities at random, but favoured those facing approximately SSE, an orientation similar to that selected by wild colonies in trees 155° (Figure 2.4b) and in cavities 132.9° (p. 59 and Table 2.13).

However, the sample is biased towards autumn-winter-spring colonies and an inspection of the table shows a south-east to south aspect for the colonies at this time of year is clearly preferred by bee-keepers.

Figure 3.3a A small colony of *Apis florea* kept in the recessed window of a house at the village of Hijār in the Ghubra Bowl, Jabal Akhdār, on 22.vii.78. The colony was well above head level, ?>2.5m, so was not particularly disturbed even though the room was used as a "majlis" (sitting/entertaining room). The colony had had its honeycomb removed and the brood comb was wedged in a split stick (not a "zoora") which was supported at either end by other sticks. The window faced approximately east so the colony probably received some direct insolation early in the morning but would have been shaded for the rest of the day. Another colony, wedged in a "zoora", but also supported by cleft sticks at each end, was in an adjacent window recess facing in the same direction. The colonies had apparently been found as natural swarms in May and brought to this site in June where they were being kept during the hot months of the year. See text Section C.1.

Figure 3.3b One of two "bee boles" for *Apis florea* at Diqāl, a village in the Bātina plain of northern Oman. They were in a stone wall that supported a bank separating date gardens from a wadi. This recess was 30cm high, 38cm wide and 25cm deep (a little smaller than its neighbour 1.6m away) and the bottom was 50cm from the ground. Behind the flat stone on top was a small gap that would help air circulation. Both recesses faced SE (145°C). I never saw them occupied but Sālim Ali said he put colonies there in the cooler months of the year for warmth (see text, p. 104.)

With a larger sample of summer colonies a bimodal distribution might have become more distinct with a tendency to select north-facing cavities in summer, as appeared to be the case with colonies kept in natural caves. The smaller summer sample is probably a result of fewer visits to bee-keepers at this time of year and of bee-keepers having fewer colonies because of absconding at the end of the "samur", *Acacia tortilis*, honey flow (Chapter VI).

3. Orientation of colonies within the cavities

With 10 out of 14 colonies being positioned so that one side faced out of the cavities (Table 3.7b) it would appear that bee-keepers preferred to site their colonies in this way rather than pointing, out of the entrance. However, the south-facing wall described in Note 2, Table 3.7b belonging to the al-Shimili family of al-Ghubby (experienced *florea* keepers eg Dutton & Free 1979), contained on 13.i.78 (winter) 4 colonies all running perpendicular to the line of the wall and pointing out of their cavities. Counting these colonies individually would boost the P (pointing) figure from 3 to 6; however, the F (facing) figure could similarly be boosted from 10 to 11 by counting individually the two wall cavities mentioned in Note 3. This data is therefore rather contradictory, but seems to point to a tendency by some bee-keepers to put colonies parallel to the cavity entrance, the way that most natural cave colonies construct their combs (p. 59-60).

However, when considered in relation to the individual sites concerned and to bee-keepers' comments, the orientation of the colony itself was obviously not a feature given priority. For instance, 2 colonies kept in cavities in ruined buildings by the afore-mentioned Humayd Sulayman al-Shimili were observed on 10.vii.80. They had been deliberately sited in cavities facing SW and S to avoid the hot north

Table 3.7a Orientation of 22 artificial caves, buildings etc used by bee-keepers for *Apis florea* in Oman. The letters b,g,h etc refer to different bee-keepers and the abbreviations in brackets to the seasons of the year in which the colonies were kept in the sites (see Table 3.4 and text, p.98 for further details).

Aspect/Bearing (degrees)	Autumn - Winter - Spring	Summer
$1^\circ - 45^\circ$	i(A)	
$46^\circ - 90^\circ$		k(Su),k(SU)
$91^\circ - 135^\circ$		j^1(Su), j^1(Su)
$136^\circ - 180^\circ$	b(W),b(W),g(W),h(W),h(W),ℓ^3(W),h^2(W-Sp),	
	h(Sp-Su)	
$181^\circ - 225^\circ$	h(Sp-Su)	
$226^\circ - 270^\circ$		
$271^\circ - 315^\circ$		
$316^\circ - 360^\circ$		

Notes:

1. These were colonies in recesses in a south-east facing wall of the inner courtyard of a house. However, a stack of *Apis mellifera jemenitica* "tubl" (date-log hives) were stacked up almost immediately in front of them, so effectively the colonies did not face in any particular direction ie like north-facing colonies with no view of the sun.
2. This refers to a specially built stone wall with a row of "artificial" caves hollowed out near the top. It contained colonies in winter and spring; 5 out of 8 cavities were occupied on one occasion, but they were counted as one as the site was constructed and used by a single family.
3. This refers to two recesses (Figure 3.3b) in a bank bounded by a stone wall that were not occupied when inspected. The bee-keeper however said he used them for *florea* in the cooler months of the year. The recesses were fairly shallow and any colonies inside would have been positioned parallel to the line of the wall.

Table 3.7b Orientation of *Apis florea* colonies within the cavities of Table 3.7a, grouping some of the colonies as in Notes 2 and 3 so that n = 14, not 22. The symbols etc are as in Table 3.6b

	F	A(F)	A(P)	P
Cooler Months (Autumn, Winter, Spring)	5	0	0	3
Hottest Months (Summer)	5	0	1	0
	10	0	1	3

Table 3.7c Shade experienced in man-made *Apis florea* cavities, grouping some of the colonies as in Notes 2 and 3 (Table 3.7a) so that n = 14, not 22. See Chapter II, p. 26 for manner of estimating these values.
+ : direct sunlight - : no direct sunlight hitting or thought to hit colony in cavity.

Shade		Season during which colony was being kept			
		Autumn, Winter, Spring		Summer	
%	Category	+	-	+	-
<75	0 - 4	1	0	0	0
75-90	5	6	0	0	0
90-100	6	0	1	2	4

winds as discussed below. The first nest had been positioned so that one side of the colony faced towards the entrance; apparently the reason for this was just to make the colony easy to inspect, not because of the wind or sun. The second nest was at an angle to the entrance closer to the perpendicular, making it more difficult to examine. I understood it was sited thus because, in this particular cavity, it was the best angle for supporting the ends of the "zoora" to which the colony was attached - again not because of the sun or wind or even for ease of inspection.

4. Shade

Table 3.7c indicates that bee-keepers generally sited their colonies so that they were well shaded in summer, but more exposed in the cooler months when they were usually put in a position to receive some direct insolation. The one colony that was an exception, being completely shaded in the "cooler" months, was observed at the beginning of November 1978 in a recess in the courtyard wall of a house. It had apparently been in the recess for about one month, having been transferred there from a well in the courtyard where the colony had arrived as a swarm. The recess was nearly completely covered over with a sack (like a curtain), which may initially have been beneficial when it was hotter, but now must primarily have been kept in place to protect passing householders from stings rather than the bees from sunlight (people regularly moving in front of an exposed colony might also have induced the bees to abscond). Furthermore, the recess faced NNE and had probably been selected only because it was the nearest convenient cavity to the well. The owner, though familiar with *florea* and techniques of using a "zoora" to support the comb, did not appear to be a serious bee-keeper, but was just making some use of this colony which had happened to land in his well. Therefore, the shading and siting of the colony was not undertaken solely with the bees in mind, and this bee-keeper's departure from the overall siting pattern is easily explained.

5. Discussion

In putting colonies in shady positions in summer and partially insolated SSE facing ones in winter, the bee-keepers were certainly implementing a practice which they often emphasised during my conversations with them - that the bees needed warmth in winter, but not excessive heat in summer and should be sited accordingly. They did not apparently site colonies with concealment from predators in mind (though they would usually keep colony locations quiet from other human beings!) but experience had presumably taught them to take account of the bees thermoregulatory requirements. To what extent they understood the biology of nest thermoregulation by honeybees, that brood should not be chilled etc I did not determine, but they must have been aware that the bees could generate a temperature greater than ambient as their warmth can be felt when fingers are used to part the protective curtain of workers round a *florea* brood comb or when scooping up handfuls of bees during colony manipulations.

The practice of most bee-keepers of putting colonies in SSE facing cavities I believe was designed to provide an appropriate degree of insolation and shade. Humayd Sulayman al-Shimili at al-Ghubby in the Dhahira however, did not just consider the sun when siting his colonies but also the wind and this is illustrated with further reference to the 2 colonies of his in ruined buildings, already mentioned when considering colony orientation within cavities (p.99-100). The colony in the SW facing cavity he said had been moved there in March and that in the S facing cavity in February. So both colonies had initially been present in cooler months and then, with the sun following a lower arc in the sky the bees had apparently been exposed to some warming insolation. In July the sun moves almost immediately overhead and no direct sunshine would strike the colonies. Humayd claimed south-facing caves were preferable in the summer as, though they were exposed to the prevailing southerly winds at this time (SW on the interior plains according to Gallagher & Woodcock 1980), these were not hot like the less frequent northerly winds (shamāl). Humayd also said that bees did not usually nest in north-facing caves in nearby mountains either, unless there was a large boulder in front, because of these hot northerly winds. Dutton & Simpson (1977) and Williams (1979) reported the same bee-keeper as saying that *florea* colonies avoided west-facing caves because the prevailing wind in the Dhahira was from that direction.

Nāsr Ahmad al-Ghaythi in the Sharqiya (eastern region of Oman) was another bee-keeper who held that wind was a factor that should be considered when choosing nest sites. At the end of June his only colony in the plains outside his village was in a type of artificial cave facing approximately WSW into the prevailing wind (Chapter IV, p. 178) and he said the cooling effect of the wind was important in autumn when he had more colonies in the plains (Chapter IV, p. 146).

These reports, some conflicting, concerning wind direction,need clarifying with careful monitoring of a number of *florea* colonies, backed up by reliable local meteorological data.

Returning to insolation, Humayd informed both myself and Dutton & Simpson (1977) that bees in the mountains preferred east-facing caves in winter where they are warmed by the morning sun, and that south-facing caves were satisfactory in summer, if the colonies were deep enough inside, as the sun passed overhead. So with wind and sun considered important, Humayd must have put some thought into selecting appropriate cavities.

However, whatever his hypotheses and success in keeping these 2 colonies in S and SW-facing cavities, he had been less successful in preventing many other colonies absconding after the end of the "samur", *Acacia tortilis*, flowering season (April and May, Chapter VII). In the middle of May (1980), a time when he would have been harvesting "samur" honey, Humayd said he had 25 colonies but towards the end of June only 8 and on the 10th July I saw he had just the 2 colonies. All these colonies would have been kept in both buildings and trees around his home; as discussed in Chapter IV, C.3 for *florea* belonging to Nāsr Ahmad al-Ghaythi and in Chapter VI, absconding at this time of year was probably due to a combination of factors (eg lack of forage, "predation" (harvesting) of the honeycomb after the main honey flow and sub-optimal nest sites) and may have been part of a seasonal cycle. Not knowing the nest sites which Humayd's bees had deserted, it was difficult to establish whether they had absconded mainly because Humayd had not, in fact, made a good nest site selection or for other reasons. Drought conditions were prevailing in 1980 and it may have been that lack of forage induced colonies to leave sites in which they would have remained in better years. So not even careful nest site selection by a specialist such as Humayd is always successful.

D. SEASONAL MOVEMENT OF *APIS FLOREA* COLONIES BY INDIVIDUAL OMANI BEE-KEEPERS AND THEIR OVERALL PATTERN OF NEST-SITE CHOICE

1. Introduction

In sections A, B and C details of *florea* colony sitings by bee-keepers within 3 different categories, namely trees, natural caves and "artificial" cavities, have been considered. However, it will have been apparent from the text and the letters a, b, c etc used to denote different beekeepers in the tables, that individual bee-keepers were observed to use sites in more than one category eg trees and "artificial" cavities at the same time or at different times during the course of a year. In order to understand better their intentions in siting colonies in these ways, this section will consider further the conceptions some bee-keepers had of the seasonal requirements of *florea* colonies, which in turn is based on their observations and interpretations of the movements of wild and kept colonies. The overall use of sites by bee-keepers will then be outlined.

2. Diqāl : Sālim Ali (farmer, Bee-keeper ℓ) and Said Ali(Badu Pastoralist, Bee-keeper d)

Around April time, Sālim Ali said he and other *florea* specialists would go and look for wild colonies in the plains and hills around their village of Diqāl, in the Batina plain near the foot of the Hajar mountains. At this season he said that colonies, of their own accord, would come from mountain caves looking for cooler sites in the date gardens and that bee-keepers too would bring the colonies into the gardens and put them in shady sites near the base of trees.

After honey, gathered during the *Acacia tortilis* flowering season (April - May),was harvested he said the bees would usually remain in their shady garden sites, but when their "sidr" (*Ziziphus spina-christi*) honey was taken in autumn some would abscond and others would stay. For the winter Sālim would put colonies in 2 specially constructed SE (145°) facing, fairly exposed recesses "mākinas" (shelter-ماكِنَس)as the bees needed warmth (see Table 3.7, note 3 and Figure 3.3b). However, if the winter was very cold the bees might abscond to a warmer site eg to the top of a tree or back to the "Jabal" (mountains). At the end of March, any colonies in the recesses would be brought to the shady tree sites.

Thus Sālim used shady tree sites in summer and open artificial cavities in winter in the belief that appropriate temperature conditions were of prime importance to the bees; despite these precautions he said the bees' acceptance of these sites could still be unpredictable and some colonies would abscond. Superficially his colony locations would appear to be the opposite of Nāsr Ahmad al-Ghaythi's, who put his colonies in trees in the winter but in recesses during the summer (Chapter IV). In fact the objectives were the same and have been achieved in each case. Nāsr's tree locations were in the plains and quite exposed (equivalent to Sālim's open, winter recesses) while Nāsr's recesses were shady, in a garden, and sheltered by date logs (like Sālim's *Citrus* tree sites under date palms).

Said Ali was a bedu pastoralist (shawāwi) living just outside the village of Diqāl whose moving of a *florea* colony from a cave to a "sidr" tree in autumn, because it was too hot in the former, has already been mentioned on p. 81-3. His usual practice was similar to Sālim Ali's in that he kept his colonies in a row of ESE (118°) facing caves in winter and moved them to trees in summer for shade. Said though, living in a sparsely vegetated natural habitat, was very restricted in his choice of suitable trees (to *Ziziphus spina-christi*) in comparison to Salim with his date garden. Sālim, in contrast, had had to make artificial caves at the edge of his garden, while Said had many natural ones available.

Said also considered that the drought conditions prevailing when I talked to him in November 1979 had made many colonies of bees migrate to the farms on the Batina coast, where irrigation provided forage, and further into the mountains where there had been some rain. The distances involved however would be approximately 20km and 10km respectively and there was no direct evidence for such an occurrence.

Though he genuinely believed the colonies moved such distances, I think it was just an easy mis-interpretation of the evidence that the numbers of colonies in the area had dropped and a case of "the other man's grass being greener". The real interpretation would almost certainly be high mortality, due to drought and man, with little or no colony replacement through reproductive swarming. Similar comments are recorded in Chapter VI.

3. Dhahira : Humayd Sulayman al-Shimili (Bee-keeper h)

Humayd and family, like Sālim Ali, kept *florea* colonies both in trees and in artificial caves and ruined buildings. In contrast, however, Humayd would use each type of site in both winter and summer and, as just discussed in Section C, his main concern appeared to be the selection of a site with the correct orientation; this applied particularly to cavities, but was less evident with colonies in trees.

It may have been that local wind conditions in the Dhahira region necessitated a colony siting tactic different from that on the Batina plain, but the overall strategy in both cases appeared to be one of selecting a site with a suitable microclimate. The seasonal pattern of natural colony movement in and around the village of al-Ghubby, as Humayd described and understood it, though similar, was not as distinct as Sālim had depicted for Diqāl, and this may explain Humayd's lack of concern as to whether colonies were put in trees or caves at a given season.

In the winter Humayd said colonies could be found in all types of site and areas, in caves in the hills, in trees in the desert "saḥara" and in the gardens. If there was winter rainfall, he said that most colonies would then reproduce and the swarms would go to the "jabal".

If the rainfall was particularly good, the colonies might stay in the "jabal" during the summer, but if it became dry they would return to the gardens for the "qayẓ" (hottest months). Any colonies in sites that faced the sun would move to another place (garden or "jabal") in summer, but sheltered ones would stay put. Thus the colonies in his new gardens and ruined village, which were rather exposed, having few trees, he thought had gone to the nearby gardens of Arāqi.

Therefore, in general, Humayd seemed to think that though there was a trend for colonies in summer to move into the shady gardens and in winter to go to the plains and hills, factors such as rainfall (and thus forage availability) and individual nest site quality were considered important too, in determining an appropriate nest site. Thus he did not have a strict routine of trees in gardens in summer, and exposed cavities in winter.

In July 1980, Humayd told me how he had been managing colonies of *florea* for people in the gardens of neighbouring Ibri, Arāqi and Araybi for a fee (apparently altogether 90 colonies for 5-10 Rials Omani each) and that most of the colonies had stayed after he had taken the honey. This was in stark contrast to the 2 colonies that remained in the cavities in his ruined village (al-Ghubby) which in May had accommodated 25 colonies. So I believe if he had adhered to a stricter policy of seasonal nest site selection, keeping colonies in summer in shady gardens (in recesses like Nāsr, Chapter IV, or trees like Sālim) and moving them to ruined buildings and his artificial caves in winter, he might have had less trouble with absconding after harvesting the "samur" honey.

4. Misfah, near al Hamra. Said Ali Āmr al-Abryīn (Bee-keeper f)

Most of the date gardens at Misfah were terraced and on the flanks of a steep, high-sided wadi. Said kept colonies of *florea* in both trees and natural caves, and the natural caves I saw him use in summer were at the foot of a cliff bordering the top edge of the date gardens. Though the cliff faced ENE, the colonies at the base were well shaded (category 6) by tall date palms immediately in front; his colony in a *Citrus* tree was also on an ENE facing terrace and fairly well shaded (category 5), though possibly exposed to early morning sunshine. He said he had 7 other colonies and though I did not see them I assumed they were in similar positions on the ENE-facing side of the wadi.

Said explained that he moved colonies to sunny or shady sites according to the season, in winter for instance to caves in the opposite side of the wadi, which had an approximately WSW aspect and was an uncultivated, exposed rocky slope. The colonies could probably have been sited to receive warming insolation during part of the day, though not very early in the morning because of the mountain slope rising to the ENE.

Thus Said was another *florea* keeper who considered that the microclimatic (temperature) properties of a nest site were of importance but, having well-shaded caves, he did not operate a strict seasonal alternation between tree and cave sites.

5. Compilation of nest site types used by bee-keepers

The following list gives a breakdown of the types of nest site I found being used by 21 *florea* bee-keepers:-

Tree Sites only	8 Bee-keepers
Natural Caves only	3 "
Man-made Cavities only	3 "
Both Tree Sites + Natural Caves	2 "
Both Tree Sites + Man-made Cavities	3 "
Both Natural and Man-made Cavities	2 "
TOTAL	21 Bee-keepers

These figures count Humayd Sulayman al-Shimili and his several relatives who also dealt with *florea* as one bee-keeper, and exclude records from people who told me about colonies they kept, but which I did not actually see. Sālim Ali of Diqāl however was included as a bee-keeper in the man-made cavity category because of the 2 special recesses he had, even though they were empty when investigated. If Nāsr Ahmad al-Ghaythi (Chapter IV) is added to this list as a bee-keeper using trees, recesses (man-made cavities) and also natural ones in the mountains, then overall I encountered colonies being sited in trees by 14 of the 22 bee-keepers (63.6%), in natural caves by 8 (36.4%) and in man-made cavities by 9 (40.9%). Only 8 out of 22 bee-keepers (36.4%) used more than one type of site, 14 (63.6%) using just a single type of site ie just trees, just natural cavities, or just man-made cavities.

If the number of colonies involved are totalled (but excluding all Nāsr Ahmad's at Zāhib and assuming Sālim Ali's 2 recesses were occupied) I recorded 27 (39.1%) kept in trees, 20 (29.0%) kept in natural caves and 22 (31.9%) in man-made cavities.

Thus trees were the sites used by most bee-keepers (63.6%) and were also the type of site adopted for most kept *florea* colonies (39.1%), with caves, natural and man-made, falling behind both in terms of numbers of bee-keepers using each of them and the total number of colonies kept in each.

However, if the *type* of cavity is ignored ie combining natural and man-made cave categories, exactly the same number of bee-keepers (14, including Nāsr) use cavities as use trees and overall more colonies are kept in cavities (42) than in trees (27), not counting the many colonies kept by Nāsr in each site type.

Therefore, depending on the way in which *cavities* are assessed, trees either are or are not the most frequently used site for colonies of *florea* . This is difficult to interpret, but from it I infer that whether a colony is put in a tree or a cavity is not important in itself and that both *can* be suitable in winter or summer. What appeared to be important to skilled bee-keepers were the characteristics of the individual nest site and its surroundings, especially with respect to temperature ie a warm site in winter and a cool one in summer. For instance Nāsr Ahmad al-Ghaythi found that with the habitat available to him, thinly-foliaged *Acacia tortilis* trees in winter and artificial cavities in a garden in summer, best met these requirements, while Sālim Ali of Diqāl in his garden without a large enclosing wall found that exposed recesses, with a south-east orientation in winter, and dense *Citrus* trees in summer, offered equivalent conditions. Most casual bee-keepers and honey-hunters probably just used whatever the local environment offered ie people on the Bātina just used trees and "hunters" in the mountains used caves, but maybe selecting the final site with shade and orientation in mind.

The records on the seasons during which colonies were kept at particular types of site were re-examined to see whether trees were being used a lot in summer but less frequently in winter, while cavities were used less in summer but a lot in winter (or vice-versa). However, the records showed that there was no overall distinction between trees and cavities in the time of year at which bee-keepers used them, which supports the conclusion that the category of nest site type is not important (tree or cavity) but its individual characteristics are eg orientation, habitat, foliage density.

I expect that one or two of the bee-keepers that I recorded as using only one type of nest site eg trees I would eventually have found also used other types had I visited them more often. However, on the whole, I gained the impression that most bee-keepers had an established pattern of nest site use that did not vary much, particularly where recesses and artificial caves had been built. Through their own trial and error and from experience passed down through the family or other mentors, bee-keepers probably got to know certain sites (even individual mountain caves and particular positions in trees) that were most likely to be suitable at each season.

Thus the prevalence of *florea* being kept by various bee-keepers in SE to S facing cavities (natural and man-made) in winter will not be a chance occurrence but a regular practice. Even though colonies would abscond from these sites, some because they had been left there in the wrong season, others because forage was scarce and their honey had been taken, the notions and experience of so many Omani bee-keepers that nest microclimate was important to *florea*, was further evidence that thermoregulatory considerations, in addition to predation (Seeley *et al* 1982), were important in determining nest site selection by this species.

PART II

MISCELLANEOUS OMANI TECHNIQUES FOR MANAGING *APIS FLOREA*

A. HONEYCOMB REMOVAL AND COLONY RE-ESTABLISHMENT

1. *Apis florea* nests in trees

At the end of the "sidr" (*Ziziphus spina-christi*) flowering season in 1978, I observed Sayf Ali Sālim of Rustaq (bee-keeper q) use a technique for removing the honey from a colony already on a "zoora", in a bush, that differs from the description of Humayd Sulayman al-Shimili's technique given by Williams (1979). It is also different from that of Nāsr Ahmad al-Ghaythi as related in Chapter IV, Part I, D.1.

On 21.x.78 the honeycomb contained a lot of honey below the "zoora", but the cells above the "zoora" were not full. On 3.xi.78 most of these cells were full and sealed, and c. 5.xi.78 the colony sent off a swarm - a prime one, presumably with the old queen. Other swarms may subsequently have left and on 20.xi.78 Sayf reckoned the bees had been consuming some of the stored honey. The honey was removed on 22.xi.78 but in retrospect it might well have been better to have removed it before then (as discussed on p. 114).

Anyway, on the afternoon of 22.xi.78, with the colony having about one half to two-thirds the original complement of adult bees, but still a very large brood and honey comb (the whole comb 32cm wide x 30cm high) that was consequently exposed in parts, Sayf prepared a new "zoora" before attempting to remove the honey from the existing one. With a knife he brushed some of the bees on the honey comb and those on the top half of the brood comb downwards so that much of the comb was exposed. Many of the bees took wing and circled in flight around the nest as a result of this disturbance, later settling on the bush in small clusters; others dropped to the floor forming 2 large clusters, while some remained on the honey and brood comb. Sayf took the prepared "zoora" and slid it horizontally 2 to 4cm below the expanded honeycomb, with the split ends of the "zoora" on either side of the brood comb. He tied the split ends together so that the comb was wedged into the new "zoora", but still supported by the old one just above it; a small area of sealed brood at the top centre of the brood comb was partly covered and squashed. The new "zoora" was then rested on 2 branches below the original one. Next Sayf took his knife and made a horizontal cut directly above the new "zoora", through the brood comb and just below the areas of honey and pollen. Thus he had removed the honey comb, with the pollen and also a little brood, in one piece and still attached to the original "zoora"; the brood comb, already attached to another "zoora", had been left in the same position as before.

The clusters of bees on the ground were attacked by ants, probably *Pachycondyla sennaarensis*, so were scooped up and draped on the brood comb where the rest of the bees were clustering. The operation had been carried out too near to dusk so the bees had not returned to their comb of their own accord as quickly as was usual and some were attracted to the lights of a house nearby.

Sayf removed the honey from another colony in the same way, but ran into problems as the brood comb was particularly elongated horizontally (45cm) and the split "zoora" he had prepared was barely long enough to clasp it. The split ends could not be tied tight and the brood comb started to slip out of it when the honeycomb and original supporting "zoora" were removed. The split ends were eventually tied properly but the edge of the brood comb was so close to the split tip of the "zoora" that it had to be squashed against the branch on which the tip of the "zoora" was resting (otherwise the "zoora" would have slipped off the branch). As a result the brood comb was rather damaged.

It was reported to me that both of these colonies absconded the following morning, so the end result of these operations was not very satisfactory. However, the principle of fixing a new "zoora" to a colony before removing the old one seemed good. Humayd Sulayman al-Shimili, according to Williams' account (1979), did not use such a method, but the sequence of his technique was not described distinctly. Disturbance and damage during honeycomb removal should be reduced if a colony's brood comb, which can be particularly soft and breakable when young, can be left in position in this way and not removed and put on the ground. Furthermore, not all the bees have to be brushed away with Sayf's method and the likelihood of the brood becoming chilled/heated and the queen lost is minimised.

It is of course necessary to have a site with suitable resting points for the new "zoora" or to have a helper to hold it when the old "zoora" and honeycomb are removed. The method is also appropriate for accessible wild colonies as well as those already on a "zoora".

The disadvantage of the method as described above was the complete removal of all the honey and pollen stores. This, along with the disturbance, would have been the main reason for both colonies absconding the following day, as feeding the remaining brood would have been difficult, particularly with the honey flow over. This highlights one of the main problems of *florea* management, namely absconding. To reduce the likelihood of absconding:-

(i) the honey should have been removed before the end of the flow so that the bees had the opportunity to obtain more stores. This might have resulted in honey with a high moisture content (>20%), but such incompletely ripened honey did not seem to concern the Omanis.

(ii) only some of the honey should have been removed, which would not have been easy with only a single, ovoid-shaped honeycomb. It would have been possible to have fixed the new "zoora" a little higher up the comb, leaving all the pollen and some honey; but to have left a still larger proportion of the honey would not have been easy as, if put high up, the "zoora" would have squeezed much of the honey out as it was tightened. The brood and honeycomb below the "zoora" might also have torn away under their own weight once damaged; such tearing might be reduced by inducing the bees to build brood combs that were wide, but not high, as was the case with the colonies of Nāsr Ahmad al Ghaythi (Chapter IV, Pt II, C.6, p. 195).

With refinement, this method of Sayf's should allow some reduction in the likelihood of subsequent absconding but it would mean a lower honey yield, at any one harvest, than Sayf had obtained on this occasion. It was estimated that the honeycombs from these 2 colonies had each weighed at least 1kg. However, a method of inducing the bees to store some of their surplus honey in a frame from which the honey could be extracted and then the frame and comb returned to the colony, would in theory be far more satisfactory (see Chapter VIII, p.412).

2. *Apis florea* nests in caves

Dutton & Free (1979) and Williams (1979) described how an Omani bee-keeper, Humayd Sulayman al-Shimili, took the honey from a natural colony in a mountain cave and how the colony was fixed to a "zoora" and installed in an artificial cave near his home. It was not stated whether Humayd ever put a colony back in its original cave after taking the honey, but Khalifa (bee-keeper c), a bedu pastoralist ("shawāwi") and hunter ("qannās- قنّاص)of bees and other animals, who managed colonies in the caves around his settlement in the Wadi Tifli (leading to the Wadi Hawasina in the northern part of the Hajar Mountains) sometimes did so. His method is described here.

The colony concerned was in a NNW facing cave (Figure 3.4) and has already been mentioned in Chapter II, C. 6.7. He called the cave "qowār" (قوار), a hole or hollow. First Khalifa cleared a small wall of stones he had built to block up the lower half of the cave entrance. He put his head and shoulders into the cave and brushed handfuls of bees from the comb onto the cave floor, which was covered with a mildly aromatic grass *Cymbopogon schoenanthus*, called "sakhbar", that was supposed to repel ants. Many of the bees also took flight. Khalifa cut away the brood comb with a knife, leaving virtually no pollen on it and no honey cells, and put it on the ground just outside the cave. Next he cut the honeycomb from the cave roof, catching it in an aluminium bowl held underneath. Then he picked up the brood comb and, holding it against the roof of the cave, propped it up with 3 sticks (probably from a *Lavandula subnuda* bush). One end of each stick was on the ground, the other penetrated the brood comb near the top, so it was squashed/pinned against the cave roof (Figure 3.5). Thus the top part of the comb was bent over and damaged, killing some of the brood, and the lower part of the comb in this case did not even hang vertically.

The bee-keeper then spread some fresher "sakhbar" leaves under the comb and moved 20m away to allow the bees to return to the comb. In the meantime the bees had been forming clusters on nearby bushes and some were also spread over rocks around the cave. No attempt had been made to find, cage or protect the queen during the operation, but the bees and presumably the queen soon re-clustered on their brood comb. The protective wall was not replaced at this stage, as I understood it to prevent further disturbance while the bees were settling.

I was subsequently informed that the bees absconded 2 days later. As with the colonies on "zoor " just described and as discussed in Chapter II, C. 6.7, the absconding of this colony was attributed partly to all the honey being removed when there was still a lot of brood to support and partly to the severe disturbance, with the brood comb being re-installed very poorly.

Khalifa's method however did not always result in immediate absconding. In July 1980 I observed 2 colonies supported in this way in caves Nos. 5 and 7 (see Chapter II, C. 6.5, 6.6 and 6.7 for earlier reference to these colonies). He had taken honey from them around the end of May and the brood combs had been pinned to their cave roofs with 2 and 4 sticks respectively (Figures 3.6 and 3.7). Both had clearly re-established themselves, reared brood and stored honey again. The colony in cave No. 7 absconded on 23.vii.80 and the colony in cave No. 5 looked as though it would soon abscond; this was 1 to 2 months after re-establishment and probably due to poor microclimate and lack of forage in an unusually dry year rather than the installment method.

The method is very similar to that described in Part II, B.2 of this chapter for "honey-hunters" in the Jabal Salakh and in the mountains near Birkat-al-Mawz and, to improve upon it, I would make the following suggestions:-

(i) that the brood comb with pollen and possibly some honey comb be put into a "zoora" before being cut away (according to the method described in the previous section) and the "zoora" then be supported within the cave by stones or by a forked or cleft stick, with one end resting on the ground.

Figure 3.4 Wild colony of *Apis florea* in a cave in the Wadi Tifli (off the Wadi Hawasina) in the Hajar mountains of northern Oman. The bee-keeper, Khalifa, was about to take the honey and re-install the brood comb, 28.xii.79.

Figure 3.5 The brood comb of the *Apis florea* colony illustrated in Figure 3.4, propped up to the cave roof with 3 sticks, immediately after Khalifa had taken the honey and before the bees had returned. The bees absconded 2 days later. Note the grass "sakhbar", *Cymbopogon schoenanthus*, spread on the cave floor to repel ants. Further details in text, p. 115-117.

Figure 3.6 An *Apis florea* colony which had been supported after honeycomb removal in a cave (No. 5) by the same method as illustrated in Figure 3.5, but on this occasion the bees had re-established themselves and not yet absconded. Wadi Tifli (off Wadi Hawasina), northern Oman, Hajar mountains; 23.vii.80. Temperature readings were also made in the cave (Figure 2.7b).

Figure 3.7 *Apis florea* colony, in a cave (No. 7), which had been propped up by sticks after honey removal. The sealed honey at the top shows the colony had initially re-established itself. The bees, however, had absconded earlier on the day of the photograph and this desertion was attributed to poor microclimate (high temperatures) in the cave and lack of forage, not to disturbance or the method of support. Wadi Tifli (off the Wadi Hawasina) Hajar mountains of northern Oman, 23.vii.80.

Figure 3.8 Colony of *Apis florea* supported on a "zoora" (split date-frond midrib) inside a cave (a) in the Wadi Tifli (off the Wadi Hawasina) in the Hajar mountains of northern Oman, 28.iii.80. This method of supporting the comb seemed more satisfactory than that illustrated in Figures 3.5, 6 and 7 and provides a horizontal dance platform.

Figure 3.9 Colony of *Apis florea* in a cave (b) in the Wadi Tifli (off the Wadi Hawasina) in the Hajar mountains of northern Oman, 28.iii.80. The colony was supported on a split stick and the honeycomb had been attached to the cave roof. If such a comb was expanded and filled with honey a cut could be made just above the supporting stick, leaving some honey attached to that and some to the cave roof. The bee-keeper could either take the honey from the cave roof and leave that round the stick for the bees, or vice versa, as long as he wedged the brood comb into a new stick and put it under the honeycomb still attached to the roof. A near horizontal dance platform is available to the bees.

Figure 3.10 The colony of *Apis florea* shown in Figure 3.9 after all the honey was taken. The bees had absconded. 13.v.80, Wadi Tifli (off the Wadi Hawasina) in the Hajar mountains of northern Oman, cave (b). Further details in text, p.118-9.

Figure 3.11 Brood comb of *Apis florea*, propped up against an angle in the roof of a cave by sticks set in a T-shape, immediately after its honeycomb had been taken by a bee-keeper, Sālim Said. Note the hexagonal wax cell remnants on the cave roof behind and to the above right of the brood comb. Jabal Salakh, west of Adam, northern Oman, 11.iii.78. Further details of honey removal in text, p. 122-3.

(ii) when the honeycomb is cut away a proportion of it should be left attached to the cave roof. Thus, until more can be gathered by the foragers,sufficient stores are left for the existing brood and young bees to be fed and for repairs to the comb to be made. The "zoora" holding the brood comb could be located immediately underneath the honeycomb (where it would catch some of the drips of honey) in the hope that the bees would soon re-attach the brood comb to the honeycomb.

Khalifa had in fact done something along these lines with 2 colonies that I saw on 28.iii.80. One colony, in cave (a), he said had come from a "salam" bush (*Acacia ehrenbergiana*) in early March and had yielded nearly 1kg of honey at the time. The brood comb had then been wedged in a "zoora", one end of which was held up by 2 sticks, while the other was supported by rocks in the cave (Figure 3.8). The honeycomb had not been attached to the cave roof, so no honey could have been left there when the honey was harvested.

The second colony had apparently come from another cave in early March and was wedged into a split "sidr" (*Ziziphus spina-christi*) twig and supported against the roof of cave (b) by sticks at either end. In this case some of the honeycomb had been attached, by the bees, to the cave roof (Figure 3.9) and when the comb was full of honey, a portion could have been left there and a portion removed by the bee-keeper. However, when I next saw the nest on 13.v.80, Khalifa said he had removed the honey the previous day; the brood comb had been wedged against the roof with 2 sticks according to the first method described in this section (Figure 3.10) and the bees had already absconded, probably earlier on the day of my visit. The comb was nearly empty of brood so the bees may have been (i) on the point of absconding anyway, or (ii) have been part way through a swarming cycle (ie the old queen and a swarm had already left, but the new queen had not started laying) and the disturbance and/or microclimate induced the new queen and the remaining bees to desert too. If the honey had been harvested earlier, when brood rearing was continuing and before swarming, and some honey had been left on the cave roof with the comb supported as suggested, the bees might have stayed (if the microclimate and forage were right!).

3. Discussion

These examples show how difficult it is to assess the effectiveness of a particular bee-keeping technique; when removing honey and re-installing a colony in a cave or at any other site it is not just the way the comb is supported which is under trial. Factors such as site microclimate, forage availability, quantity of honey and pollen stores left and quantity taken, degree of disturbance and stage in swarming cycle are all liable to influence the colony's tendency to abscond, and thus affect the outcome of any trial. Even the availability of a horizontal dancing platform may be important (see Chapter II, C. 5).

In the last 2 cases described, the photographs (Figures 3.8, 9 and 10) show that such a horizontal platform was available. In cave (a) because there was a gap between the cave roof and the top of the colony, held in the "zoora", and in cave (b), even though there was no gap in the honeycomb as it was built between the "zoora" and the cave roof, there was a nearly horizontal shoulder to the honeycomb which probably provided a satisfactory dance floor.

With the variety of colony supporting techniques employed in Oman (from wedging a comb in a split "zoora" in a tree, to tying it back to the original branch, from propping up combs in natural caves to supporting them in "zoor " in specially built artificial caves) and with the several other factors that influence absconding and thus the success of the techniques, I hesitate in recommending any particular one. However, the properties of the "zoora" and its widespread adoption by bee-keepers indicate that its use should be high among the list of priorities for traditional style *florea* management, and certainly as an alternative to vertical sticks for propping up combs in caves. However, except possibly in a cave as suggested on p. 118, it is not easy to leave sufficient honey for the colony when the bulk of it is removed still attached to the "zoora".

Maybe a combination of old and new techniques would be better, as suggested in Chapter VIII, p. 412 ie putting a small frame with foundation on top of the "zoora", which could be removed for honey extraction without disturbing the brood. Nevertheless, just using the best materials in a certain fashion at an appropriate time and place, with this sensitive species, will not substitute for the skills of the bee-keeper, both in his handling of the bees and his experience in selecting the most suitable nest site in his garden or other terrain. A combination of the two, method and skill, is the most likely recipe for success.

B. HUNTING FOR COLONIES OF *APIS FLOREA*

1. Introduction

Dutton & Simpson (1977), Dutton & Free (1979) and Williams (1979) have already described one Omani's custom of searching for wild *florea* in mountain caves and how he brought a colony to an artificial cave near his home. During the course of surveys in other parts of the country I came across a number of Omanis who also went searching in the hills and plains for wild colonies of *florea* and I accompanied some of them on such expeditions.

As might be expected, some of their practices were rather different from those of Humayd Sulayman, the bee-keeper investigated by Dutton *et al*, while others were much the same. Aspects of their practices will be considered in this section with particular reference to expeditions I made with 2 brothers, Sālim Said and Hamid Said (bee-keepers a) of Adam, to Jabal Salakh and Jabal Madmār on either side of their oasis, and with Nāsr Ahmad al-Ghaythi of Zahib to the Jabal Madar south of Muḍaybi. These 3 hills were very alike in that they were outcrops of limestone, 1014m, 740m and 766m high respectively, surrounded by gravel plains and isolated from the main Hajar mountain range. They also had a similar, characteristic vegetation. The sites were favoured by the hunters and therefore, by implication, *florea* (though few colonies were actually found on my trips!), so their vegetation, which provided the bees with forage, will be described. The survival of *florea* in these remote areas will also be discussed. Observations concerning other "honey-hunters" are mentioned where relevant, but are not considered in the same detail.

2. Hunting for *Apis florea* near Adam

On 11.iii.78 I accompanied Sālim and Hamid Said up a steep-sided, boulder-strewn wadi, fed further up by several smaller wadis, that drained down the northern side of the Jabal Salakh to the west of Adam. They searched for colonies in the numerous small caves and crannies in the sides of the wadis, using binoculars from a distance as well as looking right into some cavities from close quarters. Like Humayd Sulayman (Dutton & Simpson 1977) they looked for signs of bees flying in and out ie shimmering wings against the sun, and they looked on the rocks for the dried yellow drops of excreta (called "qatra", "kǔs", "kǔth" or "(a)rayṭa") usually produced by young bees on their first orientation flights. These drops were tiny (one large oval drop measured 6.5 x 3mm) and not easy to spot; they probably just indicated a colony was or had been in the vicinity. On this trip they were of little value and no nest was found near the large spot mentioned.

I was shown one or two empty "bee caves" with traces of wax on the roof, and other more inaccessible ones that had contained colonies in the past were pointed out. Eventually a cave actually containing a colony was found; this too had hexagonal wax remnants on the roof (Figure 3.1) so it obviously had been used by bees in the past and it was clear that the "hunters" had prior knowledge of it. Examination showed that the colony was supported by 2 sticks put there previously. Sālim took the honey from it in the following way:-

Some small twigs, with leaves on, were brushed quite vigorously against the curtain of bees so that nearly all flew into the air, just a few falling to the ground. With a knife, he immediately made a horizontal cut below the honeycomb in order to remove the brood comb, which he put on the ground. The honeycomb was cut away from the roof into a small, leather bag.

It then became quite apparent that these men were not "hunters" that destroyed their quarry but were, after a fashion, bee-keepers. They did not take the colony back to their garden like Humayd Sulayman (Dutton & Free 1979; Williams 1979) - it would have been a difficult journey in this case - but re-installed it in the same cave. Sālim took the brood comb, pressed it into the roof of the cave where there was a small right-angled kink, pushed a small twig horizontally against the top face of the comb and then propped this up with a longer stick, nearly vertical with the lower end resting on the floor of the cave (Figure 3.11). The whole operation took less than 5 minutes and the comb was placed virtually in its original position, held by the twigs. The bees flew round while this was happening and quickly started to settle again when Salim had finished. No precautions were taken to protect the queen and no honey was left for the bees, but probably only a little brood succumbed to physical damage.

Though the colony was small (brood comb 13cm wide x 11cm high; honeycomb 11.5cm wide x 6.5cm high) it had 2 concentric rings of sealed brood plus unsealed brood and these might have suffered from starvation unless the bees were able to compensate quickly for their loss of honey. The honey harvested cannot have weighed more than 100gm and was consumed on the spot by Sālim and Hamid. Considering this small yield and the risk that the bees might now abscond, it might have been better to have left the colony for a few more weeks and to have taken a greater harvest later.

The search for more colonies then continued and I gathered 2 others were found, but I did not see them as I had become separated from my guides while investigating the flora. I suspect that they too were in previously occupied caves and that the hunters already knew their location. The following day a shorter expedition up a similar, N-draining wadi of the Jabal Madmār, to the east of Adam, was made. No bees were found, not even foraging, but another cave with wax that they already knew had contained a colony was pointed out to me.

Likewise on a trip I made into the mountains near Birkat-al-Mawz on 28.ii.78 with a man called Sulayman (bee-keeper b), though he too went searching for spots of *florea* faeces (again called "kŭs"), he already knew where to find the 2 colonies that we encountered. He showed me one that was naturally established in a myrrh bush (*Commiphora* sp.) and another colony in a cave that had a vertical stick against the comb. The latter had obviously been propped up, in a way similar to that just described for Sālim Said, when Sulayman had last taken the honey. He also showed me 2 empty caves with wax remnants on the roof that were therefore once occupied.

3. Hunting for *Apis florea* in the Jabal Madar

This refers to a trip made with Nāsr Ahmad al-Ghaythi, the subject of Chapter IV. In addition to managing the colonies in and near his village of Zāhib he sometimes made 4-day long expeditions with a friend to this small mountain to look for "wild" *florea*. He said he usually went in the "qayẓ" (قيظ), the hot part of the summer towards the end of the *Acacia tortilis* flowering season, probably in May. This trip however was made at the end of the *Ziziphus spina-christi* flowering season on 12.xii.79.

As on the Jabal Salakh and Jabal Madmār trips, wadis (two) draining down the north side of the mountain were investigated and Nāsr searched the caves from a distance with binoculars and from close to. He called the caves "sarab" (سَرَبْ - literally hole, den or lair of animal). One such cavity that had contained *florea*, from wax traces of cells left on the roof, was on the west side of one "wadi" facing east and another was under the north side of a boulder, c. 4m in diameter, at the foot of the wadi. Nāsr knew of both caves already and said that on a previous visit he had re-installed the colony under the boulder with the support of a stick (presumably in the way Sālim Said had done) after taking the honey. So the aim of Nāsr's mountain expeditions was primarily to look for "wild" honey rather than to gather colonies to add to his apiaries at Zāhib.

Despite several hours searching, we did not find any living colonies, only *florea* workers foraging on flowers and gathering water. Nāsr said the bees nested in caves during the hot season, but they moved to the more open "samur" (*Acacia tortilis*) trees in the plains below for warmth in the winter, the time of year we were searching.

Unfortunately, I did not record this properly at the time, but while watching worker *A. florea* gather water from a pool, I am fairly certain that Nāsr and I discussed how he could trace a nest from watching the line of flight of such bees on their return "home", though in this case we were not successful. However, I did record Sālim Ali (bee-keeper ℓ) of Diqāl explaining to me how he and 2 other *florea* specialists would track colonies in this way from water at a dripping "falaj", rock pool etc. He said that as the bees flew straight back to the nest, if one followed this line, investigating trees (or caves) en route the nest could be found. The advantage of "bee-lining" from water is that one can sit at one spot waiting for bees to drink their fill from the one source in the knowledge that they are heading for "home" when they leave. I have tried "bee-lining" from a patch of flowers with no success as, though I could sometimes follow an individual forager for maybe 10 mins, I found I usually lost track of it amongst others before it took off for its nest. Even following the flight of *florea* from water is difficult because of the small size of the insect. Sālim Ali said that he too, and other *florea* specialists, if they noticed drops "qatār" (plural) of yellow faeces on the ground, would look for a colony in the vicinity. These drops can perhaps be a more useful sign than the Jabal Salakh trip indicated.

4. Vegetation, sources of forage and survival of *Apis florea* in mountain "wadis" where they are hunted

Plants from the Jabal Salakh and Jabal Madar were collected and pressed and these plus others recorded are listed in Table 3.8.

Table 3.8 Vegetation of limestone hills in northern Oman, where *Apis florea* specialists hunted and managed wild colonies, as indicated by lists of plants collected and/or recorded from 3 localities:- Jabal Salakh (J.S.) and Jabal Madmār (J.M.M.) to the west and east of Adam, and the Jabal Madar (J.M.D.) south of Muḍaybi. A description of the hills and vegetation are in the text (Chapter III, Pt. II B. 3 & 4). Records of foraging insects are given and of the overall flowering periods of the plants in northern Oman and whether they are a source of nectar (N) and/or pollen (P) to *A. florea* (? indicates a probable source). Further details of plants are in Table 7.3 and Appendix III.

* : plant frequent near the wadi outlets at the foot of the hills
00 : plant in flower (Fl) and in fruit (Fr) on day of visit
-- : plant not in flower or fruit " " " "
0 : plant only in flower on day of visit
-0 : " " " fruit " " " "

FAMILY	GENUS SPECIES	J.S.& J.M.M. 11.iii.78	J.M.D. 12.xii.79	MONTHS (1-12) IN FLOWER	*FLOREA* FORAGE
		Fl Fr	Fl Fr		
ACANTHACEAE	*Blepharis ciliaris*	0	0 (one plant)	1 3 8 9 10 12	
ANACARDIACEAE	*Rhus aucheri*		-0	11	
ASCLEPIADACEAE	(*Caralluma aucherana*	00 Diptera	--	3	
	(*Periploca aphylla*	0	00 *florea* Diptera	2 3 4 12	N
BURSERACEAE	*Commiphora* spp.	-0		12	
CAPPARACEAE	*Maerua crassifolia**	-	-	1 2 3	NP
COMPOSITAE	(*Grantia aucheri*	0		3	NP
	(*Helichrysum* sp. nov.	0	0	3 4 12	
	(*Launaea spinosa*		0	2 12	?
	(*Pulicaria glutinosa**		--	1 3 4 9	
	(*Vernonia arabica*	-0	-0	3	?
CONVOLVULACEAE	*Convolvulus virgatus*		0	1 6 9 12	?
CRUCIFERAE	*Physorrhynchus chamaerapistum*	0		1 2 3 12	NP
EUPHORBIACEAE	*Euphorbia larica*	0 *florea*	00	2 3 12	N?
ILLECEBRACEAE	(*Cometes surattensis*	?0		3 10	N &/or P
	(*Gymnocarpos decander*	0		3	
LABIATAE	(*Lavandula* aff. *subnuda*		0 *Colotis* sp. (Lepidopt.)	1 2 3 10 11 12	?
	(*Leucas inflata*	0	0 *florea*	3 4 12	NP
LEGUMINOSAE	(*Acacia tortilis**	--	--	4 5	NP
	(*Argyrolobium roseum*	0		1 3 12	
	(*Indigofera arabica*	00 Hymenopt.incl. *florea*,*Polistes* sp.		3 8 9 10	
	(*Taverniera glabra*	0		3 11	NP
	(*Tephrosia apollinea**		00	2 3 5 10 11 12	NP
MALVACEAE	(*Hibiscus micranthus*		-0	2	
	(*Pavonia arabica*	00		3	
MORACEAE	*Ficus pseudosycomorus*	-		?	
MORINGACEAE	*Moringa peregrina*	0	-	1 2 3 4	
NYCTAGINACEAE	*Boerhavia elegans*		0	4 8 12	
PLUMBAGINACEAE	*Dyerophytum indicum*	0	-	2 3 11	
POLYGALACEAE	(*Polygala ?erioptera*	0		3 4	
	(*Polygala mascatensis*		0	6 7 12	
RESEDACEAE	*Ochradenus* sp. nov.			1 2 3 4 11 12	NP
RHAMNACEAE	*Ziziphus spina-christi**	-	00 *florea*	1 9 10 11 12	NP
RUBIACEAE	(*Jaubertia aucheri**		-	1 2 3 4 5	NP?
	(*Pseudogaillonia hymenostephana*	00	0	2 3 12	
SALVADORACEAE	*Salvadora persica**	0 (in bud)	--	3 4	
SOLANACEAE	*Lycium shawii*		-0	1 2 3 7 10 11 12	
TILIACEAE	*Grewia erythraea*		-0	?	
ZYGOPHYLLACEAE	(*Fagonia* spp.	00	00	2 3 4 10 12	
	(*Zygophyllum coccineum**	-0?	-	2 12	?
GRAMINEAE	(*Aristida adscensionis*	0		1 3	
	(*Cenchrus ciliaris*	0	0	1 3 4 9 12	
	(*Chrysopogon aucheri*	0	0	3 12	?
	(*Enneapogon persicus*	0		3	
	(*Hyparrhenia hirta*	0		3 10	
PALMAE	?*Chamaerops* sp.	--			
GNETACEAE	*Ephedra* sp.		00	12	
		33 species recorded	31 species recorded	Mainly winter and spring flowering	c.19 bee species recorded
		Total : 47 species			

Though the botanical studies were not exhaustive and were made at different times in the year it was apparent from the floristics and habitats as seen in the field, and from the lists, that the plant communities occurring in the wadis of the 3 mountains (Jabals Salakh, Madmār and Madar) were essentially the same.

Though the plants from the neighbouring Jabal Salakh and Jabal Madmār are not listed separately, bee-plants such as *Periploca aphylla, Euphorbia larica* and *Leucas inflata* occurred at both sites. Likewise the flora occurring in the 2 wadis explored in the Jabal Madar were virtually the same. Where plants were collected or noted in one site and not the other, the omission in most cases eg *Physorrhynchus chamaerapistum, Indigofera arabica* and *Lycium shawii* is likely to have been due to incomplete recording rather than genuine absence. When collecting, photographing and recording unfamiliar plants (often not in flower) in difficult terrain with shade temperatures in the order of 30°C, in addition to searching for and examining colonies of bees with guides speaking another language, some omissions are almost inevitable!

Plants such as *Euphorbia larica* grew on the mountain slopes just above the wadi; some trees, particularly *Moringa peregrina,* and shrubs such as *Periploca aphylla* and *Dyerophytum indicum* were most frequent in rocky crevices on the steep sides of the wadi. Small specimens of the trees *Acacia tortilis* and *Ziziphus spina-christi* grew amongst the boulders in the bottom of the wadis along with small perennial shrubs and herbs such as *Leucas inflata, Argyrolobium roseum* and *Physsorrhynchus chamaerapistum.*

In an entirely separate range of mountains, another limestone wadi had a flora similar to that of the more isolated mountain outcrops just described and *florea* occurred there too. The wadi was at the southern end of the Jabal Akhdār massif near Birkat-al-Mawz, almost due north of the Jabal Salakh and separated by 60 - 70km of gravel plain, and it was hunter/bee-keeper b who had shown me wild and managed colonies (p. 123) there. Species such as *Periploca aphylla, Physorrhynchus chamaerapistum, Euphorbia larica, Acacia tortilis, Moringa peregrina* and *Fagonia* sp. were present, so perhaps a community containing such combinations of plants is particularly suited to *florea*. Though only a few sightings of foraging *florea* were made on these mountain expeditions, knowledge of the flowering seasons of other plants present and of their value as bee forage (Chapter VII, Table 7.3) did indeed indicate that this type of limestone flora offered reasonable foraging opportunities.

Plants such as *Periploca aphylla, Maerua crassifolia, Physorrhynchus chamaerapistum, Euphorbia larica, Taverniera glabra* and *Ochradenus* sp. nov. would supply nectar and pollen in winter and spring, encouraging the development of a strong colony with brood (and maybe even a honey surplus in a wet year) in time for the flowering of *Acacia tortilis*. This tree would provide the main honey crop, for the bee-keeper and/or for colony reproduction, and would see colonies with sufficient surplus through the summer months until autumn-flowering plants, particularly *Ziziphus spina-christi*, became available.

One other provision of these wadis must also be emphasised before their suitability for *florea* is fully explained, namely water. Especially in the summer months, water would be essential for the dilution of honey stores and the cooling of colonies. In both the Jabal Salakh and Jabal Madar there were small pools of water in the wadis, often only a few inches deep, that had been left after rain in the previous months and *florea* were seen collecting water from one of them (some bees had drowned too). Some of these pools, instead of being in gravelly deposits at the bottom of the wadis, were in deep depressions hollowed-out in boulders by the action of water and stones and my impression was that such pools were frequent in limestone rock formations but less so in areas of harder igneous or metamorphic rock. If this is so, the occurrence of such pools of water and the characteristic flora may help explain the apparent preference of bees and hunters for such limestone hills.

Nevertheless, I suspect some of the pools I saw would not have lasted many months without replenishment and in situations where such water supplies did dry up, the outcome to the colonies is a matter worthy of speculation.

(i) The colonies might abscond to the nearest village where water, from "falaj" or well, and forage would be available. However, in the case of the Jabal Madar the distance from the wadi, where I saw *florea* foraging, to the nearest village, Aflaj, was greater than 5km (Fig.4.1). The distance from the *florea* colony in the Jabal Salakh to Adam, the nearest oasis, was greater than 10km. The possibility of such long distance colony movements cannot be excluded, but I made no such observations in Oman and no substantiated cases have been reported in the literature. Until this study (Chapter IV, Pt. I, C. 2) *florea* was not even thought to forage much further than 400m from the nest (Lindauer 1957). Even if long distance movements were possible, to be of any survival value they would have to be made in one direction only (towards the nearest oasis), which in the case of the Jabal Salakh colony would have necessitated a round trip of greater than 20km by a scout bee.

(ii) An alternative course available to some colonies and which would provide water would be to abscond to or near a well if one was not already within foraging range. Wells, built by the bedu, were sometimes sited near the foot of such mountains as the water table would be nearer the surface, with the higher rainfall and run off. For instance, Nāsr

Ahmad showed me 3 wells 1 to 2km from the foot of the Jabal Madar, and he said they sometimes contained colonies of *florea*, with nests attached below ground level to the inside walls. None were there on 12.xii.79 when I looked. The vegetation in the outwash fan from the mountain wadis, where the wells were sited, was generally denser than in the surrounding plains; *Acacia tortilis* was dominant, but other bee-plants such as *Ziziphus spina-christi*, *Maerua crassifolia*, *Jaubertia aucheri* and *Zygophyllum coccineum* occurred too.

(iii) A third possibility is that colonies deprived of water may be able to effect some form of aestivation. By ceasing brood production, foraging etc, and if in a suitably sheltered site where temperatures did not reach lethal levels (?c. 48°C), they might be able to abandon thermoregulatory activities and let colony temperature fluctuate with ambient. Respiration/metabolism would be reduced to an absolute minimum and survival, with virtually no use of honey stores, might be feasible till further rain fell. I have no measurements of a colony deprived of water to support this speculation, but I did record a cluster temperature of 39.4°C for a colony in July in cave No. 5 in the Wadi Hawasina (Figures 2.7b and 3.6).

(iv) Demise of a colony is the final alternative, and in dry periods I expect mortality occurs, both of colonies which abscond and of those which stay.

Unless one of the first 3 alternatives is invoked, it is difficult to explain how populations of *florea* can survive in these remote hills. It also begs the question already mooted on p. 14-15 "could *florea* survive in northern Oman before man arrived, dug wells and established oasis cultivation?" Temporary pools of water are frequent in rainy periods, but not when most needed in hot, dry spells.

Reliable sources of perennial water are few and far between in northern Oman. If *florea* in Arabia did pre-date man, unless they could survive for long periods (months) without water, the populations must have been isolated and near permanent water, expanding their range in wetter spells. On the other hand, if Arabia enjoyed a wetter climate than now (and there is little concrete information on this), before man established his reliable water supplies, *florea* might have been widespread and its range now has become reduced. However, the absence of *florea* from Dhofar suggests that there has not been a wet era in this SE part of Arabia since *florea* arrived in northern Oman. Larsen (pers. comm.) reported *florea* foraging on *Ochradenus* sp. on Jazīrat al-Ghanam, an island at the NW tip of the Musandam peninsula, in late February/early March 1979; apparently dry and with no cultivation, *florea*'s presence on the island (if permanent) is remarkable. Perhaps colonies really do have some ability to cope with extended dry periods by migrating considerable distances or aestivating.

CONCLUSION

Nearly all the bee-keepers covered in this chapter, as far as I could ascertain, dealt with *florea* on a fairly regular basis. It appeared that there were never more than a handful of people in any one village or town who specialized with *florea* in this way; sometimes none could be found despite earnest enquiries. It seemed that the majority of the population did not have either the time or the inclination or the skill to manage colonies of *florea* properly.

Surveys had nevertheless shown that *florea* was widespread in northern Oman (Figure 1.1) and that colonies occurred in and around most villages. So if a man (not a specialist) found a colony that contained some honey in his garden he could either leave it, ask someone who was more of a specialist to deal with it properly (in the way that Humayd was asked, p. 107), or attempt to take the honey himself. The latter was frequently the case in the Batina date gardens, where skilled bee-keepers were scarce or absent, and on several occasions I came across brood combs discarded from colonies that had had their honey taken. Sometimes the owner would try to re-establish a colony in a "zoora", having heard of or seen other people doing this, but it would not necessarily be done well and if it was leading to painful stings the attempt might be abandoned.

Another man I knew, regularly hunted wild colonies for their honey in the gardens, scrub and plains of the Batina and made a little money by selling the extracted honey. He knew it would have been best to have kept the colonies afterwards, but did not have the knowledge of the specialist *florea* keepers that would have enabled him to do so properly.

Thus a whole range of management techniques exist in Oman that range from crude robbing of the honey and destruction of the nest to the sophisticated migratory bee-keeping of Nāsr Ahmad al-Ghaythi. This chapter and that on Nāsr (Chapter IV) have naturally concentrated on the skills employed at the top end of the spectrum. I was not convinced that all of the ideas and practices mentioned were satisfactory eg the theory of Said Ali, the bedu bee-keeper of Diqāl, that colonies absconded 20km to the Batina, and Khalifa's method of propping up cave colonies with sticks. On the other hand, I am certain that much can be learnt from the years of observation and experience that the *florea* keepers possess between them. The conviction of so many that *florea* colonies have different seasonal nest-site requirements (warm spots partly exposed to the sun in winter and shady ones in summer) and that bees would abscond if the sites were not correct can hardly be ignored. Even though numbers of their colonies did abscond, a proportion often stayed despite suffering from human "predation"; I am certain the proportion would have been much smaller if the bee-keepers had not paid so much attention to the selection of suitable nest sites.

As discussed at the end of Part I, on the basis of the bee-keeping sites investigated, it would be misleading to make a simple recommendation such as "trees are best in winter and cavities in summer" as so much depends on the type of tree and its associated vegetation and the type of cavity and its orientation, surroundings etc. Bee-keepers could be found using both trees and cavities successfully at almost any time of year. However, if appropriate sites are to be recommended in a little more detail I would propose the following:-

	Winter	Summer
Wild Habitats	Thinly foliated trees and bushes, SE quadrant eg *Acacia tortilis*. SE facing caves	Densely foliated trees eg *Ziziphus spina-christi*. Possibly N facing caves
Date Gardens	Thinly foliated trees and bushes in open, SE quadrant eg *Citrus* and grape-vine. Exposed SE facing wall recesses	Densely foliated trees and bushes under date-palms, SE quadrant eg *Citrus*. Well shaded recesses or caves

In what months the divisions between winter and summer come would be up to the bee-keeper to judge, taking into account the strength of his colonies, their degree of exposure etc, but in general colonies should probably be moved to summer sites in March or April and back to winter sites in October. The SE sector of trees should be favoured, particularly in winter; even in summer a little direct insolation in the morning might be useful, with the sun going overhead at mid-day.

In summer mountain caves did not appear to be particularly satisfactory, for instance several of Khalifa's (bee-keeper c) colonies absconded from caves at this season. Even though Humayd bn Sulayman al-Shimili said that colonies nested in south-facing caves in summer and that the sun did not penetrate deeply into them (Dutton & Simpson 1977), I believe the heating up of the enveloping rock would usually lead to an unfavourable microclimate as the cave temperature measurements in Chapter II suggested. Most colonies Humayd found in south-facing caves in summer had probably selected these sites in winter or spring, but he would have found them in May (summer) while taking the "samur" honey harvest. Cool, N facing caves might be satisfactory in summer, if sheltered from hot winds, and if shady trees are not available. Until the communication dance requirements of *florea* are understood better, all colonies in caves should be supported on a "zoora", not squashed against the cave roof, so that they have a dance platform.

The above suggestions on siting should only be a guide to intending keepers of *florea*. The bee-keepers I met had come to favour certain types of site, even individual caves, as a result of experience. New bee-keepers likewise will have to try out various sites in their own neighbourhood and then use those from which fewest abscond.

As for other management techniques, unless experiments with hives and frames are undertaken (Chapter VIII), those methods involving a "zoora", as described in this chapter and in Chapter IV on Nāsr Ahmad al-Ghaythi, were the more satisfactory. However, bee-keepers should refrain from taking their harvest at the end of a honey flow and from taking away all the honey and pollen.

CHAPTER IV

MANAGEMENT OF *APIS FLOREA* BY NĀSR AHMAD AL-GHAYTHI AND ITS ANNUAL CYCLE AT ZAHIB, SHARQIYA

INTRODUCTION

The purpose of Part I of this chapter is to record, in as great a detail as practicable, the bee-keeping methods of one Omani who specialized in the management of *Apis florea* for honey production. Operations with *florea* on the scale at which this man practised have not been recorded before and may not be matched in Oman or any other country where this species is found. Therefore, the nest sites at the two locations where his bees were kept, the vegetation at each that provided forage at different times of year and his various management techniques, are described as all may be contributory to his success. Part II of the chapter investigates the annual cycle of *florea* under these conditions and considers the suitability of this bee-keeper's methods in relation to problems such as absconding and swarming. The bee-keeper's full name was Nāsr bin Ahmad bin Sayf Al-Ghaythi, referred to hereafter as "Nāsr". He kept the bees at his date garden in the village of Zāhib and in the plains to the east of this oasis (Figure 4.1). Zāhib is in the plains just to the south of the Eastern Hajar mountains, approximately 130km SSW of Muscat in the Wāliyat of Muḍaybi in the Sharqiya (Eastern) region of Oman.

Previous descriptions of *florea* management (Dutton & Simpson 1977; Dutton & Free 1979; Williams 1979) have been qualitative and gave no data on the numbers of colonies involved or their state at different seasons. However, subsequent investigations that I made on the bee-keeping of Humayd bin Sulayman, who was the subject of the above studies, indicated that he usually worked with fewer colonies than Nāsr,

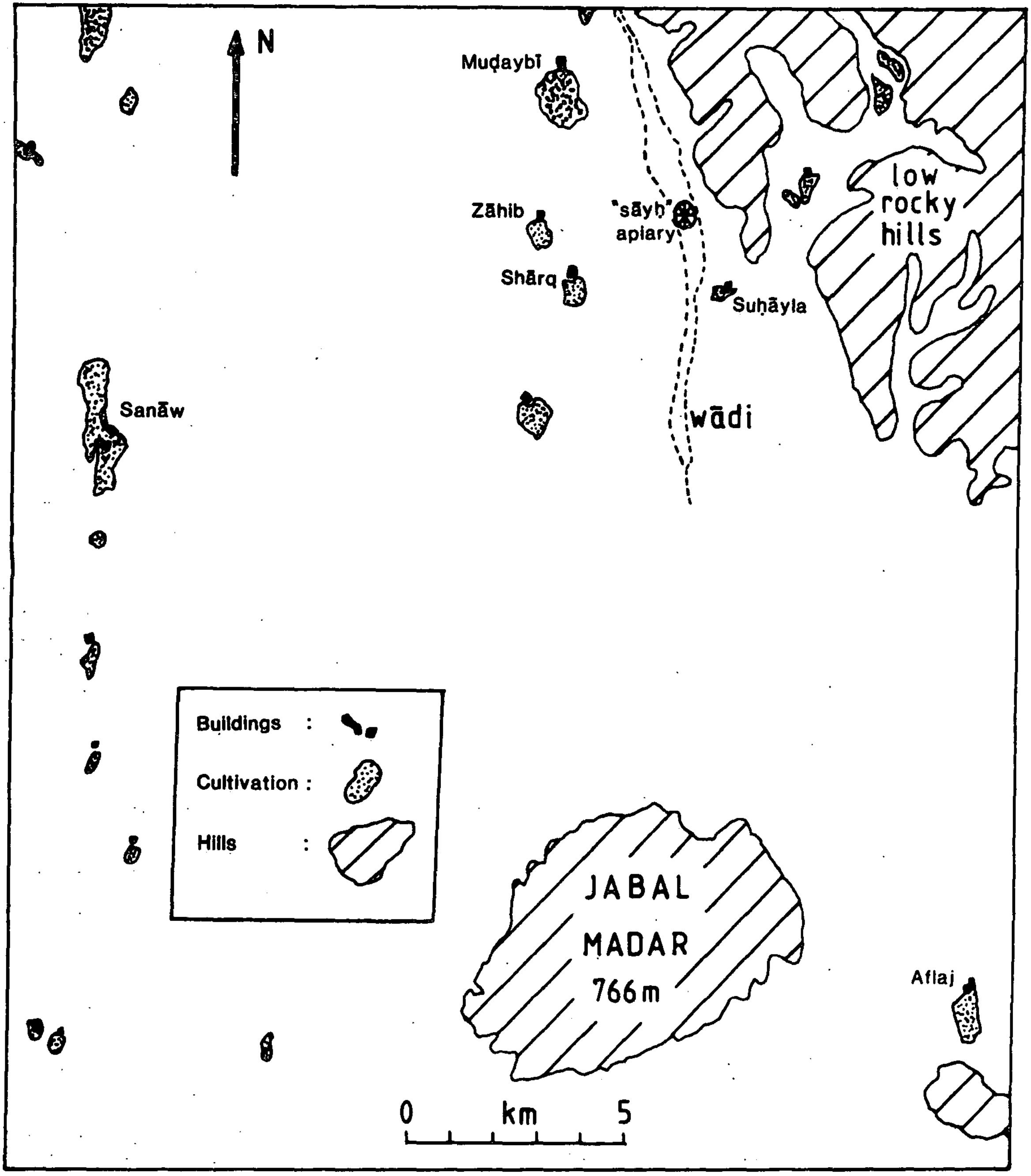


Figure 4.1 Map to show location of the village of Zahib (22°32'N, 58°07½'E), Oman and the site in the "sayḥ" (plain) where Nāsr Ahmad al-Ghaythi kept his colonies of *Apis florea*. The Jabal Madar where he hunted wild colonies (Ch.III) is also shown.

though Humayd too was very skilled in his handling of *florea*. For instance Humayd informed me that in mid-May 1980 he had approximately 25 *florea* colonies, when Nāsr had approximately 30, but on 10.vii.80 I saw Humayd had only 2 colonies, while Nāsr 3 days earlier (7.vii.80) still had 22. Most of Humayd's colonies had absconded, but comparatively few of Nāsr's.

Similarly, the experience of many other Omani *florea* bee-keepers that I encountered, and my own attempts at domestication of *florea* (Chapter VI and Chapter VIII) have shown that, because of absconding, it is difficult to keep significant numbers (>10) of *florea* colonies throughout the year, in the way that Nāsr did. This may have been accentuated between 1977 and 1980 when near-drought conditions prevailed in many areas of Oman. Therefore, with the exceptional situation of having 18 to 30 of Nāsr's colonies relatively accessible for examination at any one time, the opportunity was taken to gather much-needed, quantifiable data on the numbers, developmental state etc of *florea* colonies - albeit under management - at different times of the year, in a single area.

METHODS

The information was collected on 7 visits to Nāsr centred on the following dates (some visits were of more than one day's duration):-

I	11.ix.78	Early Autumn, before "sidr" season
II	1.xi.78	Late Autumn, end of "sidr" season
III	14.xii.78	Winter
IV	30. vi.79	Mid-Summer
V	11.xii.79	Winter
VI	11. iv.80	Spring, start of "samur" season
VII	6.vii.80	Mid-Summer

"Sidr" season : usual main flowering period of *Ziziphus spina-christi*, end of September to beginning of November

"Samur" season : usual flowering period of *Acacia tortilis*, c. 10th April to 15th May

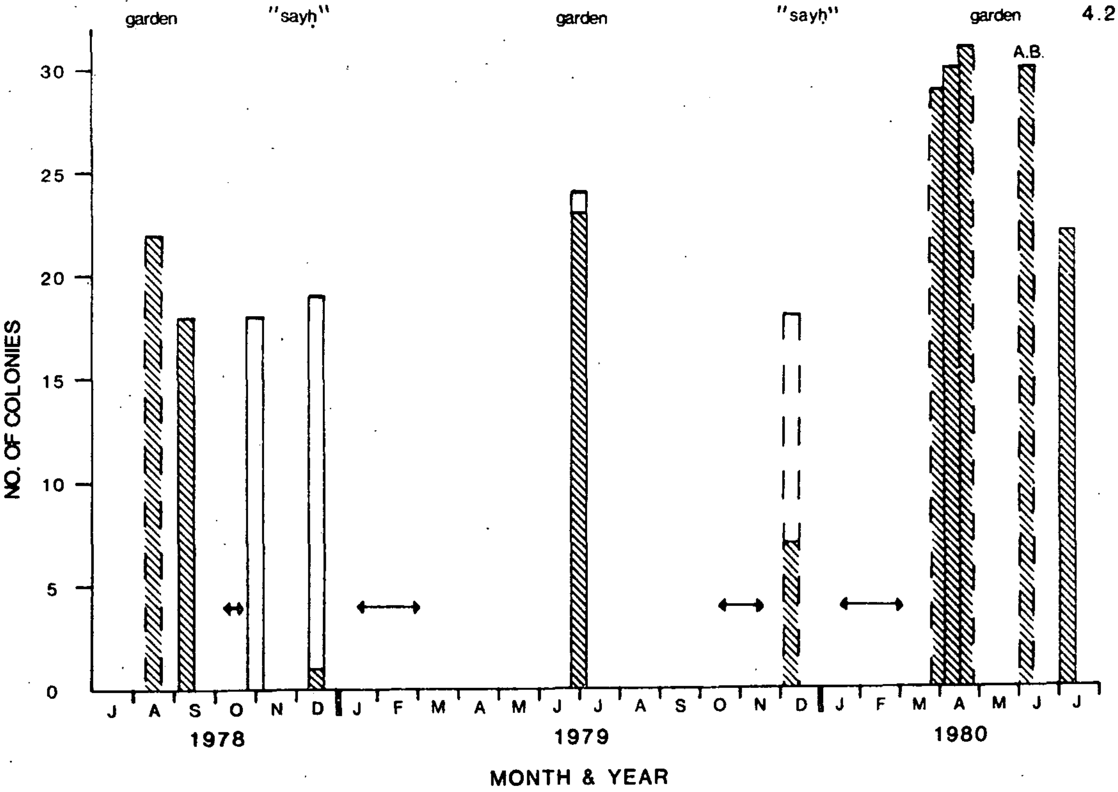
Thus most seasons were covered (illness prevented one planned visit in May) while visits III and V (December) and IV and VII (June/July) were at almost exactly the same time but in different years, and allowed a check to be made on the consistency of both Nāsr's management methods and the seasonal development of the bees.

The measurements and observations are my own but, when stated, are supplemented by Nāsr's own comments and vivid descriptions, which he kindly provided in answer to my numerous questions. He had had no school education and thus had virtually no formal knowledge of the biology of honeybees; he claimed that his uncle had introduced him to keeping *florea* but that he had also developed his own ideas and techniques. He was unable to keep any records and his various estimates of time were not always consistent, so these were adjusted appropriately according to my own knowledge of the development of *florea* colonies and the flowering seasons.

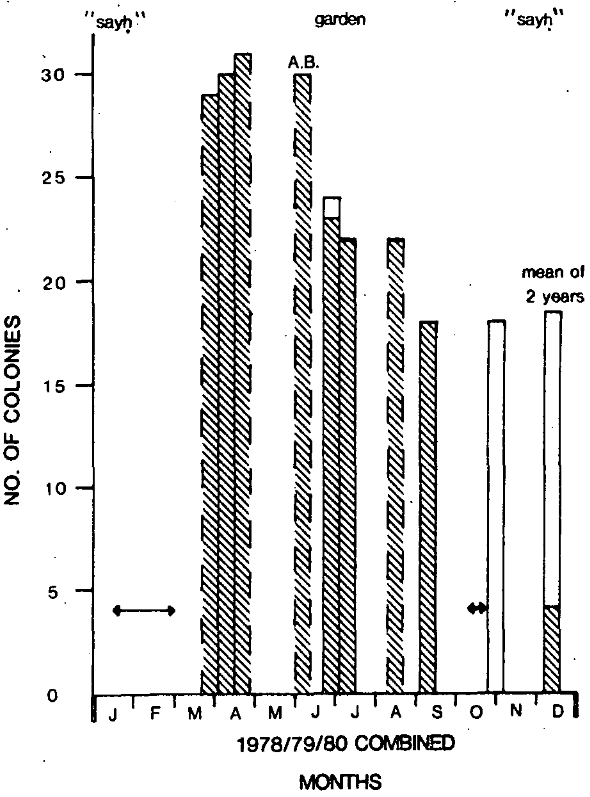
Two special features of his management system were (a) his siting of *florea* colonies in specially constructed recesses in the wall of his garden, as well as in trees, and (b) his practice of "migratory bee-keeping", moving most colonies in the cooler, winter months to trees and bushes in a region of the plains c. 3km to the east of his village. The location of the two "apiaries", at the garden and in the plain (sayḥ), are indicated in Figure 4.1 and the number of colonies kept at each site at different times of year, during the course of this study, are shown in Figures 4.2 and 4.3.

Figures 4.2 and 4.3 Number of colonies of *Apis florea* kept by Nāsr Ahmad al-Ghaythi at and near Zāhib, Oman between August 1978 and July 1980, presented in chronological order (4.2) and rearranged according to one calendar year to show the annual cycle (4.3). The numbers in his garden (hatched columns) and in trees at his apiary site in the nearby alluvial plain, "sayḥ", (unhatched columns) are distinguished. ↔ indicates the approximate periods during which Nāsr would move colonies from garden to "sayḥ" in autumn and from "sayḥ" to garden in early spring. Dashed columns indicate numbers were estimated to within 1 or 2 colonies. The data was gained from 7 visits, detailed on p. 135, supplemented by Nāsr's comments and a personal communication from Adrian Brockett (A.B.).

4.2


garden
"sayḥ"
garden
"sayḥ"
garden
A.B.
NO. OF COLONIES
0
5
10
15
20
25
30
J A S O N D J F M A M J J A S O N D J F M A M J J
1978
1979
1980
MONTH & YEAR

4.3


"sayḥ"
garden
"sayḥ"
A.B.
mean of
2 years
NO. OF COLONIES
0
5
10
15
20
25
30
J F M A M J J A S O N D
1978/79/80 COMBINED
MONTHS

When possible, the total number of colonies was counted on each visit and details of the following recorded for individual colonies:- nest site (eg type of tree, height, orientation); colony shape, height and width (with a tape measure); depth of bees in protective curtain and percentage of comb covered by them (visual estimate); worker and drone brood; adult drones; queen cells; stores of pollen and honey; recent history of the colony (information from Nāsr) eg whether it had been divided, had honey extracted etc. Usually only one side of a colony would be examined. Photographs were used to confirm some of these observations and they sometimes provided data that had not been recorded. Where height and width of a colony had been measured, a Colony Area Index (C.A.I.) was calculated, by multiplying the two dimensions. The C.A.I. gives an approximation (slight overestimate, as it assumes a rectangular shape) of the true surface area of the side of a colony and enables comparisons of colony size to be made. Sometimes colonies left areas of older brood comb and honey comb exposed, when they were not being used; then the visual estimate of percentage cover of bees x C.A.I. gave a "Colony Cover Index" (C.C.I.). This indicates the active or functional area of such colonies.

On several of the visits only a sample of the colonies could be examined and not all the details it was desired to obtain (from each colony) could be recorded because of the following problems:- (a) The inaccessibility of some of the colonies eg in the tops of thorny *Acacia* trees. (b) The need to leave the bees undisturbed, particularly to prevent absconding. (c) Nāsr's high standards; he was usually happy for me to examine some colonies (as representative of his skills as a bee-keeper) but was not always keen that I should investigate every single colony, particularly the weaker ones! However, bearing in mind that Nāsr did not really appreciate the need for detailed research (as he considered he knew all that was necessary concerning the strength of the bees, their management etc and a sample of one or two colonies would be adequate to show me), he was exceedingly co-operative and patient. Thus, particularly on the earlier visits when Nāsr was unfamiliar with my research, only a subjective assessment of the state of some of the colonies could be made and, where so, this is indicated in the text. On the later visits I was able to make closer inspections of many more of the colonies.

PART I. LOCATION OF COLONIES, VEGETATION AND BEE-KEEPING TECHNIQUES

1. Summer site of *Apis florea*; Nāsr's walled garden, Zāhib

1.1 Number and position of "Bee Boles"

Figure 4.4 is a diagram of the garden (area .239 hectares) indicating the positions of the recesses or "bee boles", in the wall enclosing it, and the various trees in which colonies of *florea* were sited. Altogether there were 24 "boles" though one of them (No. 15) was damaged where the east wall had collapsed above it and was never seen to be used. Another bole (No. 4) was not seen to be used on any of the visits either, possibly because it was shallow and a cassava bush made access difficult. The mean distance between boles (centre to centre) was 5.63m; S.E. = 0.55m; Range 3.5 - 13m; n = 19.

The distribution of "boles" in the different walls is shown in Table 4.1. This even distribution of boles per wall suggests that when the bee-keeper constructed the boles in the wall he did not consider any particular aspect was preferable for the bees. To investigate whether wall aspect had any influence on the tendency of *florea* colonies to stay at a site and not abscond, counts of the number occupied/wall

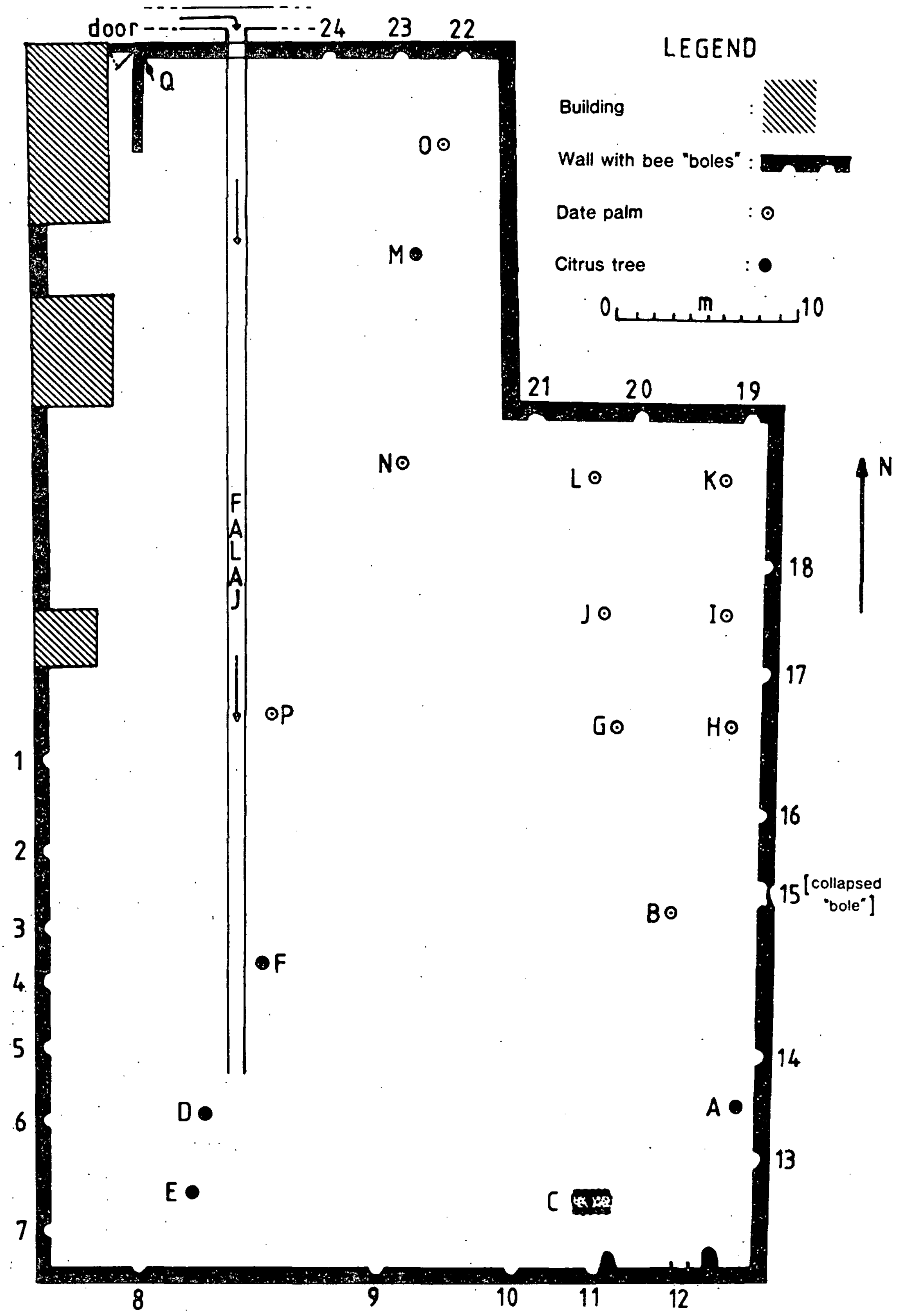


Figure 4.4 Diagram of Nāsr Ahmad al-Ghāythi's garden at Zāhib, Oman showing the position of bee "boles" (recesses in the surrounding wall) and of trees used for siting colonies of *Apis florea*. The dimensions of the garden and the positions marked for the boles are accurate to within circa 1m; the tree locations marked may be slightly less accurate in a few cases. The boles and tree sites have been allocated numbers and letters respectively, and these are referred to in the text; three of the sites were slightly different from the others and details can be found as follows:- site 12, p.141; sites C and Q, p.142. Further descriptions of the garden, boles and their use at different times of year are also given within the text and especially on pp.138-145.

Table 4.1 Number of boles (recesses) and *Apis florea* colonies in each wall of Nāsr's garden at Zāhib, Oman, on 7 separate visits. Negative figures in brackets are numbers known to have absconded recently.

			North Wall	East Wall	South Wall	West Wall	No. in trees
	Colony Aspect		South	West	North	East	
	No. of Boles		6	5 (+ 1 collapsed)	5	6 (+ 1 not used)	
No. occupied	April	Visit VI	4	3	4	6	(-1) 12→13
	June/July	Visit IV	(-1) 5	4	(-3) 3	6	5
	July	Visit VII	4	(-2) 2	(-3) 1	(*) 5	10
	September	Visit I	4	3	4	6	1
	November	Visit II	0	0	0	0	0
	December	Visit IV	(-2) 3	0	c.1?	3	0
	December	Visit III	1	0	0	0	0

* = one colony had deserted its comb to return to its original bole, in the same wall, where it united with another colony. → = new colony formed by division during visit.

were made on each visit. The counts from the 3 winter visits when the garden walls were scarcely being used are excluded from the calculations.

Summing the counts from the 4 "summer" visits, expected occupation values, assuming no difference between the walls, were calculated (Table 4.2).

Table 4.2 Influence of aspect on occupation of boles by *Apis florea* at Zāhib. Observed occupation and expected values, assuming aspect has no influence, summing 4 "summer" visits (I, IV, VI and VII). Number of boles available = number of boles in wall x number of visits. Expected number of colonies = (number of visits x available boles in wall) x (grand* total number of boles occupied) ÷ (grand* total number of boles available). * = ie sums for all walls over 4 visits.

Example : N wall. No. expected = (4x6) x 64 ÷ 88 = 17.45

Wall	North	East	South	West	TOTAL
Colony Aspect	South	West	North	East	
No. of boles available	24	20	20	24	88
No. of colonies observed	17	12	12	23	64
No. of colonies expected	17.45	14.55	14.55	17.45	64

$\chi^2_3 = 2.67$ NS

This showed that, though the West wall had a greater proportion of its boles occupied than expected and the South and East walls a rather smaller proportion, there was no significant difference ($\chi^2_3 = 2.67$) between the walls in retaining colonies of *florea*. This test assumes that the counts on each visit were independent and that equilibrium had been reached between the rate of absconding from each wall and the rate at which Nāsr replaced the colonies (if Nāsr replaced a colony as soon as it absconded no differences would be recorded). With visits being far apart and Nāsr not having a stock of colonies to replace lost ones these assumptions are not unreasonable.

1.2 Dimensions of boles

A typical bole is shaped as in Figure 4.5a, ie tending towards a rectangle, rounded at the top and bottom, with a notch at either side near the top for supporting the "zoora" (split date palm frond) on which Nāsr kept his colonies. Figure 4.5b shows a colony in bole 20. Measurements were taken of the dimensions of some of the boles (selected at random) and are presented in Table 4.3.

There was no fixed position in which the "zoor " were rested in the notches, but they were usually pushed near to or right against the back. Thus the mean distance from the "zoora" to the back of a bole was 98.5mm (S.E. = 7.2mm; Range 60-140mm; n = 10).

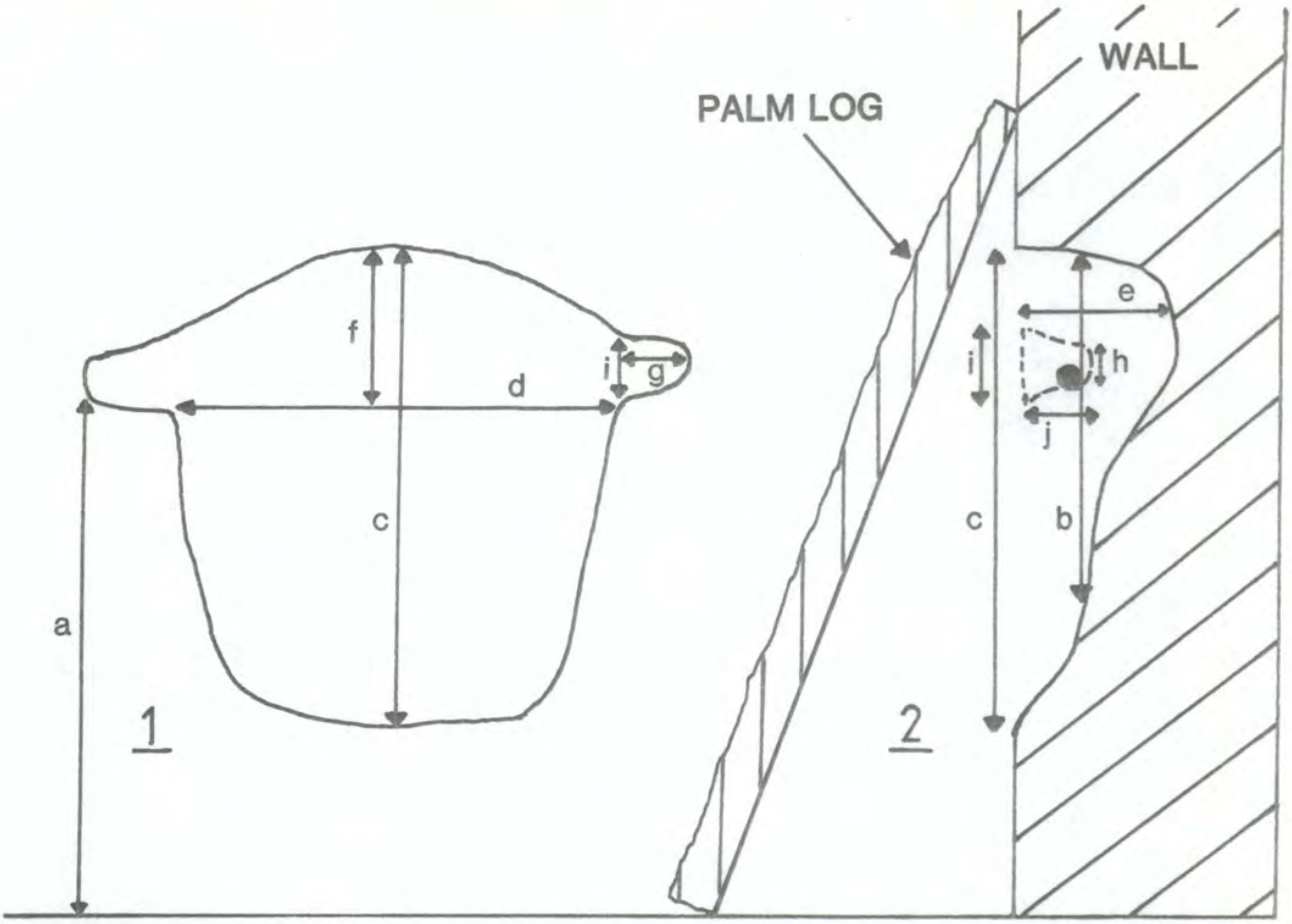


Figure 4.5a Shape of typical recess, "bee bole", for *Apis florea* in Nāsr's garden at Zāhib, Oman. (1) viewed from front, (2) cross-section. Letters a-j correspond to measurements in Table 4.3.

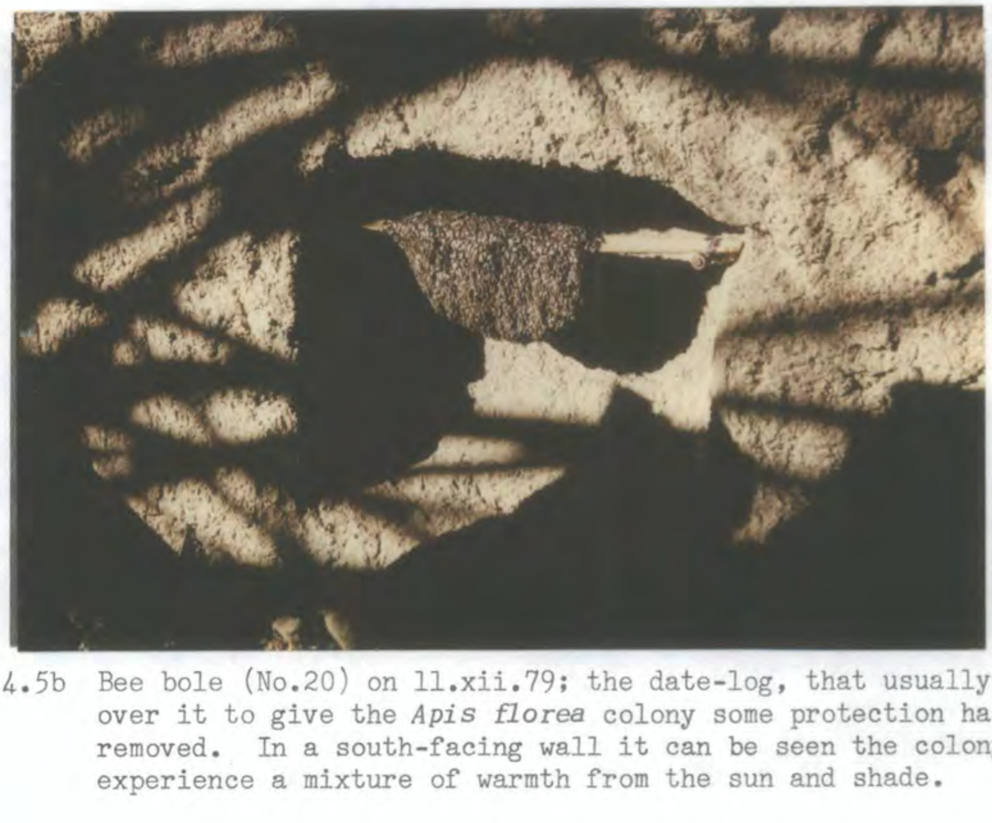


Figure 4.5b Bee bole (No.20) on 11.xii.79; the date-log, that usually leaned over it to give the *Apis florea* colony some protection has been removed. In a south-facing wall it can be seen the colony would experience a mixture of warmth from the sun and shade.

Table 4.3 Dimensions of recesses, "bee boles", for *Apis florea* in Nāsr's garden at Zāhib, Oman. Measurements were made on colonies selected at random. The letters a-j correspond to those in the diagrams of Figure 4.5.

Bole Dimensions (cm)	Mean	S.E.	Range	n
a. Ht of notch (ie colony on "zoora") from ground	83.8	5.51	60 - 150	23
b. Internal height (ie back) of bole	55.7	3.13	40 - 64	6
c. External height (ie front) of bole	59.3	3.00	51 - 68	6
d. Width of bole	58.1	1.32	55 - 63	7
e. Depth of bole	19.0	1.04	14 - 25	9
f. Height from zoora to top of bole	10.6	.73	8 - 16	10
Notch Dimensions (cm)				
g. Length	8.8	.80	6 - 10	5
h. Internal height (ie back) of notch	2.9	.29	2 - 3.5	5
i. External height (ie front) of notch	5.9	.40	4 - 7	12
j. Depth	9.73	.62	8 - 14	11

In one bole (20, Figure 4.5b) there was a protruding bolt close to one of the notches on which the "zoora", if it was short, was rested. At a second site (12) there was no proper recess, but the "zoora" was rested on two iron pegs protruding from the wall.

1.3 Other features and provisions in the garden

The height of the mud and stone walls encircling the garden and containing the boles was variable but measurements made in a few places were as follows:-

N wall : 1.80m, 1.91m, 1.56m (E corner)
E wall : 1.75m (typical height), 1.68m (near E corner)
S wall : 1.95m
W wall : Not measured. Similar to E wall, lower than S wall

The colonies were protected by the wall behind them and were usually given some shade from the front, particularly by cut sections of date-palm trunk, split down the middle, and leant against the wall (Figure 4.5) eg 3 over bole 13 had lengths 1.50m, 0.84m and 1.49m. Date-palm fronds, sacking etc were also used for shade.

In addition to shade, Nāsr made a regular supply of water available to his bees, in a circular trough resting on a block of wood; he put twigs in the water which gave the bees extra purchase while drinking. He said a raised trough was better and in December 1979 *florea* were seen to drink from this raised trough, but not from one on the ground. Presumably a raised trough is safer from predators such as toads (*Bufo* sp.). He killed one of these, on Visit VII (July), that was under a *florea* colony, claiming it ate the bees.

On Visit IV 6 of the "zoor" (split palm frond mid-ribs) Nāsr used for holding the combs were measured. Their mean length was 67.2cm (Range 63.0 - 70.0cm). Near the split end Nāsr had made a notch on either side of the mid-rib so that the strip of cloth he used for tying the ends together did not slip: it was 8.0cm from the end of one 65.0cm-long "zoora". The height of one zoora was measured as 10mm and the thickness/depth (back to front) of another that enclosed a comb was 40mm.

1.4 Siting of colonies in trees in the garden

15 different trees, 10 date-palm and 5 *Citrus* sp., were seen to be used for siting *florea* colonies over the seven visits. Two other sites were also used; one (C) so that the colony was resting between two date-palm trunks lying on the ground, and for shade was covered with branches and fabric, while at a second site (Q) the colony was supported by one end of its "zoora" that was wedged into a hole in the angle between two walls. Not being proper "boles", these sites have been included in the "tree" category.

The date-palms used were young trees and the ends of the "zoora" holding a colony would be tied to the palm fronds, at their bases close to the trunk, between waist and head height (mean = 1.21m, S.E. = 0.10m, range = 1.00 - 1.50m, n = 5). The "zoor" holding colonies in *Citrus* trees were tied to convenient branches at a range of heights from 1.50 to 3.00m (mean = 1.92m, S.E. = 0.28m, n = 5).

Therefore, though the samples are too small for satisfactory statistical tests, the colonies kept in *Citrus* trees were generally higher than those in date palms. However, this appeared to be just a reflection of the height of suitable branches on the two trees.

Combining them, the overall mean height of colonies kept in trees was 1.57m, S.E. = 0.18m, significantly higher than those kept in the bee boles, 0.838m ($d = 3.89$, $\tan \Theta = 3.267$, $P < 0.01$).

The region of the tree in which the bees were placed by Nāsr was recorded for 6 colonies on Visit VI (April 1980) as follows:-

NE	E	ESE	SE
2	1	2	1

One of the faces of the colony would be orientated in approximately the same direction. 3 of the tree sites were re-examined on Visit VII (July 1980) and they all contained colonies (probably the same ones) in the same positions. This suggested a preference for sites facing east which received the morning sun.

1.5 Discussion : overall siting of colonies in Nāsr's garden

Though there were no significant differences (Table 4.2) in absconding rate from walls with different orientation, as measured by the occupation of boles in summer, overall a greater proportion of the boles in the western wall (23/24) than in the southern (12/20) and eastern (12/20), were occupied by *florea* colonies. Continuous records of the number of colonies staying at and absconding from each wall over 2 years or so would be needed, however, to establish whether there were significant differences, between the walls, in the mean length of time that colonies stayed. The number of colonies that had absconded from each wall just prior to my visits, known from the presence of abandoned combs and Nāsr's comments (Table 4.1), did suggest that the W wall was better than the S in July. 3 colonies had recently absconded from the S wall on both July visits, but none from the W wall.

With Nāsr also positioning many of his colonies in the E sector of trees it did appear that sites receiving the early morning sun, even if filtered by palm logs etc, might be favourable; maybe the advantage of such siting patterns would have been even more evident had Nāsr kept a greater number of *florea* colonies in the garden during the cooler months.

It might have been expected that the southern wall (facing N) would be better in the summer, but with the sun virtually overhead at this time of year little shade advantage would be gained. In Nāsr's garden, the south wall may have been poorest in summer because the ground was relatively open in front of it and the microclimate consequently too hot, while there were more and larger date palms giving essential shade in the northern part of the garden. Possibly as important, the sun would not be visible for communication dances from a recess in the N facing wall.

These findings concur well with the observations in Chapter II that wild colonies tend to select nest sites in the SE quadrant of trees and to the S and E of walls. It is also especially pertinent to note that keepers of *mellifera* from Roman times to the 19th Century favoured south-facing hive sites in and against walls and buildings (Crane 1983a). Most (48.8%, n = 627) bee bole sets in Britain and Ireland face south (south-east, 15.6%, was the next preferred aspect) and warmth from the sun and shelter from the wind were the main reasons given for this choice. Columella's statement in *De re rustica*, quoted by Crane, "The heat of summer is not so harmful to this kind of creature as the cold of winter ... the bees' dwelling-places ... ought to be so arranged as to face the south-east, in order that the bees may enjoy the sun when they go out in the morning and maybe more wide-awake; for cold begets sloth" is remarkably consistent with Nāsr's and other Omanis' understanding of *florea*, and indeed my own!

Did Nāsr use boles in preference to trees? 13 was the largest number of trees he had in use at one time (Visit VI) and then most (17) of the wall recesses were occupied. On another visit (I) when exactly the same number of boles was occupied, only 1 colony was recorded in a tree. Examination of the data in this way suggested that Nāsr generally utilized the boles first and then the trees. He did not indicate that one type of site was better than the other and I suspect he used the boles first because of ease of access and the way a "zoora" could be simply rested in the notches. In trees, two level branches the right distance apart have to be found and the "zoora" ends then tied to them.

2. Winter site of colonies in plains 3km from Zāhib (Figure 4.1)

2.1 Siting of colonies

On Visits II and III the positions of 14 and 15 colonies, respectively, were recorded at this site and, as it was not possible to match all the individual colonies from one visit to the next, the measurements of the two visits are here combined. (Nāsr might move colonies from time to time eg after honey extraction, division.)

(i) 12 colonies (6 on each visit) were high in *Acacia tortilis* trees at a mean height of 4.1m (range 3 - 5m); Nāsr had to climb the trees to reach the sites, which received some shade from the surrounding twigs and small leaves.

(ii) 6 colonies, 3 on each visit, were at head height (mean 1.73m of 3 measured) in *Acacia tortilis* trees and could be inspected from the ground.

(iii) 11 colonies were close to the ground (5 on Visit II, 6 on Visit III), their "zoor" supports being from 0.2 to 0.75m from the ground; the bottom of some colonies was as little as 70 - 80mm from the ground. 5 colonies were in *Acacia tortilis* trees; 4 in *Leptadenia pyrotechnica* bushes (a colony each in the same two bushes on both visits); 1 in a small *Maerua crassifolia* bush (with a small stone wall round its base protecting the colony); 1 supported in a box shaded by a mat of brush etc.

3 additional colonies were noted in *Acacia tortilis* trees on Visit III, but their heights not recorded.

2.2 Other features and provisions

Some of the colonies, especially the lower ones, were covered and surrounded with brush etc for shade and protection. According to Nāsr, and I believe his supposition to be correct, the colonies in their fairly exposed situations benefit in winter from the warmth of the sun here and also from the cool breezes neither of which penetrates the date garden to the same extent. This sounds paradoxical but it is presumed the insolation is important in warming the colonies in the morning and the breezes are beneficial during the hotter part of the day.

Estimates were made of the distance between 6 successive colonies; the mean was 43m with a range of 10m to 100m (to the nearest colony), so the foraging areas of most of the colonies probably overlapped completely. Nāsr supplied water regularly, obtained from a well near to the centre of his bee-keeping area, in a small cement trough; he placed twigs, stones and rags inside the trough so the bees could stand and drink with little risk of drowning.

3. Vegetation

3.1 Nāsr's garden (Table 4.4)

This was a garden of area 0.24ha, irrigated by a "falaj", in which date palms were the primary tree crop supplemented by several smaller trees such as *Citrus* spp. These provided a considerable amount of shade, but there were open areas in which graminaceous crops, onions etc were grown. Weeds, as in other gardens in the interior where large basins are irrigated by "falaj", covered much of the ground throughout the garden. Aerial photographs and direct observation showed that date palm was the primary crop in other gardens in the oasis too so, though there may have been some differences in the undercrops grown, their weed flora was probably similar. All the gardens would have been in range of Nāsr's bees as his garden was near the centre of the oasis which, from aerial photographs, was approximately rectangular in shape (600m by 430m, total area 26 hectares including paths etc). Some of the neighbouring oasis of Shārqi may also have been within the foraging range of *florea* from Nāsr's garden. His garden was 1,150m from the nearest garden in Shārqi, which was very similar in size, shape and layout to Zāhib.

25 plant species were recognized in Nāsr's garden, but there was not any obvious difference in the overall composition of the flora from other gardens of the interior of Oman, to which Nāsr's success in keeping large numbers of *florea* at this site could be attributed. The weeds *Phyla nodiflora, Vernonia cinerea, Portulaca oleracea, Pimpinella* ?sp. nov. and *Euphorbia heterophylla*, however, were abundant or frequent and all are known to be sources of forage for *florea* (Chapter VII) so their combined presence must help to maintain the colonies when major sources are not flowering.

Tables 4.4 and 4.5 Vegetation of a falaj-irrigated date-garden (4.4) at Zāhib in the Sharqiya region of Oman and of the alluvial outwash plain, dissected by a wadi (4.5) that bordered the village; Nāsr Ahmad al-Ghaythi kept *Apis florea* colonies at both localities. Plants collected and/or recorded from the two sites are listed with records of whether they were in flower or fruit on visits at 4 different times of year (detailed on p. 135). The overall flowering periods of the plants in northern Oman and whether a source of nectar (N) and/or pollen (P) to *A.florea* are given. (? indicates a probable source). Further details of the plants can be found in Tables 7.1-3 and Appendix III and descriptions of the two sites on p. 147 and 148.

0 0 : plant in flower (Fl) and in fruit (Fr)
\- - : plant not in flower or fruit
0 : plant only in flower
\- 0 : plant only in fruit
(V) : plant not recorded in Nāsr's garden but pollen sample indicated its presence in the vicinity
[ ] : plant recorded at nearby oasis, Sanāw, on 14.xii.78 so likely to occur at Zāhib too
* : bee plant according to Nāsr
X : not a bee plant according to Nāsr
E : exudate of fresh dates
NP : sight or pollen record indicated definite exploitation at Zāhib

N.B. The records are not comprehensive, particularly of the plants in flower at each visit, but should cover the main components of the flora on which Nāsr's bee-keeping was based.

Table 4.4

FAMILY	GENUS SPECIES	11 April Fl	11 April Fr	30 June-6 July Fl	30 June-6 July Fr	1 Nov Fl	1 Nov Fr	11-14 Dec Fl	11-14 Dec Fr	MONTHS(1-12) IN FLOWER	*FLOREA* FORAGE
AMARANTHACEAE	*Achyranthes aspera*							0	0	1 3 4 9 12	
BORAGINACEAE	*Cordia myxa*									2	N
COMPOSITAE	(*Blumea aurita*	0	-	0	0					4 7	
	(*Carthamus tinctorius* (V)									2 3	NP
	(*Eclipta alba*	0						0		4 6 8 12	N *
	(*Flaveria trinerva*	0		0						1 2 4 6 7 8 9 10	NP
	(*Launaea* sp.	0		0				0		4 7 10 12	NP
	(*Vernonia cinerea*	?	0	0		0		0	0	1 3 4 5 6 7 9 11 12	NP
CONVOLVULACEAE	*Convolvulus arvensis*			0						1 2 3 4 5 6 7 9	*
CUCURBITACEAE	(*Citrullus lanatus*									6 7 8	NP
	(*Cucumis melo* (V)			0						5 6 7	NP
EUPHORBIACEAE	(*Euphorbia helioscopia/peplus*									1 2 4	NP
	(*Euphorbia heterophylla*							0		1 11 12	NP
	(*Euphorbia indica/prostrata*	0	0	0				0		3 4 7 9 12	
	(*Manihot esculenta*									?	
	(*Phyllanthus maderaspatensis*			0	0			0	0	6 7 8 12	
(at Suhayla) →	(*Ricinus communis*									?	P
LABIATAE	*Ocimum* sp. (V)									1 2 4 6 7 8 9 10 12	NP
LEGUMINOSAE	(*Cassia italica*			0				0		3 4 7 8 12	
	(*Medicago sativa* (?V)									4 5 6 7 8	NP
	(*Melilotus indicus*	0								2 3 4	NP
	(*Tamarindus indica*									6 10 11	
LYTHRACEAE	*Lawsonia inermis*			0						5 7 8	NP
MALVACEAE	(*Abutilon* sp.									?	
	(*Sida spinosa*							0	0	2 3 9 10 11 12	
MORACEAE	(*Ficus carica*									?	
	(*Morus* sp.							0?		1 2 3	
MYRTACEAE	indet. (V)										P
OXALIDACEAE	*Oxalis corniculata*							-		1 7 8 12	
PORTULACACEAE	(*Portulaca oleracea*			0						3 4 5 6 7 8 9 11	NP
	(*Portulaca quadrifida*							0		2 10 11 12	?
PRIMULACEAE	*Anagallis arvensis*	-	0					0		1 2 3 4	?
PUNICACEAE	*Punica granatum*	-	-							4 6	? *
RHAMNACEAE	*Ziziphus spina-christi*					0				9 10 11	NP
RUTACEAE	*Citrus* (≥2 spp.)					-	0	-	0	1 2 3	NP
SOLANACEAE	(*Solanum incanum*							0		1 6 10 12	
	(*Solanum nigrum*		0	0				0		2 3 4 7 12	
	(*Withania somnifera*			0	0			0		7 12	
TILIACEAE	*Corchorus trilocularis*	0						0	0	2 3 4 5 6 7 11 12	
UMBELLIFERAE	*Anethum graveolens*	0								3 4 5 6	NP
	Pimpinella sp.	0								4	NP
VERBENACEAE	*Phyla nodiflora*	0	0					0		1 2 3 4 5 6 7 8 9 10 11 12	NP*
MUSACEAE	*Musa* sp.									1 2 3 4 6 7 12	N
GRAMINEAE	(*Cynodon dactylon*							0		4 6 7 11 12	P
	(*?Eragrostis* sp.			0						?	
	(*Setaria verticillata*	0								3 4 8 9	
	(*Sorghum* sp.									3 6 8 10 12	?
LILIACEAE	*Allium cepa*	-	-							2 3 4	NP
PALMAE	*Phoenix dactylifera*				0					1 2(♂) 6 7 8(fr.)	EP
TOTALS NO. OF SPECIES	50	11		16		2		18		Mixture of winter, spring, summer and all year flowerers	31

Table 4.5

		11 April		30 June - 6 July		1 Nov		11-14 Dec		MONTHS (1-12) IN FLOWER	*FLOREA* FORAGE
FAMILY	GENUS SPECIES	Fl	Fr	Fl	Fr	Fl	Fr	Fl	Fr		
APOCYNACEAE	*Rhazya stricta*	-	0					0		1 2 12	*
ASCLEPIADACEAE	*(Calotropis procera*	0								2 3 4 6 7 8 10	N*
	(Leptadenia pyrotechnica	-	0			0		0		2 11 12	N
	(Pentatropis spiralis							-		?	
CAPPARACEAE	*(Dipterygium glaucum*							0		2 3 7 9 12	NP*
	(Maerua crassifolia	-				-				1 2 3	NP*
CRUCIFERAE	*Morettia* sp.	0								?	
CUCURBITACEAE	*(Citrullus* cv.									6 7 8	NP
	(Cucumis cv.									5 6 7	NP
EUPHORBIACEAE	*Euphorbia granulata*									1 2 3 4 12	
LEGUMINOSAE	*(Acacia ehrenbergiana*	0						0		3 4 12	NP?*
	(Acacia tortilis	0		-		-		-		4 5	NP*
	(Cassia italica	0		0				0		3 4 7 8 12	X *
	(Crotalaria aegyptiaca	0						0		1 2 3 4 12	*
	(Indigofera sp.									?	
	(Prosopis cineraria	0		-				-		3 4 5	NP*
RESEDACEAE	*Ochradenus* sp. nov.	-	0			-		0		1 2 3 4 11 12	NP*
RHAMNACEAE	*Ziziphus spina-christi*	-		-		0				9 10 11	NP*
RUBIACEAE	*Jaubertia aucheri*									1 2 3 4 5	NP?
SOLANACEAE	*Lycium shawii*									1 3 4 7 10 11 12	
	Tribulus sp.	0								1 2 3 4 12	?P
ZYGOPHYLLACEAE	*Zygophyllum coccineum*	-	0							2 12	?*
	Zygophyllum simplex									1 2 3 4 5	NP
TOTALS NO. OF SPECIES	23	8		1		2		7		Mainly winter and spring flowering	19

3.2 Plain ("Sayḥ" or "Saḥara"), Table 4.5

The winter site for Nāsr's bees, c. 3km from Zāhib, was an area of alluvial outwash plain, dissected by a broad, shallow wadi that drained from the plains and the hills and mountains of the Hajar range to the North. Some of the hills and plains near to this site have very scant vegetation but closer to the wadi, with fewer stones and a greater depth of silt at the surface, a considerable increase in the density of *Acacia tortilis* trees was apparent. This was the dominant tree, with smaller numbers of *Prosopis cineraria* and *Ziziphus spina-christi*, all important sources of forage for *florea*. The shrub layer was sparse; it included 3 known sources of forage, *Maerua crassifolia*, *Ochradenus* sp. nov. and *Leptadenia pyrotechnica*, but none were abundant. *Zygophyllum coccineum*, *Rhazya stricta* and *Cassia italica* were the main undershrubs; the first-named, abundant in patches, was not seen in flower on any of my visits, but Nāsr claimed it was a source of forage to *florea*. This was likely as a closely related annual species, *Zygophyllum simplex*, is certainly used by *florea*. Elsewhere in Oman *Z. coccineum* was recorded in flower from the latter half of December to the beginning of February and on 14.xii.78 Nāsr said it was about to flower, at a season when little else was available in the plains. Nāsr also claimed that the bees used the flowers of *Rhazya stricta*, but I have not been able to confirm this; it is a plant avoided by and probably toxic to livestock. *Cassia italica* was not used by bees, according to Nāsr, and my observations supported this. Very few ephemeral plants were seen on my visits, but after rain plants such as *Asphodelus fistulosus*, *Zygophyllum simplex* and *Tribulus* sp. are probably valuable sources of forage.

Bright-red pollen being gathered by many colonies in December 78, subsequently identified as *Euphorbia heterophylla*, showed that the bees did forage at date gardens some distance away while being kept at this site. It was difficult to pin-point on aerial photographs the exact site Nāsr used near this wadi, but from a 1:100,000 map it was c. 3.0km East of Zahib, 2.5km ENE of Shāriq and 1.5km NW of Suḥayla, a small uninhabited oasis (Figure 4.1). It was not known whether the weed *E. heterophylla* occurred at the two latter sites but it did not occur "wild" in the intermediate plains. Therefore, unless this weed was growing at a nearer cultivated site that was not located, *florea* must have been foraging at sources c. 1.5 - 3.00km from their nests, considerably further than the 400m which has been reported before (Lindauer 1957).

4. Major management techniques employed by Nāsr

The most important operations of Nāsr's *florea* management will be described here while other minor practices will be mentioned at appropriate points elsewhere in the text.

4.1 Honey removal

On the afternoon of 10.iv.80, during the course of Visit VI, Nāsr demonstrated his method for removing a *florea* honeycomb using colony H, held on a split "zoora" resting in a date palm. Though the colony was strong with the brood comb fully occupied and being extended and its honeycomb was filled with honey, the honey was nearly all in unsealed cells which could have been extended much further ie honey extraction was rather premature, from this colony, but still allowed satisfactory observations of Nāsr's technique.

He took the colony from the tree and slowly turned it upside down; he then rested one end of the "zoora" in a little hole in the wall and, with his waist, leant against the other end. The colony was thus well supported and both his hands were free to brush the bees very gently down away from the brood comb which was now protruding vertically above the "zoora". When all the bees were hanging in a cluster around and below the honeycomb he cut with a knife (previously held in his mouth) between the brood and honeycombs, through the middle of the pollen storage area. He was therefore able to lift away the brood comb almost completely free of adult bees.

He was able to leave the "zoora", with honeycomb plus bees, supported by the one end wedged in the wall while he inserted the brood comb into another "zoora" already split down the middle for c. 95% of its length. The split ends of the "zoora" were tied together, with a strip of cloth ("khartֹ"), so that the brood comb was sandwiched in the middle, its pollen storage cells and some brood cells being enclosed and squashed a little. He then held this new "zoora" and brood comb adjacent to the cluster of bees hanging from the honeycomb and gently brushed and "patted" the bees so that they walked up onto their original brood comb. He returned the bees and brood comb to their site in the palm tree nearby. The following day the bees were still present and from the presence of eggs in recently completed cells the queen was deduced to be ovipositing still; it appeared, then, that the colony would not abscond.

The honeycomb was therefore free of bees and still attached neatly to the "zoora". He cut away and discarded the band of pollen cells still present immediately below the honeycomb which was now ready for expressing and straining. This particular comb was given away still attached to the "zoora", but he had already explained his simple technique of extracting the honey on Visit III.

All the honeycomb is cut and scraped away from around the "zoora" with a knife so it falls into a large tin (eg that had contained powdered milk). The honey is separated from the wax by straining through a colander (called "mōkhal - موخَل ; classical Arabic for a sieve is "munkhal" - مُنخَل) into another tin. The tin Nāsr used had a nick in it so the honey could then be poured more easily in through the narrow top of a soft-drink bottle. A little wax and pollen sediment usually floats to the top of the honey and is left; this sediment is considered by some Omanis to be a sign of the natural origin of the honey. The rest of the wax is discarded; Nāsr did not indicate he had any use for it.

4.2 "Making increase" through colony division

(i) Division

On the morning (09.15 - 10.00h) of 11.iv.80, Visit VI, Nāsr demonstrated a method of creating extra colonies which I shall call "division", though as two colonies are used to produce a third, it is not the splitting of one colony into two. Initially he had said he would divide one of the colonies used, I, in about 2 days' time, but in order to show me he kindly performed the operation a little earlier than he had intended.

Having selected colony I, on a "zoora" resting in a date palm and measuring 16cm high by 34cm wide with a large brood area, he gently brushed the bees away from the left-hand side of the comb. This revealed a lobe of white, relatively new brood comb which he cut away from just below the honey area (Figure 4.6), through the bottom of the bands of pollen cells. He squeezed, with finger and thumb, the cut pollen and brood cells remaining on the parent comb, thus evening out the slightly

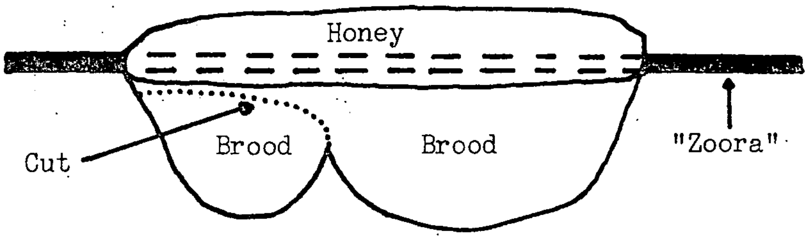


Figure 4.6 Diagram to illustrate removal of portion of brood comb from *Apis florea* colony I during Nāsr's colony "division" procedure. Details in text.

damaged edge. He blew and brushed off the few bees still on the removed portion of comb and wedged it into a prepared, split "zoora", as with the cut brood comb described in the honey-removal section. He checked the comb was in the centre of the "zoora" by measuring the distance from either end with his out-stretched hand.

The parent brood comb (I) was left in the date palm but the "new" comb was taken to bole 20 approximately 12m away; the resident colony from this bole was removed and the new "zoora" and brood comb put in its place. Nāsr then gently patted and brushed the bees, first on the top, then on the sides, of "removed" colony 20, which he was holding by its "zoora" in one hand. This too was a large colony (18cm high by 35cm wide) and did have 1 or 2 queen cells which Nāsr had removed earlier in the day, before he had decided to perform the division. Considerable numbers of worker and drone bees took off from the colony and clustered round the introduced brood comb at their original nest site. The queen was also seen to take off but not to land. She could have settled again on her own brood comb, but a cluster of bees had started to form on the introduced "zoora", a few cm from the brood comb; this suggested the queen had settled here and that some bees were clustering around her. Nāsr brushed this cluster off the "zoora" so that all the bees settled on the adjacent brood comb.

Nāsr then moved the colony originally in bole 20 to a *Citrus* tree (A) at the opposite end of his garden, 37m to the south, where he tied it to convenient branches (having first removed the comb of a colony which had recently absconded). He presumably moved this second "parent" colony to the tree once he thought a proportion of the workers, sufficient to form a viable colony, had joined the new, introduced comb; this may have been c. 40% of the worker population. Nāsr had thus used a section of brood comb from one colony and a portion of the worker population of a second colony to produce a third one.

(ii) Advantages and problems of division technique

Nāsr's method would appear to be far preferable to a method involving the division of the bees and brood of one comb only, as each colony would suffer only a partial setback in its own development. Observations were not possible over the following days to investigate whether the worker bees accepted the brood of this other colony; there were no initial signs of rejection and presumably Nāsr would not use this method if such a problem was acute. However, one slight drawback, which would apply also to one colony divided in two, was that during the day more workers from the second parent colony, now in the *Citrus* tree (A), returned to their original site in bole 20, strengthening the new colony but depleting their own. Observations by Free & Williams (1979) indicated that *florea* workers could remember a previous nest site and some of the bees in this case, presumably foragers in the main, were still orientated on bole 20. The final proportions of workers attached to the new and the parent colony were not known, but if imbalanced some re-adjustment might have been made by brushing bees from one colony to the other. Alternative solutions might be (i) to brush fewer bees onto the new colony in the first place or (ii) move the second parent colony further away, beyond the range from which workers are likely to return. This distance would need to be determined experimentally.

(iii) Queen rearing and introduction

In the case described above either the new colony or the second parent colony would be left without a queen. Though Nāsr was not aware of the biological processes involved he realized that a colony without a queen reared no brood and if a queen recently emerged from a queen cell was introduced, he said there would be brood after approximately one week. He did not know, either, that a virgin queen went on a mating flight and had never seen such an occurrence. He realized that the drones did not forage on flowers or for water, but had no idea they were involved with fertilizing the queen. He had seen them fly upwards towards the sun and believed they came back from such flights to feed the workers; so he had seen food exchange between workers and drones but thought food was passing in the opposite direction.

However, despite this misunderstanding of the reproductive biology of honeybees, his techniques for providing a new queen to a queenless colony appeared satisfactory. Nāsr's "re-queening" of one portion of the divided colony was not seen but he showed me the process he used. His new queens came from queen cells (which must be sealed, though he did not specify this) that are removed from a colony and stored in a large powdered milk tin for up to c. 5 days until the adults emerge. I saw queen cells stored in this way, including one which he said he would introduce to the queenless colony just created. It already had a hole exposing the queen's thorax, but it may have been nibbled by worker bees before the cell was put in the tin rather than the queen within her cell. Presumably the temperatures of early summer (mean c. 29°C at Seeb on the Batina and likely to be similar here) are sufficiently high to allow metamorphosis and eclosure away from the nest.

With the division described above Nāsr had in fact already removed 1 or more queen cells from each of the parent colonies before he had decided to perform the division for my edification. In normal circumstances he might have cut the brood comb, that formed the new colony, in such a way that it had one queen cell and left another queen cell with the colony which provided the adult bees. Nāsr would have been able to identify the colony without the queen by searching for it and from the absence of new brood and the construction of emergency queen cells. He would then leave the queen cell on the queenless colony and remove it from the queen-right one. Under the existing circumstances he would also have identified the queenless colony and then introduced to it the virgin queen, after it had emerged in the tin.

(iv) Swarm Control and Success of Divisions

The advantage of removing all queen cells from a colony and allowing queens to emerge elsewhere, rather than trying to catch virgin queens that have emerged _in situ_, is that swarming by the old queen (and new queens) is unlikely. If a colony is used in a division as well as having its queen cells removed, the depletion of the worker or brood complement should reduce the tendency of the colony to produce more queen cells. Thus Nāsr's practices of division and queen cell removal should achieve a degree of swarm control in addition to the production of extra colonies.

It was not possible to follow precisely the outcome of this particular division, but on Visit VII 3 months later (July), a strong colony was still present in bole 20 and had had, according to Nāsr, honey removed from it c. 1 month previously. Likewise there was a strong colony in palm tree I which had had honey removed c. 15 days ago. There was no colony in the *Citrus* tree. Therefore, assuming Nāsr had not moved either, the new colony and the one which had provided the brood comb had both stayed and produced honey. The second parent colony removed to the *Citrus* may (i) have absconded soon after the division with or without the virgin queen (ii) have stayed, produced honey and absconded when this was removed or (iii) have been moved to another site by Nāsr.

Discussions with Nāsr and examinations of his colonies indicated that he would sometimes divide the one colony into two. For instance on Visit IV colony D had had, by a horizontal cut right along its length, the bottom portion of its brood comb removed to make a new colony and the worker population had apparently been divided too. However, Nāsr said he would only divide his colonies in two and no more.

The overall success rate of Nāsr's techniques of "making increase" were not easy to assess. Amongst some pieces of brood comb I obtained from Nāsr on Visit VII, 12 looked as though they had been deserted recently and some of these (not counted), from their shape and his neat "fingermarks" along the comb edge, looked as though they were combs produced by divisions. Therefore, in one season, he must lose several colonies after divisions. However, his colony numbers rise from c. 20 to c. 30 between winter and summer (Figure 4.3) and even if a proportion of this increase is from gathering wild colonies his methods, though not perfect, must be quite effective and have the added advantage that those colonies involved are inhibited from swarming.

4.3 Prevention of absconding

Nāsr thought that a colony might abscond if (a) it had no brood (b) its workers clustered loosely and (c) when brushed away, the workers took wing, did not return quickly and hung loosely under the comb before re-forming a cluster. This description matches fairly well my observations of the behaviour of *florea* within a day or so of absconding.

One piece of action Nāsr took in summer (I observed this in July 1980) to prevent absconding was to sprinkle water on the ground underneath colonies, every day, presumably in the belief that the cooler, locally moist atmosphere created was beneficial. The efficacy of this was not assessed.

Nāsr said that once the queen took off he knew all the bees would go (however, large numbers of workers usually take off first, by which time it is obvious absconding is happening) and if he was present he would catch the queen in his hand. He said he would hold her in his hand close against the comb which the bees were leaving, till they returned; he indicated he would hold the comb in the air, amongst the departing bees, if necessary. A queen cage, as was used successfully on colony IC on 17.vii.80 at Khabura (Chapter VIII, p. 382),would probably be an easier way of achieving the same end, but it too depends on noticing that a colony is likely to abscond.

Nāsr also said that if he saw a swarm passing "over his head" he would leap up and catch the larger queen (which must be easier said than done); he would then hold the queen against a comb in a "zoora", if available, till the bees settle. No assessment was made of how often this treatment of absconding colonies and swarms took place, nor of its success.

4.4 Gathering a wild *Apis florea* colony

(i) Introduction

In addition to dividing his own colonies, Nāsr would also gather wild colonies from Zāhib and its vicinity to supplement his stocks; colonies would probably include ones of his own which had absconded. He also used to look for *florea* in the Jabal Madar (Chapter III); he would take the honey from these but probably did not bring the colonies back to his apiaries. I was never present when he did gather a wild colony from a tree, but he did enact and describe his method vividly enough for it to be recorded here.

(ii) Method

(a) The bees are brushed away (by hand) from all round the whole comb, so that they take wing. Recently emerged bees presumably remain on the brood comb.

(b) The twig, supporting the comb, is cut away from the tree.

(c) The brood and honeycomb are separated with a knife and, apart from a small piece that is cut away from the brood comb, are temporarily put to one side. The main portion of brood comb is put in his hat!

(d) The small piece of brood comb is impaled on the thorns of a twig, some honey smeared on it and the twig rested in the tree in the position where the colony had been.

(e) While the bees are settling round the piece of comb and twig, the honeycomb can be scraped from the twig to a container.

(f) When all the bees have settled, the twig and piece of comb round which they are clustered are picked up and very gently moved into a small sack which is then tied shut quickly so that no bees escape.

(g) The bees in the sack, the brood comb in his hat and the honey in the container are then taken, by donkey, to the new site.

(h) The brood comb is wedged into a "zoora" and is put in the required position, with some honey smeared on it.

(i) The sack is opened in front of the comb and all the bees rush out and eventually settle on the comb in the "zoora". The small piece of brood comb impaled on the twig is discarded.

(iii) Discussion

This procedure for gathering wild *florea* differs slightly from that of Humayd bn Sulayman of al-Ghubby (180km away, but several hours by road, and there would have been no contact between the two beekeepers) as described by Dutton & Free (1979). The initial brushing and scooping of handfuls of bees away from the comb is common to the two methods. However, Humayd wedges the brood comb into the "zoora" at the original site, allows the bees to settle on it and carries the comb and bees <u>together</u> to their new site. Nāsr takes the main piece of brood comb to the new site, <u>separately</u> from the bees. The advantage of Humayd's method is that the workers can envelop the brood as usual and may be able to provide food and thermoregulation. However, my own experience has shown that a brood comb, particularly one of soft, fresh wax, that has just been fixed into a "zoora" or frame, can easily tear loose if shaken in transit. The brood comb is thus damaged and when it falls away can crush and suffocate some of the adult bees (workers, drones and queen) also in the sack. This problem is avoided if the brood comb is not inserted in the "zoora" till at the new nest site, as with Nāsr's method. However, this way there may be some mortality of the brood if temperatures are extreme in transit. Gathering a colony at a time of day when the temperature is between 25° and 30°C and moving it quickly should avoid this; in these circumstances Nāsr's method should be favourable.

Moving a recently established colony, which has already secured its comb to a "zoora", by enclosing both comb and bees in the same sack, should also be satisfactory. Similarly, a small wild colony with insufficient honey for harvesting could be moved "intact", but it is probably advisable to separate the honey, brood comb and bees of a large colony before moving (Nāsr's method) if the honeycomb is likely to get damaged or the brood comb to tear away from the honeycomb under its own weight (cf colony FD on 27.v.80, Table 6.3).

Finally, at the beginning of such colony gathering operations, if the queen can be caught and caged, and then placed where it is desired that the bees should settle, the chances of the bees re-settling in the "wrong" position (at their original site or away from their new one) should be greatly reduced. Methods of enclosing a queen in a hive, to the same end, are considered in Chapter VIII.

PART II STATE OF *APIS FLOREA* COLONIES AT DIFFERENT SEASONS AT ZĀHIB

A. INTRODUCTION

The state of the colonies under Nāsr's management at the time of each visit will now be considered, taking the visits, not in strict chronological order, but re-arranging them according to the seasons as if they all occurred in the one year. On some of the visits, particularly the early ones, it was not possible to gain much more than qualitative information. No attempt was made to trace each colony from one visit to the next as his movement of colonies from garden to plain, during divisions etc, made this almost impossible without labelling of "zoora", and these would have been changed when honey was extracted. The stage of development of each colony at any one time is primarily a result of the natural environmental conditions of forage, temperature etc that prevailed in the previous months, but is also affected by Nāsr's treatment. His division of colonies mimics reproductive swarming and was done at times when colonies would have been reproducing anyway. Therefore, his *florea* were manipulated to reproduce in a similar way to wild ones, but had their honey taken from them at intervals which was in fact the fate of most colonies found by man in Oman. His local migration of the colonies, to a micro-environment considered more suitable, should have ameliorated the effect of honey-extraction and may also have matched the selection, by swarms, of different micro-environments at equivalent seasons. Finally, the effect of his removal of drone comb from some colonies was probably minor, but may have delayed swarming and promoted honey production. Therefore, overall, despite Nāsr's "interference", the development of his colonies should approximate to the natural development cycle of *florea* in this region of Oman.

B. OBSERVATIONS

1. Spring, Visit VI, 11.iv.80. Start of "samur" season

GARDEN SITE

1.1 Colony Number, Shape and Size

On this visit Nāsr had 12 colonies in "tree" sites, which became 13 after a division, and 17 colonies in boles, giving a total of

29 + 1 (Table 4.1). The mean dimensions of the colonies are given in Tables 4.6 and 4.7. These show that the colonies were significantly wider than they were tall (1.61 times) but there was no significant difference in the size, as measured by the Colony Area Index, of colonies kept in trees as opposed to those kept in boles.

1.2 Worker brood

All 29 colonies contained brood at one stage or another. Most (25) had both sealed and unsealed brood. 3 colonies (3, 7 and E) had only a little sealed brood and no eggs or larvae, having become queenless probably because they were recently involved in colony divisions; Nāsr, however, had requeened them and oviposition was likely to start again soon. A fourth colony (13) also had no eggs or larvae, only a little sealed worker brood, its queen having been taken to a new colony by Nāsr during the course of a colony division (possibly involving workers too, from this colony). Many (17) queen cells were present so this colony also would soon have had a new queen and brood rearing been continued.

Therefore all colonies with fertile queens were actively rearing worker brood and those without queens or with unfertilised ones had been rearing brood recently. The area of brood in each colony was not measured, but a large proportion of the brood comb was occupied in those colonies examined more closely, and some combs were still being extended (new wax); it appeared that most colonies were similarly strong and rearing comparable quantities of brood.

1.3 Drone comb and drones

6 colonies had drone comb with brood at various stages of development, including some with eggs only and others with emerging

Table 4.6 Dimensions in cm of *Apis florea* colonies in Nāsr's garden, Zāhib, 11.iv.80, with comparison of height and width

	Colony Height (cm)	Colony Width (cm)
Mean	16.59	26.75
Standard Error	0.60	1.07
n	28	28

F-test showed variances not equal

Fisher-Behrens d = 8.255, Significant, $p << .01$

Ratio, Mean Width/Mean Height is 1.61 : 1

Table 4.7 Colony Area Indices of *Apis florea* colonies in "boles" and in trees in Nāsr's garden, Zāhib, 11.iv.80. Measurements in cm^2

	C.A.I. (Height x Width) cm^2		
	Colonies in Boles	Colonies in Trees	Colonies in Both Sites
Mean	458	439.1	450.6
Standard Error	38.6	39.5	27.7
n	17	11	28

Differences between colonies in boles and trees not significant.

N.B. Bee Cover Index ≈ 100%; ie all combs were well covered by a curtain of bees and significant areas of comb were not exposed.

adults. Nāsr cut the drone comb away from one of these colonies (22) while my inspections were being made, pinching, with finger and thumb, the bottom of the damaged comb remaining to tidy up the edge. A large comb, from which the bees had absconded and which was left in a *Citrus* tree, also had an area of drone comb with empty cells from which drones had already emerged and sealed drone cells from which drones were still emerging. Two other colonies, E and H, showed signs of having had their drone comb removed recently in a similar fashion. Adult drones were seen on 17 of the colonies (only a few on 3 of these) which suggested that either (i) there is extensive drifting from colony to colony by the drones and/or (ii) Nāsr had already removed drone comb from a significant proportion of the colonies, having allowed at least some of the adults to emerge. He said he would cut drone comb away sometimes, but not always; his criteria for doing so were not clear. In fact the drone comb (85mm high x 90mm wide) on one of the 6 colonies (19) had been cut away from the worker brood comb and attached, by a thorn, directly beneath the "zoora" just to the right of the main brood comb. A few drones were still emerging, but most of the cells were empty and no more eggs had been laid in them. Nāsr said he had not yet divided the colony and had removed the drone comb so that the colony would make more worker comb below; he gave no reason for retaining the drone comb till the adults had emerged.

1.4 Queen cells

8 colonies had queen cells (from cups to sealed cells) as detailed in Table 4.8. Therefore, from those colonies which I inspected with Nāsr present, he removed some or all of the queen cells whenever they were found; he was not present when I saw the queen cup on colony K. Colony E also showed signs of queen cells having been removed.

Table 4.8 Queen cell status of 8 *Apis florea* colonies, kept by Nāsr in his garden at Zahib, Oman, on 11.iv.80

Where recorded:- S, Sealed US, Unsealed Em, Emergency Queen Cells

	In Boles				In Trees			
Colony Identifier	13	16	20	23	B	G	I	K
No. of Queen Cells	17 (S+US)	Several (US)	c.2	3 (Em)	6(US)	2(US)	1	1(US)
No. removed by Nāsr	Some	All	c.2	3	6	2	1	0

This colony had apparently lost its queen; it may therefore have produced queen cells, which Nāsr then removed when he released a new queen to the colony.

1.5 Colonies involved in division

Some of the colonies cited above had produced queen cells as a result of Nāsr's activities in dividing colonies, leaving part queenless. Nāsr's comments, confirmed by examination of the colonies for (i) shape of their comb, (ii) for recently cut edges, (iii) absence of honeycomb, and (iv) absence of queen and the presence of queen cells indicated that some colonies had fairly recently (apparently in the last week) been divided.

Three colonies (23, J, M) appeared to have been formed around sections of brood comb removed from other colonies, two of them taking the original queen and one having a new queen introduced. It was difficult to deduce whether or not in each case bees had been provided from a second "parent" colony to cluster round the "new" brood comb, as in the division already described (Part I, 4.2). However, it was concluded that one of the new colonies (J) may have been produced from two "parent" colonies in this way, while the other two new colonies may have been produced by taking both brood and bees from the one "parent" colony only.

In addition to the 3 new colonies mentioned above, two other colonies were used to create a third during the course of this Visit VI (as described in Part I, 4.2) and Nāsr stated that he would split yet another colony (G), a large one in a tree, in about two days' time. Therefore, if successful, 5 new colonies would have been produced in less than a month, ie c. 7 strong colonies being used to create 12, taking Nāsr's total number of colonies to 31.

1.6 Honey Production

11 colonies had had honey taken from them within, approximately, the last two weeks according to Nāsr's comments and my examinations of the combs (Table 4.9). It was thought that most of the colonies had had honey extracted from them when they were in the garden some time after being brought in from the "sayḥ", but Nāsr did not always give full details. At least one colony, however, had had its honey extracted in the sayḥ <u>before</u> being brought to the garden. A large, recently abandoned comb Nāsr had left in a *Citrus* tree, still with some brood emerging, had clearly had all its honey removed and this was likely to have been a major cause of their absconding. Nāsr did not say that any other colonies had absconded recently and it did not look as if any

Table 4.9 Honey extraction from and recovery of eleven *Apis florea* colonies in Nāsr's garden, Zāhib, 10.iv.80. G: Garden, S: Sayḥ, US: Unsealed Honey, - : absent, + : present

Colony Symbol	1	2	5	6	8	12	16	P	H	K	L	TOTALS (No.of colonies)
Location when honey taken	S?	G	S	G?	G	G	G?	G	G	G?	G?	
Time when honey taken (No. of days ago)	7	9	7	2	14	1	5	1	0	14	<7	
Time when brought from sayḥ (No. of days ago)	7	14	<7	?	?	?	?	?	?	?	?	
Presence of fresh honey again	US	-	-	-	US	-	US	-	-	-	-	3
Presence of new honeycomb	-	+	+	-	+	-	+	-	-	+	-	5

of the colonies listed in Table 4.9 would abscond; if this was the case, losing only one colony after honey extraction from 12 gave Nāsr a high success rate for *florea*.

Excluding those 11 colonies in Table 4.9, 10 colonies had sealed and/or unsealed honey (7 with unsealed honey only); 3 colonies had been created only recently from sections of brood comb, as detailed in the last section, and as might be expected had not yet built any proper honeycomb. The remaining 5 colonies in Nāsr's garden had no recorded honey.

"SAYḤ" (PLAINS SITE)

1.7 Status of *Apis florea*, Visit VI, 11.iv.80

In order to assess the status of *florea* outside the oases at this season and for Nāsr to check whether he had left any of his colonies behind in the "sayḥ", the trees and scrub at his apiary site near the broad wadi and around the small uninhabited date garden at Suḥayli were searched. It appeared that he obtained wild colonies from this latter site, 4km ESE of Zāhib (Figure 4.1) and sometimes kept a few colonies here.

No bees were found at either site nor were any drinking from either the small falaj running into Suḥayli (12.00h) or the water trough next to the well at his main "apiary" (13.15h); drinking bees would have been expected at this time of day if colonies had been in the vicinity. However, near Suḥayli there was the remains of a comb in an *Acacia tortilis* tree and Nāsr said he had removed 2 other wild colonies about 2 weeks ago; one from an *Acacia tortilis* tree, the other from a large *Prosopis cineraria*. These might otherwise still have been present. Nāsr said that any colonies which were still in the area would have gone to shady sites, away from the tops of trees where they would have been more exposed to the sun.

2. Mid-summer, Visit VII, 6.vii.80

GARDEN SITE

2.1 Colony Number, Shape and Size

The number of colonies in Nāsr's garden had dropped to 22 from the 30 (to 31) of the previous visit in April (Figures 4.2 and 4.3). 12 colonies were in boles (see Table 4.1 for distribution) and 10 were in "tree" sites including C, rested between two horizontal palm trunks, and Q, supported by one end of its "zoora" in the angle between 2 walls.

Table 4.10 shows that, though the colonies in trees are a little taller than those in boles, there is no significant difference in height or width of colonies kept in the two site types, and the ratio of Height/Width is 1.65 : 1, similar to the value of 1.61 : 1 in April, Visit VI.

Table 4.11 shows there is no significant difference between the size of colonies (C.A.I.) kept in boles or "trees", nor in the area of comb covered by bees as measured by the "Colony Cover Index". The area of comb covered by bees <u>in boles</u> ranged from 60% to 100%, but in trees the range was 80% to 100% cover, ie exposed comb, no longer used for brood rearing or honey storage was frequent at this time of year, whereas in April (Visit VI) all combs were effectively completely covered by bees. Furthermore, considering all nest sites, the Colony Area Index in July, 359.9cm^2 (Table 4.11) was significantly smaller than that in April, 450.6cm^2 (Table 4.7); $t_{48} = 2.456$, significant at $p < 0.02$. The difference is even greater if the areas of comb covered by bees are compared: 329.8cm^2 (Table 4.11) in July and 450.6cm^2 (Table 4.7) in April.

From Tables 4.6 and 4.10 it can be seen that this reduction in colony area between April and July has been brought about by reductions in both the height and widths of the colonies. This will have been

Table 4.10 Dimensions in cm of *Apis florea* colonies in Nāsr's garden at Zāhib, Oman, on 11.iv.80, comparing height and width of those colonies in boles with those colonies in "trees"

	Colony Height (cm)			Colony Width (cm)		
	In Boles	In "Trees"	Both Sites	In Boles	In "Trees"	Both Sites
Mean	13.92	15.25	14.50	23.88	24.0	23.93
Standard Error	.879	.506	.552	1.48	1.202	.965
n	13	10	23	13	10	23

Boles versus "Trees":- (1) Colony height, Fisher Behrens d = 1.311, $\Theta = 30^{\circ}$, not significant.
(2) Colony width, not significant

Colony Height versus Colony Width (Both Sites), significant, $P << .01$.
Ratio, Mean Width/Mean Height is 1.65 : 1

Table 4.11 Colony Area Indices and Cover Indices of *Apis florea* colonies in Nāsr's garden, Zāhib, 6.vii.80. Measurements in cm^2. For each colony, Colony Cover Index = C.A.I. x % Cover of Bees

	C.A.I. (Height x Width), cm^2			Colony Cover Index, cm^2		
	In Boles	In "Trees"	All Sites	In Boles	In "Trees"	All Sites
Mean	352.8	368.4	359.9	311.1	352.2	329.8
Standard Error	34.0	28.2	22.1	31.8	28.7	21.6
n	12	10	22	12	10	22

Colonies in Boles versus those in "Trees":- (1) C.A.I., NS
(2) Colony Cover Index, $t_{20} = 0.9438$, NS

the result of recent honey comb removal (p. 170). As the combs are widest at the honey storage area, both the height and widths of the colonies will have been reduced when their honey was cut away and it did not appear that the combs had been re-extended to any great degree since then.

2.2 Density of Bees in curtain

For most colonies the thickness of the protective curtain of bees covering the centre of the brood comb was estimated in terms of number of bees after making an opening in the curtain with a pencil; for some colonies the depth in mm of the curtain, from its surface to that of the brood comb, was also measured. In most cases, as bees in different layers overlapped and moved, it was not possible to specify an integral number of bees in the curtain, but an estimate of eg between 4 and 5 bees thick would be scored 4.5. No records were made on the presence, absence or size of the gap between the comb and the bees of the curtain that Lindauer (1957) observed at high temperatures.

For 19 colonies measured, the mean thickness of bees in the centre of the curtain was 3.4 bees (range 1.5 to 5.5 bees); the mean depth of the curtain, measured for 13 colonies, was 15.0mm (range 6.0 - 25.0mm). Considering the 12 colonies for which thickness was measured in terms of both number of bees and depth in mm it has been calculated that each bee occupied, on average, 3.99mm of the depth of the curtain.

The data suggested that for the colonies in the trees there were more bees in the curtain and that they were a little more tightly packed than in the colonies in the boles, maybe because there was more shade at the former sites. However, this slight difference may partly have been a consequence of the fact that more colonies in boles were measured in the late evening, while several of the "tree" colonies were measured in the early morning, when it was cooler; Lindauer (1957) observed that bees in the curtain became more tightly packed when it was cooler. More detailed examinations are needed to determine such diurnal changes in the composition of the bee curtain. Similar measurements were not made on visits at other times of the year and these would be necessary too if seasonal changes in the curtain are to be investigated.

2.3 Worker brood

All 22 colonies had brood at one or more stages (eggs, larvae, sealed pupae), 17 having sealed brood. Only one colony, 12, did not have eggs and this had only a little, old sealed brood and a recently emerged, apparently virgin queen. The bees were nervous during the inspection, readily taking wing, and with little food stored in the comb it appeared possible that this colony would abscond and not resume brood rearing. Excluding 12, the estimated brood area of the colonies ranged from almost 100% (colony 1 with which the bees from colony 6, previously kept at bole 1, had united) to 10%; most colonies had more than this bottom figure, 5 colonies having an estimated 80% of their brood comb containing brood.

2.4 Drone comb, drones, queen cells and colony divisions

No adult drones, nor drone brood, were recorded on any of the colonies. Even if Nāsr had still been removing drone comb, some drone cells and adult drones would have been expected at this date (6th July) if the colony reproductive season was still in progress.

Only colony 12 had any queen cells and these, 2 emergency and 1 normal queen cell, were all empty. Therefore, unless other colonies nearby in the oasis contained drones, the virgin queen on colony 12 would be unlikely to mate. The natural dwindling of drones at this time of year was probably accelerated by Nāsr's practice of removing drone comb from numbers of his colonies of *florea*. If colonies regularly become queenless at this season and virgin queens consequently need drones for fertilization, Nāsr might be advised to try and keep at least one colony stocked with drones for as long as possible.

Colony 12 may have become queenless after being involved in a division, but otherwise it did not appear that any colonies had been recently divided nor would it be advisable at this season without drones and with little forage.

2.5 Honey and pollen

Nāsr said he had taken honey from 4 of the colonies in the last 3 weeks, from one of them only 5 days ago, and honey must have been extracted from most of the others some time earlier. Though some colonies were difficult to categorize it was considered that c. 10 colonies had little or no fresh comb built above the "zoora" since honey removal, while c. 4 colonies had properly-formed but empty honeycombs and the remaining c. 8 colonies possessed a certain amount of filled honeycomb above the "zoora". Sealed honey was recorded in 13 out of the 22 colonies, as much as 80% of the honeycomb in a smaller colony (3), but in other colonies as little as 5% or only a few cells. In at least 9 colonies, some or all of the honey and/or nectar was stored in old brood comb below the "zoora", the honeycomb not having been expanded much since honey extraction. Fresh nectar was found in all 22 colonies, some of it quite dark. It may have been gathered from the exudate of drying fresh dates, "rutab", and/or from *Phyla nodiflora*; according to Nāsr, though *florea* forage on "rutab" what they gather is for their own consumption and does not yield surplus honey.

20 out of the 22 colonies were inspected for pollen. In only one colony was no pollen recorded, while 19 had some present; no colony had large quantities of pollen present and 5 had only a little. It was usually stored between brood and honey, but in 4 colonies it was scattered amongst the brood. Much of the pollen was pale brown in colour and may have been from *Phyla nodiflora*; one colony, Q, had a large proportion of orange-brown pollen which was identified as that of melon, *Cucumis melo*, from a pollen load of the same colour gathered by a returning forager (08.50h).

2.6 Absconding

There was direct evidence in terms of abandoned combs on "zoor" that 5 colonies had absconded in the last month or so; in addition colony 6 had united with colony 1. Nāsr said that only 4 or 5 colonies abscond per season but on the previous visit in April he had 30 colonies and had been planning to divide another, making 31. Therefore, including colony 6, at least 9 colonies must have abandoned their combs since mid-April and as mentioned on p. 156, 12 fairly fresh, abandoned combs (including ones involved in divisions) were given to me on this visit. So, combining these two figures, in the order of 30% of his maximum number of colonies had absconded soon after the end of the "samur" season, following divisions and honey removal. In September 1978 (Visit I), only 18 colonies were present in the garden so, if 1980 and 1978 are comparable years, the loss of a few more colonies during the rest of the 1980 summer might be expected and colony 12 would be the next to go.

"SAYḤ" (PLAINS SITE)

2.7 Status of *Apis florea,* Visit VII, 6.vii.80

Tree sites where Nāsr had previously kept or found bees, both near the uninhabited oasis of Suḥayla and at his "apiary" next to the broad wadi, were investigated. Nāsr claimed that *florea* colonies often returned to the same site, and near Suḥayla he searched in a particular *Acacia* tree from which he had earlier taken a (?wild) colony to his garden. It had absconded after he had taken the honey this season and he thought it might then have returned here, c. 4km away. No bees were however found in this tree or neighbouring trees, nor at a small, deserted well-garden nearby. Apparently there had been a colony in the well within the last month, but the bees must have absconded of their own accord or after the garden owner took any honey present.

Likewise no *florea* colonies were found in the trees at the wadi site and there was no water in the trough which, at other seasons, Nāsr kept full for the bees. At another well-garden closer (?1.5km) to Zāhib, where a few melons were still being grown, there had apparently been a colony of *florea* in a pile of *Acacia* branches and others in *Acacia* trees nearby. This was substantiated by the presence of split "zoor", one containing a brood comb which the bees had abandoned after their honey had been taken. Nāsr said he had taken honey from the colonies here during/at the end of the "samur" (*Acacia tortilis*) flowering season, but then left the combs and bees "for the bedū". Two or three of these colonies had still been present in the last few weeks, but all had now absconded. The causes of absconding were probably a combination of (i) unsuitable, exposed nest sites in *Acacia* trees with few leaves (ii) lack of honey and pollen stores (iii) lack of forage in the vicinity (iv) further predation by bedū.

It appeared therefore that nest sites in the plains outside the oases were most unsuitable at this hot time of year (July). However, Nāsr contradicted this by stating that the bees which absconded from his garden after the end of the "samur" season and also after the "rutab" season returned to the "sayḥ", and that he had followed one such colony to an *Acacia tortilis* tree. He claimed the advantage of such a site would be exposure to cooler breezes which would not reach colonies in his garden.

However, it may have been the case that most of his *florea* absconded to other gardens within the oasis. Detailed studies of marked colonies would be needed to elucidate this paradox. If most absconding *florea* really do settle in trees in the "sayḥ" at this time of year, maybe they select very well shaded sites (which are hard to find) that are close to oases and so have forage nearby.

3. Mid-summer. Visit IV, 30.vi.79

GARDEN SITE

3.1 Colony number, shape and size

Visit IV corresponds, in season, to Visit VII of 1980. Visit VII was discussed first, even though it was a few days later in the year than Visit IV, as it followed on directly from Visit VI in April 1980.

23 colonies were present in the garden (Table 4.1) with 18 of them in boles and 5 in trees; a few days later in the next year, 1980, there were 22 colonies with only 12 in boles but 10 in trees. The overall numbers in mid-summer 1979 and 1980 were therefore effectively the same, but the distribution rather different.

Table 4.12 Dimensions in cm of *Apis florea* colonies in Nāsr's garden, Zāhib, Oman on 30.vi.79

	Colony Height (cm)	Colony Width (cm)
Mean	13.91	25.63
Standard Error	.565	1.145
n	23	23

Ratio, Mean Width/Mean Height is 1.84 : 1

Table 4.13 Colony Area Indices (C.A.I.) and Colony Cover Indices (C.C.I.) of *Apis florea* colonies in Nāsr's garden, Zāhib, 30.vi.79. Measurements in cm^2. For each colony, Colony Cover Index = C.A.I. x % Cover of Bees

	C.A.I. (Height x Width) cm^2			C.C.I. cm^2		
	In Boles	In "Trees"	All Sites	In Boles	In "Trees"	All Sites
Mean	355.4	363.4	357.2	319.0	348.5	325.4
Standard Error	27.4	41.8	22.9	25.0	42.8	21.5
n	18	5	23	18	5	23

The standard errors in Table 4.12 indicate that the width of the colonies was significantly greater than their height, ratio 1.84:1. Comparing the mean 1979 colony dimensions with those in 1980 (Table 4.10) at the same season, the mean heights are almost the same, 13.91cm and 14.50cm respectively; the mean 1979 width, 25.63cm is a little greater than the mean 1980 width, 23.93cm, but the difference is not significant, $t_{44} = 1.135$.

The standard errors in Table 4.13 indicate that there were no significant differences between the Comb Area Indices and Colony Cover Indices of colonies in boles and in trees; this was the case on other visits too. As with the 1980 Summer Visit, the C.A.I. on this summer 1979 Visit, 357.2cm^2, was significantly smaller than that, 450.6cm^2, on Visit VI in April 1980 ($t_{49} = 2.527$, Significant $P < 0.02$).

In fact, for the summers of 1979 and 1980, the respective C.A.I.s (357.2cm^2 and 359.9cm^2) and C.C.I.s (325.4cm^2 and 329.8cm^2) are almost exactly the same. Therefore, though the 1979 and 1980 summer combs are a little different in shape, the mean size reached by a colony under Nāsr's management regime appeared to be most consistent at this time of year. This evidence suggested that Nāsr could remove, at the right times, the appropriate quantity of honey from his colonies, according to their health and the forage available, in order to maintain colony size at a satisfactory level. Taking too much honey in a poor season could lead to extinction of a colony and allowing colonies to develop too much in a rainy year could lead to swarming.

3.2 Density of bees in curtain

This was not measured accurately as on Visit VII, but it was estimated that the typical density of the curtain was 4 bees thick, ranging from a minimum of 2 to a maximum of 6. These values were of the same order as the values on Visit VII (mean 3.4, range 1.5 to 5.5), suggesting that they were typical for this time of year.

3.3 Worker brood

Only 8 colonies were examined at all closely for this, by brushing away part of the curtain of bees. All 8 had sealed brood (pupae) but only 2 were estimated to have had a large area of it.

One of the weaker colonies examined, though it had brood, had no eggs at the edge of the comb; their presence would have indicated a strong, growing colony. Therefore, though brood rearing appeared to be continuing in June/July in most of the colonies, there was no rapid growth.

3.4 Drone comb, drones and queen cells

Drone comb was only recorded on 2 colonies (9 and A) and it was not protected by bees on either of these 2 colonies. Though not every colony was searched thoroughly round the periphery, drone comb was not apparent on any of the other colonies. The sizes (height x width) of the 2 pieces of drone comb were 3.5 x 7.0cm (24.50cm^2) and 3.5 x 9.0cm (31.50cm^2), being 4.9% and 9.1% of the area, respectively, of the rest of their combs. The first (9) piece of drone comb contained one egg, the second (A) was completely empty.

Adult drones were only recorded on one colony (13) and then only 1 or 2 were visible at a time.

Queen cells were not recorded on any of the colonies and it is unlikely that any went unnoticed as their presence is usually obvious at the bottom of a colony. It appeared that Nāsr had cut away the drone comb and queen cells from nearly all the colonies.

3.5 Honey and pollen

All the colonies showed signs of honey having been harvested recently ie of having had honeycomb removed from above the brood comb. Some (11) colonies still had empty brood comb protruding to a maximum height of 30mm above the "zoora" following honey harvesting, but little had been reconstructed with fresh wax.

Sealed honey was recorded on only one colony and that was below the "zoora"; a little unsealed honey was present on some, probably most, of the colonies.

Nāsr said he had harvested the honey 2 months ago (beginning of May), but I expect harvesting had continued for 2 weeks or so on either side of this. He said he had recently sold 18 squash bottles of honey for approximately 300 Rials Omani, ie 16-17 RO/bottle. Whether this represented his total harvest was not clear. He claimed that 2 to 3 bottles of honey could be obtained from a single colony during the *Acacia tortilis* season. This is probably the yield of the best rather than of average colonies but not an exaggeration as the lengths of wax left in the centre of 3 "zoor" from which he had harvested honey measured 42, 48 and 59cm. This would have been the maximum widths of the colonies just prior to honey extraction; the last value being double the present mean width, indicates a very large colony.

Pollen stores were not investigated.

3.6 Absconding

Abandoned combs and Nāsr's comments indicated that a minimum of 6 colonies had absconded since honey harvesting, including 2 from the one bole (10) - Nāsr having replaced the first colony to abscond, with another which did the same! They cannot all have absconded immediately after honey removal as one colony had absconded on 29.vi.79 and another on 30.vi.79.

3.7 Overall assessment

A subjective assessment (based on size, density of bees etc) of the condition of 14 colonies chosen at random was made in the field:-

	Strong	Quite Strong	Small but Healthy	Weak
No. of colonies	2	5	3	4

Therefore, despite the scarcity of flowers, Nāsr had succeeded in maintaining most of his colonies that had not absconded in a satisfactory state. Figures for autumn visits (Figures 4.2 and 3) indicate that a few more colonies might abscond but sufficient healthy stock would be left for the "sidr" (*Ziziphus spina-christi*) honey flow in autumn. The state of the colonies, with virtually no drones, only a little honey remaining and so on, thus corresponds very closely to that found in 1980 a few days later in the year.

"SAYḤ" (PLAINS SITE)

3.8 Status of *Apis florea*, Visit IV, 30.vi.79

Only one colony was present at the apiary site near the wadi and this was in an "artificial cave" of stones, similar to that described by Dutton & Free (1979); it was probably the same site, under a small, low growing *Maerua crassifolia* tree, as was recorded on Visit II. According to Nāsr the "cave" entrance was orientated so that it faced into the prevailing wind (probably WSW but not recorded) to keep the colony cool, and the "zoora" was put at right angles to this, so that one of the brood surfaces of the comb was exposed to the entrance. A small opening had been left at the back of the "cave" to allow air to flow through it.

The condition of this colony was not recorded. Its presence serves to indicate that *florea* could be left in the "sayḥ" during summer - giving support to Nāsr's claim (Visit VII) that colonies absconding from his garden went to the "sayḥ" - though with what chance of survival and for how long were not known.

4. Early Autumn. Visit I, 11.ix.78. Before "Sidr" Season

Apart from making a count of the number of colonies in the garden only a little detailed information was gathered on this first visit. 18 colonies were observed, 17 in "boles" and just 1 in a *Citrus* tree (not being familiar with the garden it was possible, but unlikely, that 1 or 2 colonies in other trees might have been missed). The condition of 5 colonies examined more closely was as follows:-

(a) One was very weak, probably without brood, and Nāsr reckoned it would abscond.

(b) A second had adult drones, drone comb and at least two queen cells (the drone and queen cells were probably sealed but full details were not recorded). The queen cells were not emergency ones and Nāsr explained how he would take the queen from one of them to another colony without a queen, which I understood had been created by division from this colony with queen cells. Prior to the division this parent colony must have been quite strong.

(c) A third colony that had now been re-queened Nāsr said had lost its queen to a pest, probably a robber fly (Asilidae). This explanation sounded rather unlikely as the robber flies in Oman were not observed to take bees from within the protective curtain of *florea* colonies. A queen might only fall prey if forced to take flight during an inspection, or on a mating flight.

(d) A fourth colony was medium-sized and considered healthy, having brood, though no adult drones or drone or queen cells. Nāsr said drones would appear after a month, during the "sidr" season, when there would be more honey.

(e) A fifth colony was considered to be strong, and returning foragers were dancing.

A count of abandoned combs in "boles" indicated that 4 colonies must have absconded in the last month or so, including one which had apparently gone, 5 days ago, to an *Acacia tortilis* tree in the "sayḥ". No visit was made to the apiary site in the "sayḥ" but Nāsr did not mention that any other colonies of *florea* were present there at the time.

The state and size of most colonies, therefore, appeared in general to be similar to that of mid-summer (July) with brood rearing occurring, but not at a high level. Little or no surplus honey had been stored. One colony had been divided, another was dwindling and some had recently absconded, suggesting that Nāsr's colonies steadily decline in number from a peak of just over 30 at the end of the "samur" season to just under 20 at the beginning of the "sidr" season.

5. Late Autumn. Visit II, 1.xi.78. End of "Sidr" Season

There were no *florea* colonies in the garden on this visit at the end of the "sidr" season, all having been moved to the "sayḥ" approximately 15 days previously. The greatest temperature drop (see Appendix II) occurs in October, so moving the bees from the cooler garden sites to the warmer tree sites in the middle of this month appeared to be appropriate. 14 colonies were seen at the wadi apiary (details of siting of colonies given on p. 145) and Nāsr said there were 4 others he had moved near to the uninhabited oasis Suḥayli.

No detailed inspections were made (to avoid disturbance and because of the inaccessibility of many colonies in the tops of thorny *Acacia* trees) but most colonies, though of various sizes, appeared to be relatively healthy. With thick protective curtains of bees over the brood combs, it was assumed that most were still rearing brood; yellow pollen, probably of *Ziziphus spina-christi*, was being gathered (15.45h, 1.xi.78) by at least one colony, and this also suggested brood rearing.

Water was being collected from the nearby trough (15.15-16.30h) indicating cooling of the colonies and their brood and/or dilution of honey for consumption. The honeycombs of two colonies were inspected; one contained a fair quantity of honey, the other was rather empty. Nāsr said he had removed "sidr" honey from many of the colonies (probably in the last 3 weeks) and reckoned he had obtained 20 bottles.

Drones were definitely not present on 3 colonies (though they had apparently been present on one of them, recently) but were recorded on a fourth, large colony. At least 11 queen cells had been removed from this colony by Nāsr, and dropped on the ground within the last 2 days; this, presumably, was to prevent swarming.

One of the colonies belonged to a friend of Nāsr and I understood Nāsr had removed the honey and brought it here that day, probably from a wild nest site in the "sayḥ" or the man's garden.

Just before the "sidr" season Nāsr had 18 colonies, including one about to abscond; on this visit he had 17 colonies, plus the one belonging to a friend, so if more colonies had absconded in recent weeks he had made good any loss. It was probable, however, that no further colonies had absconded during the "sidr" season and the 17 colonies that remained had produced sufficient quantities of honey for extraction, and at least one reached a swarming stage. The colonies had been moved from garden to plains in the "sidr" season, but it was likely that most of the honey was removed once the bees were in their "sayḥ" site, since Nāsr claimed it was from here that they foraged on *Ziziphus* trees near Suḥayli and also in the village of Shārqi.

6. Winter. Visit III, 14.xii.78

6.1 *Apis florea* at the garden site

One colony was being kept in the garden, in "bole" 19, on this visit. It measured approximately 18cm high by 17cm wide and apparently came from a wild colony Nāsr had found in an *Acacia tortilis* tree in the "sayḥ" on the previous day. Photographs indicated the honeycomb had been removed when the colony was gathered, but a curtain of bees completely enveloped the remaining comb which was not examined. Foragers were gathering pollen, including that of *Euphorbia heterophylla*, so brood rearing was probably being continued.

6.2 Numbers of colonies in "sayḥ"

18 colonies were present, all at the wadi site. Nāsr did not mention any being near the Suḥayli oasis; the 4 colonies that had been at Suḥayli had probably been moved to join the 14 that were at the wadi site in November. The details of the trees in which Nāsr put the colonies are given on p. 145.

6.3 Brood rearing and colony strength, "sayḥ"

Only one large colony was inspected for brood and quite a large proportion of its brood comb had sealed cells; a closer look for eggs and larvae was not made but they were presumed to be present. A subjective assessment of the size/condition of all but one of the colonies was made as follows:

	Large, Strong	Medium, Quite Healthy	Small, Healthy	Small, Weak
No. of colonies	2	4	9	2

6.4 Drones, "sayḥ"

Drones, from a few to large numbers, were seen on 5 colonies and were definitely absent from 3; they were not recorded from the 10 other colonies, but inspections were not thorough enough to state categorically their absence. Those drones present would be the remnant of those produced by colonies which had grown strong during the "sidr" season.

6.5 Honey

5 colonies were examined and their stores assessed as follows:-

No Honey	Very Little Honey	Small Quantity of Honey
1	3	1

From one of the large colonies, which had drones present, Nāsr said he had harvested honey three times during the "sidr" season that had finished about one month earlier. He obtained 3 "squash bottles" of honey for which he received 12 Rials Omani each. From another colony he said he had harvested honey twice. Altogether Nāsr reckoned he had obtained 20 bottles of honey from the "sidr" this year, which is in the order of 1 bottle (approximately 1 kilo)/colony.

6.6 Sources of forage and location of colonies

Foraging activity was observed on 16 of the 18 colonies between 11.30 and 13.30h on 14.xii.78; the remaining 2 colonies were not sufficiently accessible for such activity to be seen. A bright red/orange pollen, identified as *Euphorbia heterophylla* was being gathered by a minimum of 9 of the colonies, and a pale buff pollen (possibly *Vernonia cinerea*) was also being gathered by one of these 9 colonies. Workers were gathering nectar (not pollen which is in the form of pollinia) from *Leptadenia pyrotechnica* and this and/or water was probably the forage being gathered by bees without pollen loads that were observed on 5 colonies. On 5 other colonies, only unspecified foraging activity could be seen.

Therefore, in December, these colonies in the "sayḥ" were not on the whole large, nor did they have significant quantities of honey left to them after the "sidr" season but their foraging activity did suggest most would be rearing brood. Apart from the few, scattered bushes of *Leptadenia pyrotechnica* there were virtually no flowers available to the bees in the "sayḥ" and most forage appeared to be coming from weeds in the date gardens. This suggested that the advantage (if any) of the "sayḥ" at this time of year was the greater insolation and thus warming of the *florea* colonies, reducing the energy consumption required for thermoregulation.

However, *Zygophyllum coccineum* ("tharmad"), an abundant succulent shrublet in the plains near Zāhib, was, according to Nāsr, a source of forage to *florea* and about to flower. *Z. coccineum* might, therefore, be a critical source of forage to *florea* in the plains, till the *Citrus* trees are in flower, when Nāsr said he would take the bees back to his garden. This would be in 1-2 months' time towards the end of January; the bees would then be in the garden just before the temperature rises rapidly in March and April.

7. Winter. Visit V, 11.xii.79

7.1 Introduction

This 1979 visit was made at virtually the same time of year as Visit III in 1978. It was primarily to explore the Jabal Madar (see Chapter III where Nāsr sometimes looked for wild *florea* but a brief assessment of his kept colonies was made; their siting was rather different from 1978, with some colonies at the wadi site, but also several in his garden.

7.2 *Apis florea* at the garden site

c. 7 colonies were present altogether, 3 in boles in the north wall and 3 in the west wall; 1 colony might have been present in the south wall, but this wall was not checked properly, and there were none in the trees. There were two recently abandoned combs in the north wall and Nāsr thought one of the colonies still present might soon abscond too, as it had no brood and its honey was in old drone cells, not new comb. Nāsr attributed the absconding to it being too cold for the colonies in this wall for, though facing south, the "boles" were well shaded by trees. However, another of the colonies in the north wall was quite large, measuring c. 18cm high by 29cm wide, and was completely enveloped by a thick curtain of bees; it almost certainly was rearing brood and though its honeycomb was only drawn out a little,more honey had been stored since the last harvest a little over one month ago at the end of the "sidr" season. This colony was not likely to abscond and, despite saying the north wall was too cold, Nāsr was still providing the colony with some shade from date-palm logs.

As is also discussed in Chapter VI, the sizes of the colonies might be the explanation to this paradox. In winter, in a cool micro-environment, colonies with a large population of bees and some honey may be able to generate sufficient heat for brood rearing, while weak colonies may not, particularly when forage is scarce. Therefore, smaller colonies in the garden may abscond to a nest site with a more favourable micro-environment, such as a tree in the "sayḥ". Consistent with this explanation was the fact that Nāsr had tracked (by following workers collecting wax from the old comb) one of his colonies, that had absconded about 5 days ago, to an *Acacia tortilis* tree c. 500m to the east of his garden. It was a fairly dense, young tree c. 2.5m high and the colony had settled near its centre but towards the E side, where it was fairly well shaded but might receive some morning sunshine.

Of the colonies in the western wall, only the comb of one was inspected. It had no sealed brood, only eggs, so might have been on the point of brood rearing; alternatively the queen may have been ovipositing without the workers tending the eggs. Pollen (*Euphorbia heterophylla* and possibly *Vernonia cinerea*) was being gathered by foragers of the other 2 colonies, suggesting brood rearing was in progress or imminent.

7.3 *Apis florea* in "sayḥ"

Not all the colonies at the wadi site were seen, but there were more than in the garden and it was estimated that 9 were present in *Acacia tortilis* trees (in addition to the one which had absconded from the garden) and 1 was in the centre of a *Leptadenia pyrotechnica* bush. Only this last colony was inspected; it was in a very shady position and was rearing brood, but its honeycomb had not been drawn out since honey had last been removed from it (maybe 1 month ago).

7.4 Nāsr's "migration" of colonies, 1979-1980

On this visit,11.xii.79, Nāsr said he would, within a few days (ie mid to late December), move from his garden to sites in the "sayḥ" any colonies that he thought might abscond, such as the broodless colony in the N wall. His observations that colonies without brood, and on which some bees hung loosely below the comb and did not re-cluster quickly when brushed aside, were likely to abscond, were consistent with my own observations. However, the colony which had already absconded to the *Acacia* tree he said he would bring back to the garden fairly soon, maybe in 10 days' time which seemed premature. Re-considering this Nāsr said he might move the colony when the male date-palms flowered; this would be more than 45 days later in February at a similar time to *Citrus* flowering which is the time he had said he would move his bees, from the "sayḥ" to the garden the previous year. Indeed, when Nāsr visited Khabura on 22.i.80 he told me half his colonies were in the "sayḥ" and half in the garden; the bees were foraging on *Citrus* and already storing some honey. So there appeared to be no specific date for moving all colonies from "sayḥ" to gardens, but a general period from mid-January to March.

There was similar confusion concerning the time Nāsr had moved his bees from the garden to the "sayḥ" in autumn 1979. On 11.xii.79 he said he had moved them there 20 days earlier, but this would have been the middle of November, after the end of the main *Ziziphus* flowering season; in 1978 the bees had been moved from the garden to the "sayḥ" in mid-October. Whether the colonies were moved to the "sayḥ" at different times in the 2 years or whether Nāsr underestimated the number of days which had elapsed since he had moved them in 1979 is discussed below.

7.5 "Migration" of colonies to "sayḥ"; differences between 1978 and 1979

The main difference between the December visits of 1978 and 1979 was that there was only one colony in the garden in 1978 but about 7 in 1979. In 1978 Nāsr had been concerned about aerial applications of insecticides to the oases, which apparently had killed some of his bees 2 years earlier, so that autumn he may have been more wary of keeping too many colonies in his garden unnecessarily, so had kept nearly all colonies in the "sayḥ". As "sidr", *Ziziphus spina-christi* trees, grew both at the oases of Zāhib and Shārqi and at the wadi site and nearby Suḥayli, Nāsr's *florea* should produce some "sidr" honey, whether kept in his garden or the plains. Experience may have taught Nāsr that one site was rather better than the other, in general, but if an autumn was particularly hot, or plants were not flowering well, or certain colonies in the garden were about to abscond, or pesticide applications were likely etc., the timing of "migration" of all or some of the colonies could be adjusted. Therefore Nāsr may have moved his bees to the "sayḥ" in mid-October both in 1978 and 1979 (and in error told me it was mid-November in 1979), but the alternative is that he did in fact move the bees to the "sayḥ" in 1979, in mid-November, a month later than in 1978. With 1979 being the second dry year in succession, the flowering of *Ziziphus spina-christi* in the oases may have been better than that in the "sayḥ", so with little danger of pesticide applications in the gardens some colonies were kept there longer.

Therefore, whichever alternative was correct, the differences between the garden and "sayḥ" apiaries in terms of either microclimate or forage availability (or both) may have influenced Nāsr's timing of colony "migration". Furthermore, Nāsr did not have to move all the colonies during one day or week and his timing of "migration" for individual colonies may have been influenced by their condition or their location in particularly favourable nest sites.

C. DISCUSSION

1. Overall cycle of *Apis florea*

The principal events in the developmental cycle of the managed *florea* colonies at Zahib are given in Table 4.14. The features detailed for months when no visits were made are based on (a) interpolation of observed colony development at Zāhib, (b) knowledge of colony development

(Chapter VI) and plant flowering times (Chapter VII), at other localities in Oman and (c) Nāsr's answers to questions on this subject. The actual number of colonies kept fluctuated and was determined by the balance between those colonies lost through absconding and those gained from divisions and the gathering of wild colonies. The overall numbers and their distribution between the garden and the "sayḥ" at different times of year have already been presented (Figures 4.2 and 4.3) and indicate that the maximum occurs in April/May and the minimum in September. Crucial points in the cycle are considered below.

2. Importance of sources of forage prior to *Acacia tortilis*

Though most honey is extracted during the flowering of the "samur" tree, *Acacia tortilis*, and much of it is probably derived from this source, the greatest increase in colony numbers (from approximately 18 to 30) has taken place before the "samur" starts to flower. Similarly, all colonies with fertile queens were strong and rearing brood in early April and several colonies had drone and/or queen cells, 17 having adult drones (see Part II B. 1). Therefore, plants other than *Acacia tortilis* must be providing quantities of nectar and pollen sufficient for growth and reproduction, though not for maximal honey production, at this time of year.

When the honeycomb was removed from colony H on 10.iv.80 (Part I, 4.1) a band of nearly full pollen cells was exposed beneath the honeycomb. Over 80% of this was yellow to dull orange in colour and microscopic analysis showed it to be *Prosopis cineraria*; also identified were smaller quantities of *Euphorbia heterophylla, Pimpinella* sp. and *Acacia* sp. (*ehrenbergiana* or *tortilis*). Therefore, these plants and other known sources of forage that flower in February, March and April

Table 4.14 Summary of annual cycle of *Apis florea* under management of Nāsr Ahmad at Zāhib, Sultanate of Oman

(December) January	Cool. Most colonies in "sayḥ"; strong colonies rearing brood but little growth, no honey surplus. Forage from weeds and desert shrubs.
February	Cool. Some colonies now in garden as tree crops (*Citrus* spp., *Phoenix dactylifera, Mangifera indica*) and annuals flower. Brood rearing starts to increase.
March	Warm. Remaining colonies moved to garden. Development accelerating, particularly if winter rain has increased flowering of annuals and shrubs.
Early April	Becoming hot. *Prosopis cineraria* starts flowering, colony growth continues. Drone and queen cells produced, some removed. Larger colonies divided; surplus honey being stored and extracted from some colonies.
Mid-April to Mid-May	Hot. *Acacia tortilis* flowering. Maximum "samur" honey production and harvesting. Swarm control still required.
Mid-May to Late June	Hot. Remaining honey extracted from a few colonies. Little forage except for garden weeds, melons etc. Several colonies abscond, others continue brood rearing, but negligible growth. Most remaining drone and queen cells removed; drones dwindle.
July, August Early September	Hot. Forage still scarce. Sugary exudate of fresh dates available. A few more colonies abscond, brood rearing reduced.
Late September October	Temperature dropping. *Ziziphus spina-christi* flowering. Most colonies moved to the "sayḥ". Active brood rearing; some drone and queen production. "Sidr" honey harvested.
November December	Cool. *Ziziphus* flowers finishing, brood rearing reduced. Forage from *Leptadenia pyrotechnica, Euphorbia heterophylla* etc. Some colonies abscond from garden to "sayḥ".

(see Tables 4.4 and 5) must be critical to the successful build-up of *florea* before the "samur" season and are probably as important as *Acacia tortilis* if "samur" honey is to be produced. The flowers of *Citrus* sp. and of various weeds (eg *Phyla nodiflora*) and herbs (eg *Ocimum* sp.), being irrigated, should be available every year in the oases as should the flowers of the deep-rooted *Prosopis cineraria* (whether in oasis or plain) but abundant flowering of desert annuals and shrubs in spring is dependent on winter rainfall. Without winter rain, but with forage from the oasis flora, colony growth and reproduction will proceed in spring; however, both should be enhanced after heavy rainfall so that more and larger colonies are able to exploit the *Acacia* honey flow.

3. Absconding after "Samur" Honey Flow

It appears that Nāsr loses in the order of 40% (12 out of 30) of his maximum number of colonies through absconding during the summer months after extraction of the "samur" honey. Though it may be the stimulus in some cases, the disturbance associated with extracting the honey is probably not the major factor that induces absconding, as Nāsr claimed he could extract honey 2 or 3 times in a season from a strong colony. The main cause of absconding at this season is likely to be a combination of (i) scarcity of forage when colony stores have been depleted and (ii) sub-optimal nest sites at the high temperatures prevailing in the summer months at the end of the "samur" honey flow (monthly mean temperatures for June and July at Seeb, on the coast, are approximately 35°C and are possibly higher at locations like Zāhib in the interior of Oman - see Appendix II). This absconding appears then to be equivalent to the "resource-related" or "seasonal" absconding described by Winston *et al* (1979) for Africanized *Apis mellifera* in South America. In Oman, predation of *florea* colonies (by Nāsr in this case), though it may be a contributory factor and the "final straw", in some cases does not then appear to be the fundamental reason for absconding. This conclusion is different from that reached by Seeley *et al* (1982) and Seeley (1983) based on studies of *florea* in Thailand and discussed in Chapter II; they deduced that it was predation that caused frequent shifts in nest site, and did not consider environmental conditions such as temperature and forage availability to be as important.

With the number of colonies dropping from about 30 to 22 by the beginning of July, in the order of 8 colonies (c. 27%) must abscond within 1½ months of the end of the "samur" honey flow. 4 or 5 more (c. 15%) might be expected to abscond in the remaining 2½ months or so before the start of "sidr" flowering. It is possible that those colonies which had had nearly all their honey taken right at the end of the "samur" honey flow absconded soon afterwards, while those that had had honey taken earlier and been able to replenish their honey and pollen stores, or had been left a sufficient amount, stayed. The few colonies in which these stores subsequently became depleted, particularly if they were in an unfavourable nest site, might be the ones to abscond later in the summer.

The shortage of forage in summer when temperatures are very high does therefore appear to play a critical role in the cycle of *florea* in Oman. In this species of honeybee with a small, exposed nest, absconding is evidently a good adaptation to an environment with a patchy distribution of forage and with a wide range of temperatures where one nest site may not be suitable for all seasons.

If absconding is to be reduced in a bee-keeping situation such as Nāsr's, it would be worthwhile to determine whether or not leaving a portion of a colony's honey, or extracting the honey early enough for the comb to be re-built and filled, does induce the bees to stay longer. This could best be done experimentally at a well-organized apiary such as Nāsr's. The balance between reducing the "samur" honey harvest (eg by taking honey once not twice from strong colonies) and increasing the number of colonies held at the beginning of the "sidr" season would have to be established. Leaving some honey for a colony might be easier if a method of inducing *florea* to re-use comb in a frame, from which honey can be extracted, can be found (Chapter VIII). Also honey yields might not be reduced at all this way as *Acacia* nectar would no longer be diverted to comb building after each honey extraction.

Finally, encouraging the cultivation of summer-flowering crops such as melons and lucerne, or moving bees near to such crops, might help to supplement the little forage that is available from weeds (*Phyla nodiflora, Portulaca oleracea*) and fresh dates, "rutab" (Chapter VII). Feeding sugar syrup to the bees would be an additional help, as long as the bees did not store surplus sugar just prior to the start of the "sidr" season as, with only one honeycomb, sugar and nectar honey would become mixed.

4. "Sidr" (*Ziziphus spina-christi*) season; end of September - beginning of November

Apart from "sidr" itself, very few plants are in flower either before or during this season (Tables 4.4 and 5 and Chapter VII). Nāsr's *florea*, whether in the gardens or the "sayḥ", were primarily dependent on the nectar and pollen of the "sidr" for their own growth from fairly weak colonies in September, with little brood or stores, to strong colonies by October/November that could gather surplus honey. Thus the absence of alternative sources of forage must be the main reason that there was little or no build-up in colony strength or numbers before the "sidr" season as there was before the "samur" season. Similarly, though some stronger colonies might reach a swarming stage with drone and queen cell production, the flowering season appeared to be too short for Nāsr to exploit the limited potential for dividing colonies and replenishing his stocks. Instead of producing a few extra small colonies which might not survive the following 2 or 3 cooler months with limited forage, he concentrated on honey production. This would appear to be the best strategy in the circumstances.

5. Nāsr's "migration" of colonies : for microclimate or forage?

Nāsr's movement of colonies from garden to "sayḥ" in the autumn and the possibility that its timing and the numbers of colonies involved might vary according to circumstances, such as pesticide application or differences in "sidr" flowering intensity between the two sites, has already been considered (Part II, B. 7.5). It appeared that some colonies were usually kept in the garden and some in the "sayḥ" in winter and early spring, and that a certain number of *florea* colonies were left in the "sayḥ" during the spring flowering of *Citrus* sp. and of garden weeds; some of them were still present there at the end of March (p. 165). However, except for the one colony in the "sayḥ" in July 1979 (p. 178), all colonies were brought into the garden before the "samur" started to flower in the "sayḥ". They were kept there throughout its flowering season and until the end of summer.

Therefore, in winter when plants such as *Euphorbia heterophylla* were being exploited (p. 149) and in spring when date-palm, *Citrus* spp. etc were important, a number of colonies were kept in the "sayḥ" away from their main sources of forage. Similarly, when the main source of forage was "samur", *Acacia tortilis*, all the bees were kept in the oasis, not in the "sayḥ". Assuming that Nāsr's experience had taught him that this strategy was successful (and it would be of interest to compare the initial state and subsequent development of those colonies kept in the "sayḥ" in spring with those moved to the garden), this evidence suggests that the primary advantage of moving the colonies was to provide them with nest sites that offered a favourable micro-climate in a particular season; the shady garden in summer, and in winter the "sayḥ" with greater insolation, but also cooling breezes. Meteorological measurements are needed to determine the magnitude of the differences in conditions at the two sites.

Nāsr did not appear to be entirely aware of the fact that when the bees were at his wadi site some were foraging in the oases; he thought that the bright orange/red pollen from the weed *Euphorbia heterophylla* was from the desert shrub *Leptadenia pyrotechnica* which the bees were using at the time, but which produces only tiny, yellow pollinia. However, he was keen to establish a garden/farm around the well at his wadi site and the cultivation of flowering crops (and weeds!) could only help the bees here, as long as trees and shrubs useful to them were not grubbed up.

6. Shape of combs under Nāsr's management

Table 6.2 and the associated text in Chapter VI show that colonies under Nāsr's management were considerably wider (1.6 to 1.8 times) than they were high, while the width and height of wild colonies were approximately the same. This is attributable to Nāsr's regular removal of drone and honeycomb, and maybe to other less apparent features of his management, and presumably contributes to the suppression of swarming. As detailed in Chapter VI, frames with this width : height ratio, for combs of *florea* in hives (Chapter VIII), should be investigated, considering the success Nāsr has with colonies maintained to such a shape.

7. Overall honey yields

It was difficult to determine the yields of honey at different seasons as Nāsr did not seem to keep count of the number of bottles harvested. In 1978 he reckoned he had obtained c. 20 bottles of "sidr" honey. More colonies were kept in the "samur" season and each probably yielded a greater quantity of honey (having developed considerably before the *Acacia* flow started) and in June 1980 Nāsr told A. Brockett (pers. comm.) that he had already gathered 900 Rials' worth of honey and,might even have 1,000 Rials' worth when he had harvested a little more. He had been selling most of the honey in Al Ain (Abu Dhabi) where it was probably fetching 18-20 Rials Omani. If these figures were correct, his 30 colonies must have produced 45-50 bottles of honey ie approximately 1½kg each. This figure seemed high for a dry year, but not impossible if yields of 1kg or less from smaller colonies were balanced by larger colonies producing 2 or even 3 harvests of 1kg, as he said they did.

Therefore, in one year his *florea* might produce up to 70 bottles (kg) of honey which at the (exorbitant) 1980 prices of 18 Rials/bottle would give an income of 1,260 Rials Omani. Though the yield per colony was small compared to that which *mellifera* can produce in Oman, the price of the honey makes Nāsr's enterprise worthwhile. The material costs were negligible, but hard work and skill were essential. An even greater understanding of Nāsr's management system and techniques would therefore be worthwhile, with a view to their adoption by other *florea* keepers in Oman.

CHAPTER V

COLONY TEMPERATURE REGULATION AND WORKER FORAGING ACTIVITY: *APIS FLOREA* AND *APIS MELLIFERA*

A. INTRODUCTION

This chapter considers brood-nest and honeycomb temperature regulation and the diurnal pattern of foraging, particularly with respect to temperature, of *Apis florea* and *Apis mellifera jemenitica*. The primary aim was to investigate any differences between the two species in their temperature relations and thus in their adaptation to the hot and arid Omani environment. Since northern Oman, other than parts of Iran, is probably the only region in the world where *florea* and *mellifera* have overlapped in their range for any length of time, it was an unusual opportunity for comparative studies to be performed; it was hoped they might shed light on aspects of competition or co-existence between the two species. There are many processes and environmental factors influencing the two activities under examination and some of these are considered, but comprehensive studies to evaluate their respective roles were not attempted.

1. Colony temperature regulation

It has long been known that colonies of *mellifera* maintain their brood-nest temperature at around 34 - 35°C, while temperatures in broodless areas of the nest may fluctuate widely (eg Lensky 1964a). Seeley & Heinrich (1981) have recently reviewed the subject of thermoregulation by honeybees, especially *mellifera*, and other social insects and most of the information in this section of the introduction is derived from this source. Heinrich (1974, 1975d, 1981a, b and c), Chappell (1982), Kronenberg & Heller (1982) and Ritter (1982), provided further background details on honeybee and insect thermoregulation.

Brood rearing by *mellifera* can occur at air temperatures external to the hive of -40°C to 40°C or more and, according to Free (1977) colonies can even maintain a stable brood temperature of about 35°C for short periods at air temperatures of 70°C provided the bees have access to water. Various investigations have shown that the principal source of a colony's heat is the flight muscles of adult bees and that flight muscle activity does not need to involve wing movements. Conservation of heat or cooling can be brought about by the clustering or dispersal of the adults and further cooling by fanning of the wings and water evaporation. Both the materials and construction of the multiple-combed nests of *mellifera* and *cerana*, with the brood being surrounded and buffered by wax combs containing honey and pollen, and the cavity nest sites chosen, with south-facing entrances at the bottom (see Chapter II, p. 16), facilitate thermoregulation at low temperatures and must have been pre-requisites for the spread of these species from the tropics and sub-tropics to colder latitudes.

There have been relatively few studies of thermoregulation by tropical races of *cerana* (eg Kapil 1960; Free & Spencer-Booth 1961; Verma 1970; Verma & Edwards 1971) and *mellifera* (eg Darchen 1973; Taylor 1977; Heinrich 1979b; Taylor & Spivak 1984) but most evidence suggests they are less well adapted to temperate conditions. Comparable studies on *dorsata* and *florea* are also few. With air temperatures of 20° - 34°C *dorsata* colonies have been shown to maintain a fairly constant brood-nest temperature of 30° - 33°C, but this is a little lower than the brood-nest temperature of *mellifera* (Viswanathan 1950; Morse & Laigo 1969). Lindauer (1957), Akratanakul (1977), Free & Williams (1979) and Kshirsagar *et al* (1980) have measured *florea* brood-nest temperatures but no detailed investigation of their relationship with ambient temperatures have been made, nor of colonies without brood (unless some of the data given by Kshirsagar *et al* came from a broodless colony); in these studies, *florea* cluster/brood temperatures ranged from 29° - 38°C with environmental temperatures of 18° - 42°C. Thermoregulation by *florea* was therefore clearly in evidence but control appeared to be less exact than for *mellifera*, even though at a given season daily brood temperatures seemed not to fluctuate by more than about 4°C. Arboreal and ground-nesting Meliponini also actively maintain brood-nest temperatures at optima above 30°C, but their thermoregulation too seems less precise than that of *mellifera* (Fletcher & Crewe 1981).

As with *mellifera*, movements of *florea* workers in the cluster appear to be associated with thermoregulation, a gap forming between the comb and protective bee "curtain" and the bees becoming less tightly packed at higher temperatures (Lindauer 1957; Akratanakul 1977). However, Free (1982) has pointed out there is some discrepancy in the descriptions as to whether the bees become more or less tightly packed under such circumstances; my impression was that the bees in the curtain were more tightly packed at lower temperatures. With some colonies I have also observed that during the night, when it is cooler, most of the bees may cluster round the brood area leaving parts of the honeycomb exposed, but as it becomes warmer in the morning larger numbers move up over the honeycomb. Foragers, since they use the crest as a dance platform, may be particularly involved, but this movement, despite its association with the onset of foraging, must also be involved in colony thermoregulation. Furthermore, on occasions in summer, I have even observed a portion of the workers from *florea* colonies kept in hives desert the brood comb and form a "beard" outside the hive, at or near the entrance; Seeley & Heinrich (1981) refer to such behaviour by *mellifera* at extremely high temperatures and humidity and the action is presumed to be necessary when ventilation and evaporative cooling were already being applied in full force within the nest.

Also as in *mellifera*, wing fanning to bring about cooling has been recorded for *florea* (Lindauer 1957; Akratanakul 1977; Free & Williams 1979) and I observed this behaviour frequently in Oman. Free & Williams (1979) and Free (1981 and 1982) reported that fanning only occurred in direct sunlight and that it would cease immediately the colony was shaded; however, on at least 3 occasions and with different colonies I have seen workers fanning when the nest has been completely shaded. These observations were made in particularly hot and sometimes humid periods (May, June and July; see Appendix II). On one occasion, 24.vi.80, fanning was observed on a wild colony, in a *Citrus* tree, that was rearing brood; it was in the evening (18.15h) and the atmosphere felt particularly humid as well as hot (maximum temperature 24-25.vi.80 was 39.5°C, minimum 31.0°C and relative humidity, at 09.00h on 25.vi.80, was 74%). Another colony was in a cave (5) in the Wadi Hawasina (see Chapter II, Figure 2.7b) and not rearing brood, but on 24.vii.80 fanning was observed under the following conditions:-

Time h (O.S.T.*)	Cluster Temperature °C	Cave Temperature °C	R.H. %
06.15	36.0	37.4	78
08.00	36.0	37.0	65
09.00	35.5	37.7	59
10.00	34.3	38.0	51

* Oman Standard Time : GMT + 4h

Cooling seemed to become more effective as the Relative Humidity dropped, suggesting that evaporation of water was occurring. A third colony, kept in a hive (22), was reducing brood rearing before absconding (see Table 8.4) and many bees were observed fanning at 14.30h on 31.v.79 when it felt extremely hot (maximum temperature 38.0°C and R.H. 50% at 09.15h; on 1.vi.79, R.H. at 08.00h was 96%, shade temperature 32.5°C).

Finally, Free (1981) points out that observations are needed to determine the extent to which the bees collect water and use it to cool the comb. Frequent observations of *florea* workers collecting water (from wadis, pools, taps etc) and crop contents of returning foragers (eg Figure 5.10) revealed water was gathered in most months of the year in Oman (ii - viii, xi, xii and probably the others), but the proportions used for cooling and for dilution of honey stores were not investigated.

The likely role in *florea* thermoregulation of the nest sites selected by the bees (Chapter II) and by man (Chapters III and IV), and of seasonal movements/absconding (Chapter VI) are considered elsewhere and the property of the expanded honeycomb to protect the brood comb below from sun and rain (p. 50).

Honeybees, therefore, have several means at their disposal to regulate their colony temperature and all are probably used, as conditions dictate, by the 4 species of *Apis*. Individual worker honeybees are heterothermic at certain times and ambient temperatures in that they have a remarkable capacity to regulate their own temperature (eg Allen 1959; Heinrich 1979b, 1980a and b), but overall they are poikilothermic, their body temperature being variable and partly dependent on ambient temperatures. However, when as a colony rearing brood, *Apis* spp. appear to be fairly effective homeotherms and endothermic ie much of the heat that determines the colony temperature is produced by the honeybees' own metabolism (see Heinrich 1981a for definitions of these terms). The evidence, though, tends to suggest that temperate races of the multi-combed *mellifera* are better thermoregulators, at least at low temperatures, than the tropical *Apis*, including the single-combed *florea*, and this is reflected in their world distribution. This chapter investigates more closely the differences between *A.m.jemenitica* and *A. florea*.

2. Foraging activity

2.1 Influence of forage

The foraging activity of honeybees and other pollinators is partly determined by the availability and attractiveness of nectar and pollen sources (eg Butler 1945; Percival 1955; Schaffer *et al* 1979; Frankie & Haber 1983). The quantity, quality and availability of these resources at different times of day varies from one plant species to another and is affected by physical factors such as nutrition, soil type and prevailing meteorological conditions, including temperature (Wykes 1952, 1953a and b; Beutler 1953; Percival 1955, 1961; Baker & Baker 1975, 1983; Corbet 1978; Corbet *et al* 1979). The timing of nectar secretion, though influenced by such abiotic factors, to be effective must also have evolved to meet the requirements of pollinating insects (ie co-evolution), within a plant's physiological limits. This does not mean, however, that the timing of nectar secretion in a particular plant and the foraging activity of polytropic and "opportunistic" pollinators such as honeybees are necessarily well correlated. For instance, a fairly typical pattern of nectar secretion (with a peak volume fairly early in the morning and a decline during the day), as found in a cruciferous crop in Bangladesh, and the corresponding foraging activity of *florea* and *cerana*, is given in Murrell & Nash (1981). The peak and overall foraging times for the two honeybee species on this one crop were different from each other and from the pattern of nectar availability so, with some nectar present throughout the day, their foraging activity cannot have been entirely determined by the floral rewards of this crop. The two species may therefore have been "choosing" their own"optimum" foraging times. The times chosen were likely to have been determined in part by factors such as ambient temperature, insolation and alternative sources of forage.

There have been many studies similar to Murrell & Nash's on the activity of the *Apis* species on various flowers, especially on crops (eg Boch 1961; Dhaliwal & Atwal 1976; Panchabhavi & Devaiah 1977; Jadhav 1981; Swaminathan & Bhardwaj 1982) but, as Boch was aware, the availability and exploitation of alternative sources of forage would affect the numbers of foragers observed at any time. So field counts on flowers do not necessarily give a good measure of the relationship between honeybee activity and meteorological factors. Also, where the 3 Asian honeybees were concerned, counts rarely took any account of the numbers of colonies of each species providing the foragers nor their proximity to the crop and these must affect the relative number of bees recorded. Therefore, to obtain comparative data on the activities of *florea* and *jemenitica* and an indication of their relationship with ambient temperatures, counts in this study were made on adjacent colonies of the two species and under a range of natural conditions. It had to be assumed that several species of plant would prove to be suitable for the honeybees at each site and that at least some nectar and pollen (and preferably from the same sources for each *Apis*) would be available throughout the day; under these circumstances any differential influence of forage on activity would be minimized. Analysis of the pollen and nectar/water carried by the returning foragers was undertaken to check the accuracy of these assumptions.

2.2 Influence of other factors

Excluding food availability, various explanations have been given for the activity patterns of honeybees and other insects. For instance, Taylor (1963) hypothesized that there may be upper and lower temperature thresholds for insect flight, but between these limits the proportion of insects in flight may be independent of temperature, and gave the even flight activity of *Vespula germanica* above 15°C as an example. He concluded that *Vespula* did not show a regression of activity against temperature. However, in a mixed community of aculeate Hymenoptera in Finland, Käpylä (1974) found, using regression analysis, that flight activity was correlated best with temperature and then with light intensity, while relative humidity had no significant effect. I believe this relationship could be explained by the temperature threshold of more and more species being reached as the temperature rose and/or by the increased activity (numbers) of individual species. For bumblebees in northern Sweden, Lundberg (1980) also found that the combined effect of light and temperature was the most important factor regulating flight activity.

For honeybees, however, Butler & Finney (1942) claimed it was difficult to determine whether the diurnal cycle of activity was associated with light, temperature or any other property showing a diurnal cycle. They calculated that 30% of the variability of honeybee activity (from the diurnal cycle) could be ascribed to irregularities in light intensity, but that changes in temperature were too regular and the minor variations were insufficient to detect variations in bee activity. Indeed, by moving hives to different longitudes and latitudes overnight, Renner (1960) has shown that honeybees do have a time sense based on endogenous and exogenous factors. They can learn a time of nectar/pollen presentation and will set off, according to their endogenous rhythm and time of dawn, to find particular flowers even if it is too early locally because the hive has been moved. However, the endogenous clock adjusts to exogenous rhythms indicating that there are direct, proximate (internal rhythms) and indirect, ultimate (forage availability) factors determining flight activity times; meteorological conditions such as light and temperature may even act both directly and indirectly.

Using controlled environment rooms Kefuss & Nye (1970) too have shown that all honeybee castes have a flight rhythm controlled or influenced by photoperiod, but concluded that in workers the rhythm was not normally evident because it was overshadowed by exogenous factors such as weather and foraging opportunities. Consistent with this latter conclusion Nelson & Jay (1968), using a flight room, showed that the level of flight activity was determined by the temperature of the room but that more "winter" than "summer" bees flew at lower temperatures and fewer at higher temperatures, indicating seasonal acclimatization; nevertheless, bimodal patterns in daily flight cycles were also observed (indicating a degree of endogenous rhythm).

With colonies outside, Szabo (1980) showed that the most important factors in determining honeybee activity, both having similar positive correlations, were temperature and solar radiation, while relative humidity and wind had little effect. Burrill & Dietz (1981) however concluded that honeybees responded to temperature and solar radiation differently. For temperature the response was positive (increasing flight departures) but with solar radiation intensity there was a positive response at low levels that changed to a negative response (decreasing flight departures) at higher radiation levels. Gary (1967) recorded honeybee activity in a hot (28^{o} - 46^{o}C), dry desert area of

California; in contrast to most of the studies above and others (eg Lundie 1925; Lewis & Taylor 1964) that were conducted under temperate conditions, he found that there were very few flights at midday, but very many at dawn and dusk. Bodenheimer & Ben Nerya (1937) found flight activity varied with temperature and humidity, with separate peaks at 24°C and 37°C, the latter probably associated with water-gathering.

Foraging activity studies of the Asian honeybees have been limited. Morse & Laigo (1969) found that *dorsata* in the Philippines were active on flowers as much as 30 to 60 mins before *indica* and *mellifera* were active in the morning and that they also worked later at night. Apart from a secondary peak in the evening, *dorsata* foraging activity, from the nest, generally declined from a maximum in the early morning. *Dorsata* visits to sunflower at Udaipur in India (Swaminathan & Bhardwaj 1982) concurred with this pattern, while in contrast the number of *florea* visits was low early in the morning, peaked at 14.00 - 16.00h and stopped by 18.00h. On *Trifolium alexandrinum* at Ludhiana (India) differences in the foraging patterns of the 4 *Apis* species were not very marked (Atwal *et al* 1970); this may have been a consequence of the presence and differential exploitation of other sources of forage as already discussed. Nevertheless, Jhajj & Goyal (1979) also found that *cerana* and *mellifera* showed similar foraging patterns to each other at Ludhiana, when observing bees at the hive entrance. Cherian *et al* (1947) found correlations between *cerana* activity and meteorological conditions, with an optimum of c. 24° - 27°C and reduced foraging when temperatures were higher. In Thailand, Akratanakul (1977) observed that only a few *florea* started foraging before 07.30h but that foraging activity increased at about 08.00h when the air temperature reached 30°C; during the warmest period of the day activity decreased and after 16.30h it was noticeably reduced. However, a concentrated sucrose solution near the nest induced the bees to start foraging earlier (soon after sunrise, c. 06.00h) and continue later (15 mins after sunset).

To summarize "Flight rhythms of worker bees have been studied from the tropics to the Arctic Circle, and these investigations have shown that outdoor flight activity is correlated with nectar flow, pollen collection, temperature and weather" (Kefuss & Nye 1970). The conclusion of Lewis & Taylor (1964) for insects in general, that light intensity is usually the factor that affects the time of flight whereas temperature influences amplitude appears to be an oversimplification for honeybees. Furthermore, because they are interrelated it seems to be particularly difficult to distinguish the influences of air temperature and radiation on honeybee activity. Nevertheless there presumably are certain lower and upper thresholds of light and temperature for the activity of the various bee species and the duration of suitable light intensity could limit the period when temperature conditions make flight possible and vice-versa. Near maximum visual acuity in *mellifera* is reached at a light intensity rather brighter than that at sunrise/sunset but is reduced to 50% before light fades to Civil Twilight (Lewis & Taylor 1964). In the U.K. honeybees rarely continue to fly so late, probably because cold inhibits them. However, even such low light levels may not totally inhibit flight activity, since in the tropics there are various reports of *florea*, *dorsata* and *A.m. adansonii* foraging at night, though usually near times of full moon (Dover 1929; Diwan & Salvi 1965; Fletcher & Tribe 1977).

Thus the factors determining honeybee flight activity are many and their interactions complex and the discussion above should be borne in mind in these attempts to identify some of those key factors in Oman and while the differences between the honeybee species are considered.

B. METHODS

1. Study sites

To make comparative recordings of nest temperatures and foraging activity over a range of environmental temperatures, experimental colonies of *florea* and *mellifera* were established at several sites. Presented here are representative recordings from 3 sites in cultivated areas, where the bees also had access to surrounding natural vegetation.

(a) Khabura, on the Batina coast (altitude 10m), where temperatures and relative humidity can be high (Appendix II).

(b) Sayq, a village high in the Jabal Akhdār (altitude c. 1950m), where temperatures sometimes drop below 0°C in the winter (Horn *et al* 1977).

(c) Rustaq, at the foot of the central Jabal Akhdār range (altitude c. 300m), with maximum and minimum temperatures rather more extreme than on the coast and the relative humidity generally lower (Appendix II).

For various reasons it was not possible to replicate the experiments as much as would have been desirable. For instance, insufficient hives of *jemenitica* were available, due to drought and the understandable reluctance of bee-keepers to part with surviving colonies in "tubūl", and then the absconding habit of *florea* made it difficult to keep more than one or two colonies at a given site for any length of time.

2. Materials and measurements

For these recordings *jemenitica* were kept in Langstroth hives and 3 of the *florea* colonies were kept in experimental plywood hives, with mesh on either side of the honeycomb to provide access and ventilation (the hive, No. 2, used for recordings at Khabura is described in Chapter VIII and the others were similar in principle). Recordings on a fourth *florea* colony, FD (see Chapter VI, Table 6.3 for details), that had established itself naturally on a *Bougainvillea* branch at Khabura allowed comparison between temperature regulation by a wild colony and a colony in a hive.

Using mercury thermometers and a whirling hygrometer, measurements were made during the day of atmospheric temperature and relative humidity (in the shade, close to the hives, ie <10m away and a little, c. 0.5m, off the ground), the brood temperatures of the *mellifera* and *florea* colonies and in one case (Hive 2, Khabura) the honeycomb temperature of a *florea* colony. The numbers of bees per min, based on counts over 2 min periods or a little longer when activity was low, leaving and returning to the colonies, were counted at intervals during the day. Estimates were made of the proportions carrying water, nectar and/or pollen, by counts and dissection in the field of samples of approximately 10 returning workers; pollen in the bees' corbiculae and on their bodies was analysed in the U.K. (see Chapter VII, Methods 3). Recordings were usually made on 2 consecutive days, starting on the afternoon of the first day, then continuing again from dawn on the second day and stopping in the afternoon ie over 24 hours but not during the course of a single day; the days have been reversed on the graphs.

The following abbreviations are used in the text:- T_A: Ambient temperature, T_B: Brood temperature, T_C: Cluster temperature (no brood) and T_H: Honeycomb temperature.

C. RESULTS

1. Colony temperature regulation

(a) Khabura, early summer (8-9.v.80)

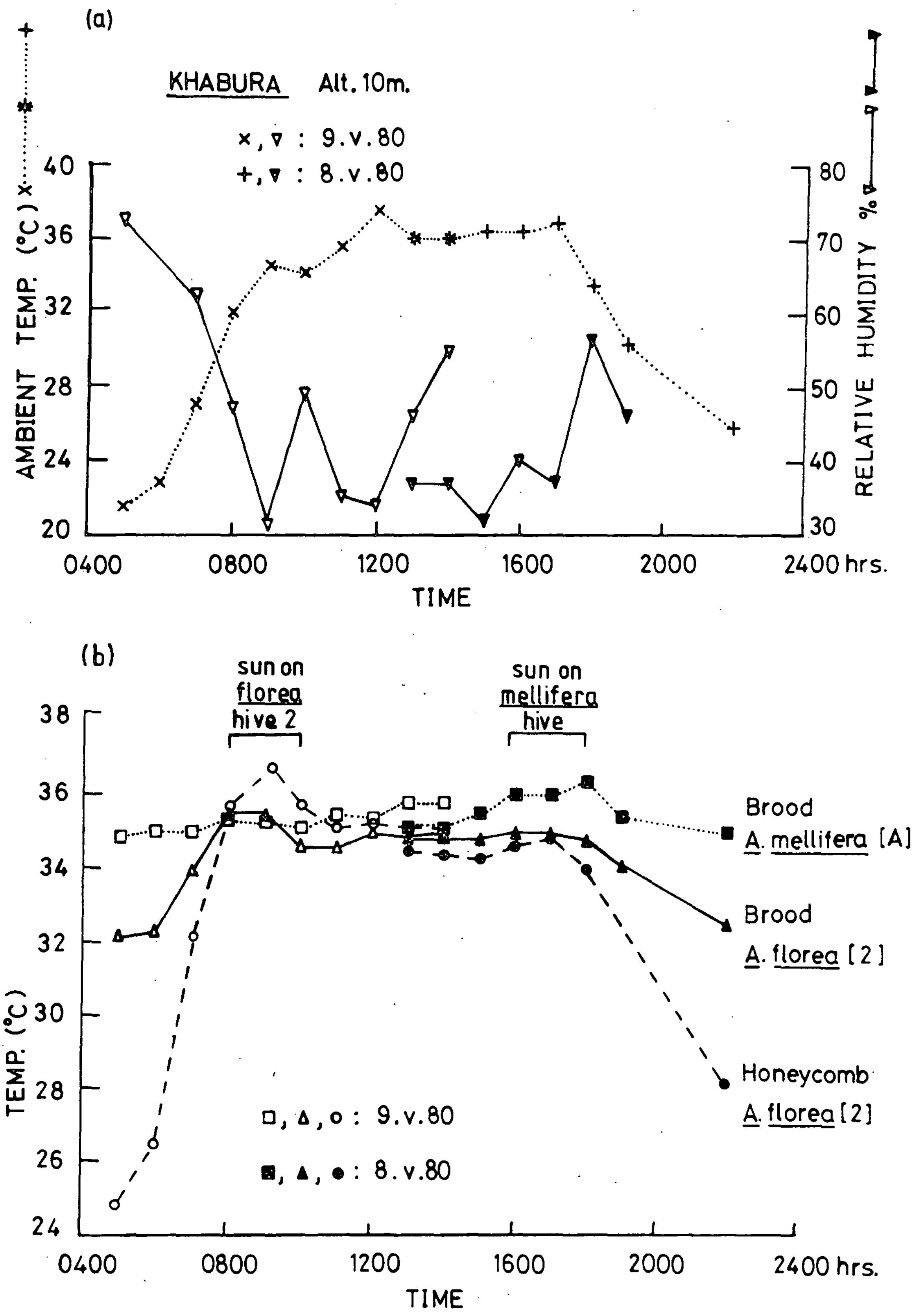
As with most days in Oman, there was virtually no cloud so the uninterrupted sunshine gave rise to steady temperature changes during the day, with only minor fluctuations (Figure 5.1a); such a temperature pattern suited experimental recordings of this nature, being close to the controlled temperature changes that might be applied under laboratory conditions. The relative humidity (R.H.) over the 2 days did fluctuate to some extent and may have accounted for a small component of the variation in *jemenitica* and *florea* brood and honeycomb temperatures, but the graphs (Figures 5.1a and b) indicated that T_B and T_H followed changes in T_A much more closely than changes in R.H.

Despite a range of T_A of 18°C, *jemenitica* T_B remained fairly constant throughout the day (Figure 5.1b). *Florea* 2 however was not able to keep T_B so high during the coldest hours in the early morning nor in the evening. T_B of the "natural" colony of *florea* (FD) followed virtually the same pattern during the 2 days as T_B of colony 2 in the hive, so is not graphed. The maximum T_B of *florea* 2 at c. 09.00h corresponded with a short period of sunlight striking the colony as did the peak T_B at c. 18.00h for *jemenitica*. This demonstrated that direct insolation influences the temperature control of both species; this could be beneficial or harmful according to whether the insolation occurs at a season or time of day when warming or cooling is required. The colonies were in shade for the rest of the time.

In contrast, T_H of *A. florea* 2 (Figure 5.1b) was, at most, only a few degrees above ambient so the honeycomb did not appear to be subjected to such direct temperature control.

Figure 5.1 (a) Ambient temperature and relative humidity at Khabura, Oman, on 8 and 9.v.80 (early summer).

(b) Corresponding records of the brood nest temperature for *Apis mellifera jemenitica* in a Langstroth hive (A) and *Apis florea* in an experimental hive (2), and of the *A. florea* honeycomb temperature. Both colonies were rearing brood.


(a)
KHABURA Alt. 10m.
×, ▿ : 9.v.80
+, ▾ : 8.v.80
AMBIENT TEMP. (°C) ×
40
36
32
28
24
20
RELATIVE HUMIDITY %
80
70
60
50
40
30
0400
0800
1200
1600
2000
2400 hrs.
TIME
(b)
sun on florea hive 2
sun on mellifera hive
TEMP. (°C)
38
36
34
32
30
28
26
24
Brood A. mellifera [A]
Brood A. florea [2]
Honeycomb A. florea [2]
□, △, ○ : 9.v.80
■, ▲, ● : 8.v.80
0400
0800
1200
1600
2000
2400 hrs.
TIME

To assess in more detail the ability of each species to thermoregulate, regression lines were plotted of colony temperatures against T_A. For *jemenitica* a better correlation was obtained by plotting the T_B values recorded one hour after each T_A reading, than by plotting concurrent readings of T_B and T_A. This delayed effect is explained by the solid materials used in the construction of the hive and by the protection of honeycombs on either side of the brood.

For *jemenitica* (Figure 5.2) there was a significant correlation between T_A and T_B, so the colony was not 100% homiothermic; if it were, both the gradient of the regression line and the correlation coefficient would be zero. However, the brood temperature was maintained within limits of 1.6°C, despite T_A varying over a range of greater than 16°C, with actual temperatures reaching 37°C.

Turning to *florea* 2 (Figure 5.3) a similar pattern to *jemenitica* was followed with a significant correlation between T_A and T_B, but the gradient was steeper and T_B was not kept within such tight limits (2.9°C). The natural colony of *florea* FD (Figure 5.4) responded to T_A in much the same way as did *florea* 2. The regression line gradient for FD, 0.144, was slightly shallower than that for Hive 2 (0.187) and the variation in its T_B slightly less (range 2.3°C as opposed to 2.9°C); this could be attributed to the greater size of the natural colony (and thus better ability to thermoregulate) or to the effect of the hive on *florea* 2. However, there was no significant difference between the regression lines (Figure 5.6) which at least indicates that a hived *florea* colony does not thermoregulate atypically to any great extent.

The *florea* honeycomb temperature regression line (Figure 5.5) has a gradient near to 1 (when $T_H = T_A$), so is almost "poikilothermic", indicating that little energy is devoted to the control of its temperature. In fact at the lower temperatures in the early morning, when the bees

Figure 5.2 Regression of *Apis mellifera jemenitica* (in a Langstroth hive) brood nest temperature (T_B) on ambient temperature (T_A) one hour previously, at Khabura, Oman in early summer.

Figure 5.3 Regression of *Apis florea* (in experimental Hive 2) brood nest temperature (T_B) on ambient temperature (T_A), at Khabura, Oman in early summer.

Figure 5.4 Regression of a wild *Apis florea* colony (FD) brood nest temperature (T_B) on ambient temperature (T_A) at Khabura, Oman in early summer.

Figure 5.5 Regression of *Apis florea* (in experimental Hive 2) honeycomb temperature (T_H) on ambient temperature (T_A) at Khabura, Oman in early summer. The colony was rearing brood.

Figure 5.6 Comparison of brood nest thermoregulation by *Apis mellifera jemenitica* in a Langstroth hive, by a wild colony of *Apis florea* (FD) and by a colony of *A. florea* in an experimental hive (2) and of honeycomb thermoregulation by the *A. florea* in the hive. All recordings were made on the same two days (8 and 9.v.80) at Khabura, Oman in early summer and the individual regressions of colony temperatures on ambient are presented in Figures 5.2 - 5.

Fig. 5.2

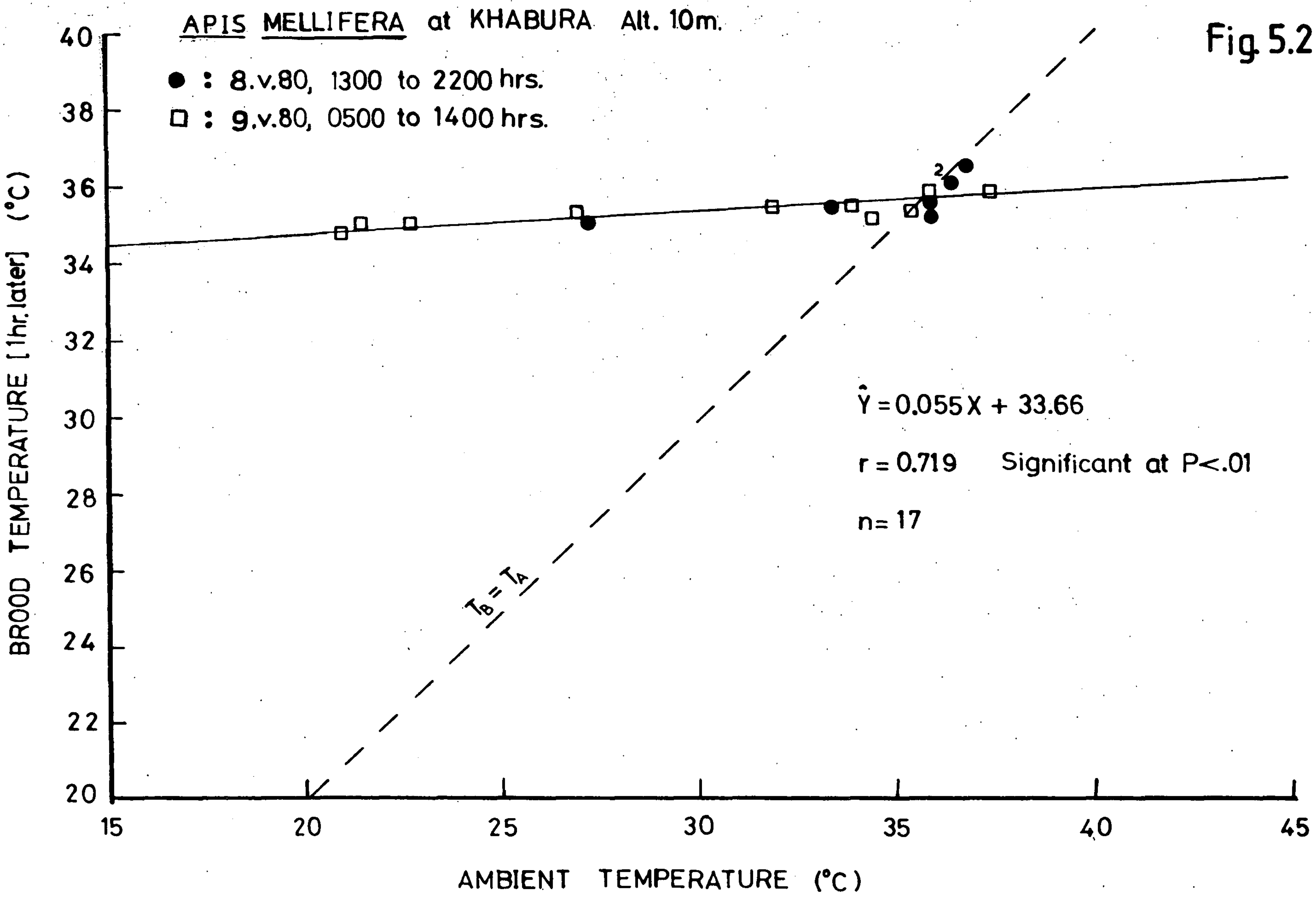
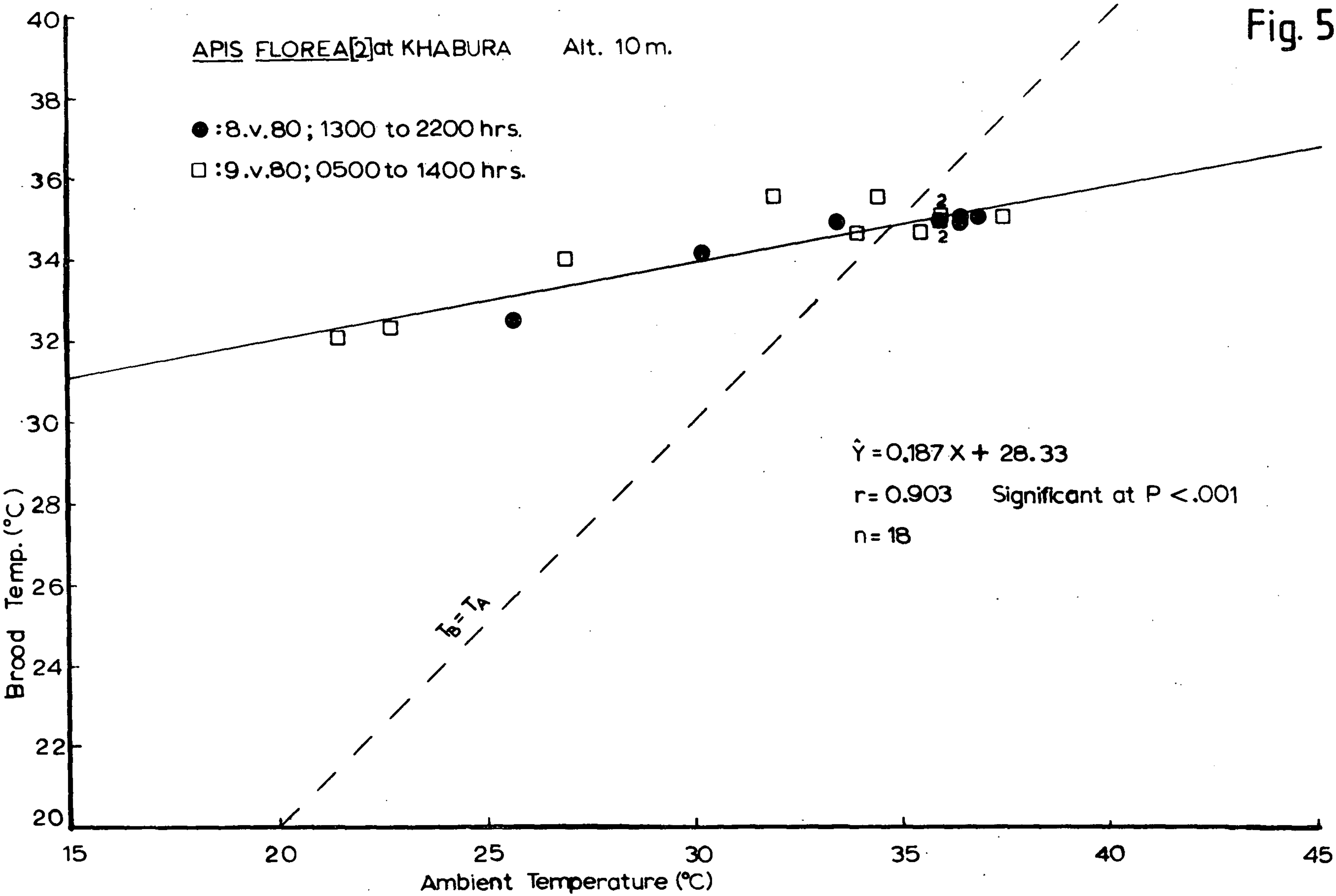

APIS MELLIFERA at KHABURA Alt. 10m.
● : 8.v.80, 1300 to 2200 hrs.
□ : 9.v.80, 0500 to 1400 hrs.
BROOD TEMPERATURE [1hr. later] (°C)
40
38
36
34
32
30
28
26
24
22
20
15
20
25
30
35
40
45
AMBIENT TEMPERATURE (°C)
2
$T_B = T_A$
$\hat{Y} = 0.055X + 33.66$
r = 0.719 Significant at P<.01
n= 17

Fig. 5.3


APIS FLOREA[2] at KHABURA Alt. 10 m.
● : 8.v.80 ; 1300 to 2200 hrs.
□ : 9.v.80 ; 0500 to 1400 hrs.
$\hat{Y} = 0.187X + 28.33$
r = 0.903 Significant at P < .001
n = 18
$T_B = T_A$
2
2
Brood Temp. (°C)
Ambient Temperature (°C)
40
38
36
34
32
30
28
26
24
22
20
15
20
25
30
35
40
45

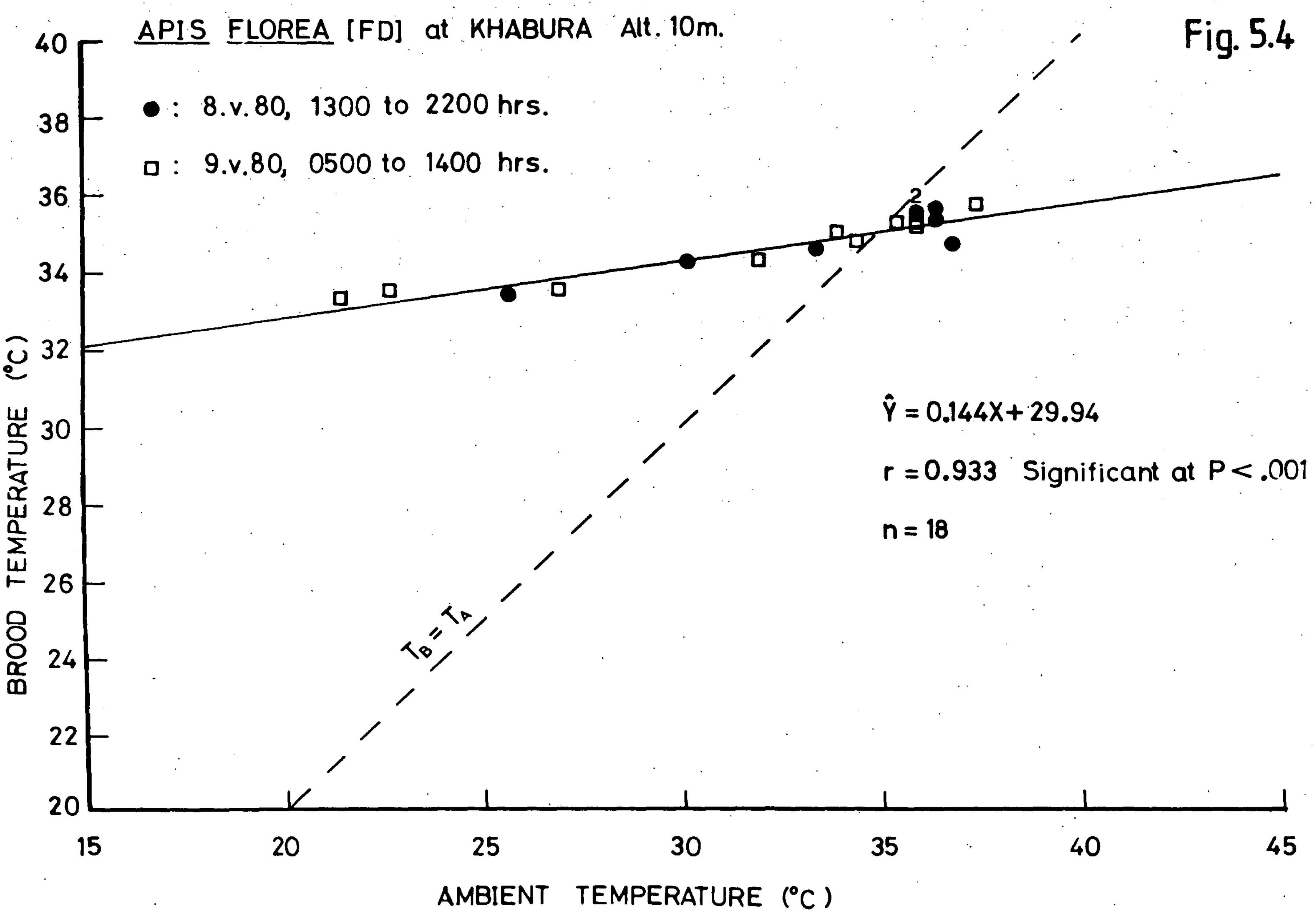

APIS FLOREA [FD] at KHABURA Alt. 10m.
●: 8.v.80, 1300 to 2200 hrs.
□: 9.v.80, 0500 to 1400 hrs.
$\hat{Y} = 0.144X + 29.94$
r = 0.933 Significant at P < .001
n = 18
$T_B = T_A$
2
BROOD TEMPERATURE (°C)
AMBIENT TEMPERATURE (°C)
20
22
24
26
28
30
32
34
36
38
40
15
20
25
30
35
40
45

Fig. 5.4

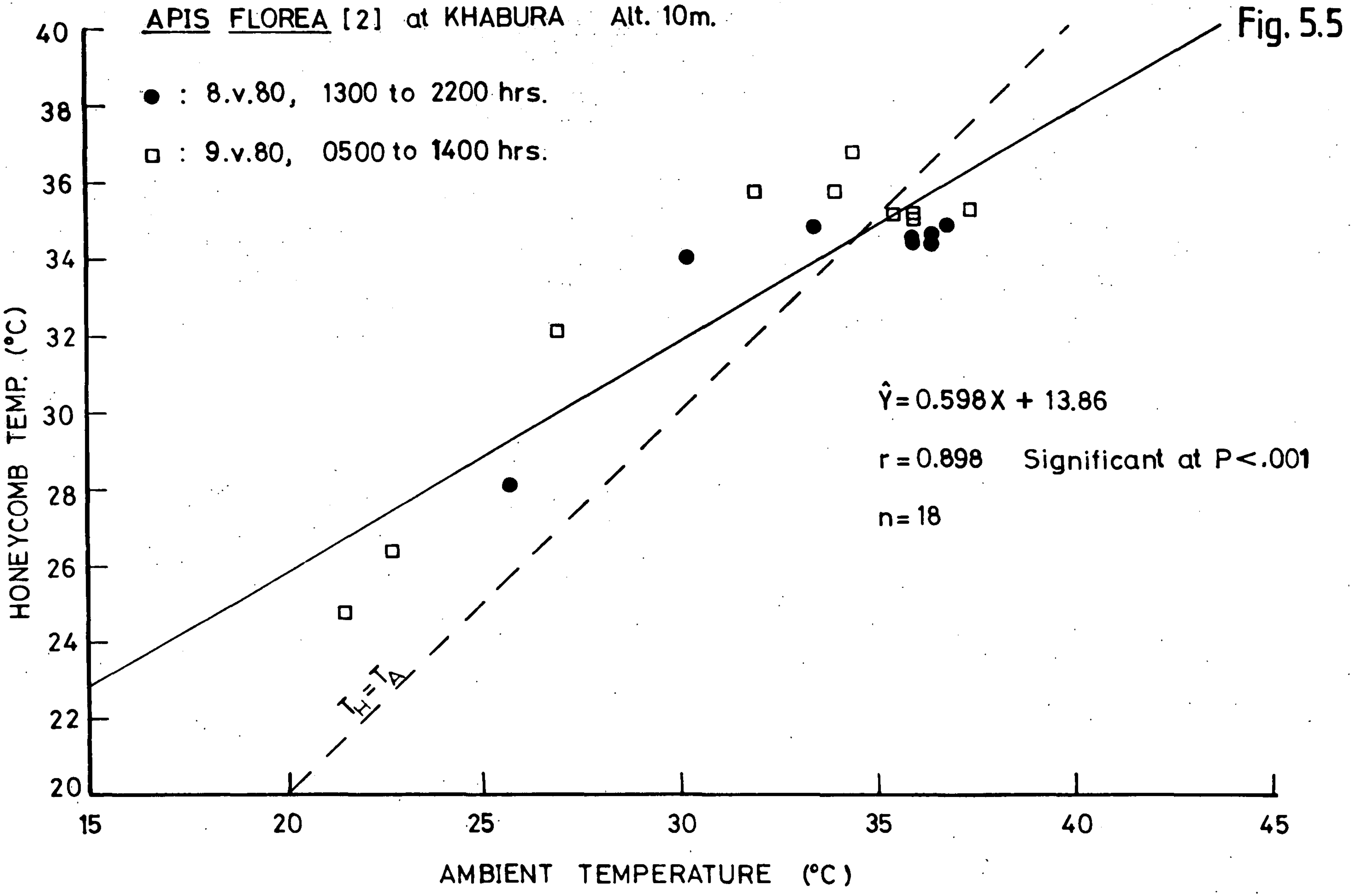

APIS FLOREA [2] at KHABURA Alt. 10m.
● : 8.v.80, 1300 to 2200 hrs.
□ : 9.v.80, 0500 to 1400 hrs.
$\hat{Y} = 0.598X + 13.86$
r = 0.898 Significant at P<.001
n = 18
$T_H = T_A$
HONEYCOMB TEMP. (°C)
AMBIENT TEMPERATURE (°C)
40
38
36
34
32
30
28
26
24
22
20
15
20
25
30
35
40
45

Fig. 5.5

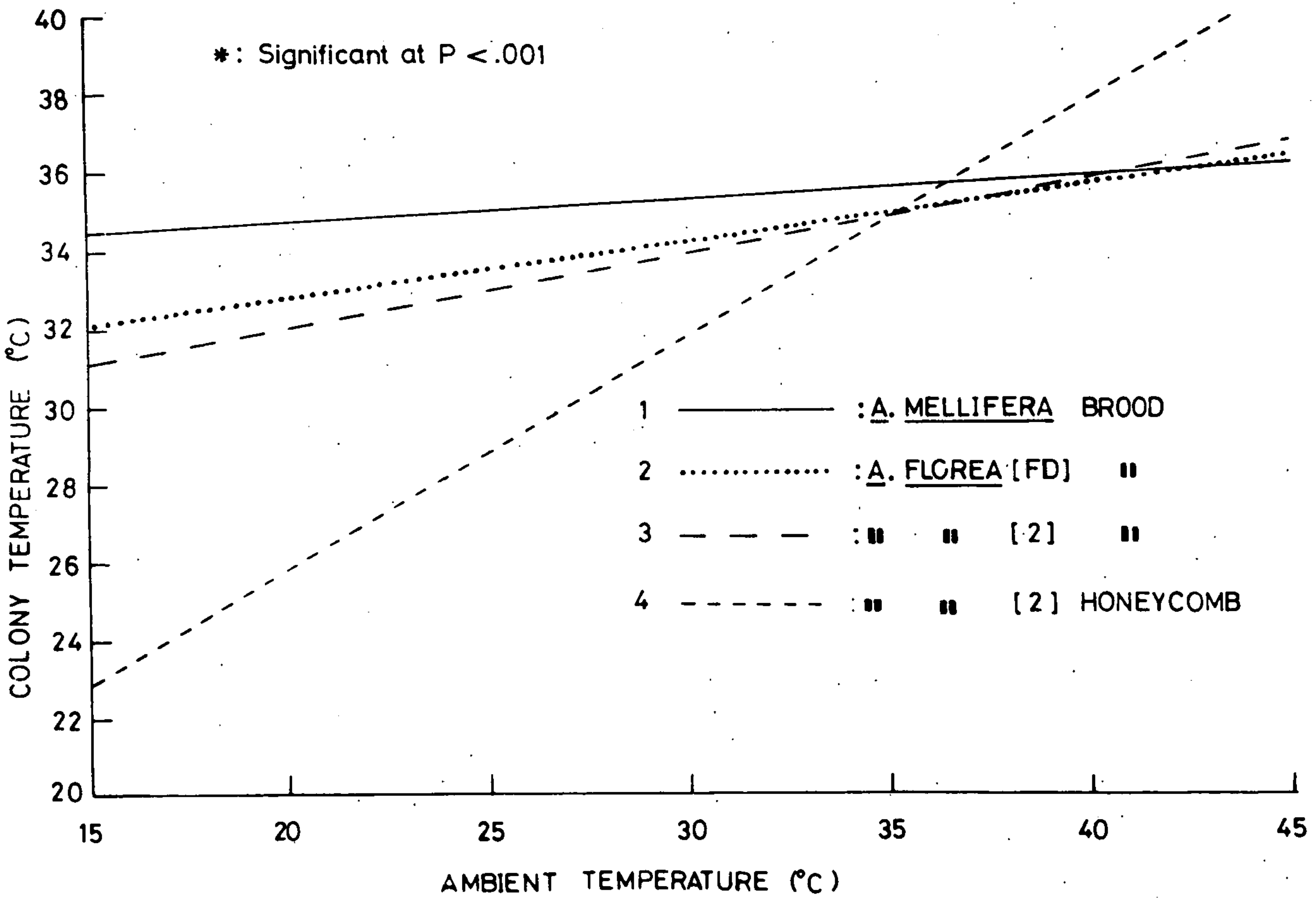
SLOPE COMPARISONS: t VALUES

	2	3	4
1	4.88^{*}	5.39^{*}	7.74^{*}
2		1.75^{ns}	6.47^{*}
3			5.70^{*}

<u>KHABURA</u> Alt. 10m.

8-9.v.80

Fig. 5.6



are not foraging and most were around the brood comb, the gradient appears to be particularly close to 1. The line levels off at higher T_A (in the middle of the day), suggesting that only then is T_H being regulated. However, I believe this regulation of T_H is primarily a passive effect due to the presence of bees that have moved onto the top of the comb (to dance, bring water etc) rather than a deliberate attempt to keep the honeycomb cool.

A comparison of the 4 regression lines (Figure 5.6) gives an indication of the relative ability of the two species to thermoregulate. The lines are all significantly different except for the brood temperatures of the two *florea* colonies.

(b) Sayq, early spring (17-18.ii.80)

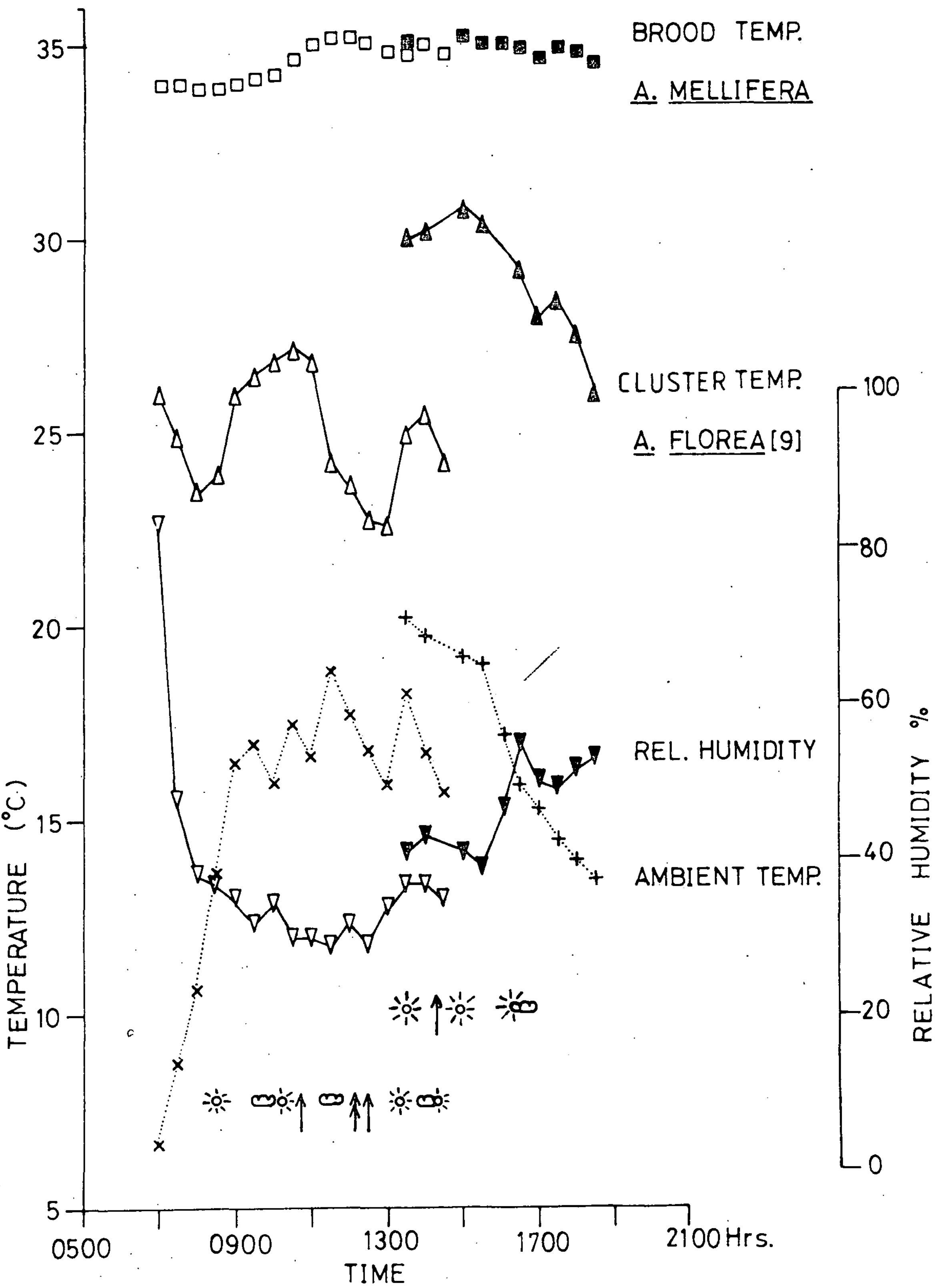
Despite night-time temperatures near to freezing, *jemenitica* were rearing brood at Sayq (1950m) in February 1980. From the presence of eggs in the comb it was apparent that the queen of the *florea* colony in Hive 9 was fertile, but the workers were not rearing the eggs to the adult stage as no larvae or pupae were present. On 18.ii.80, despite changeable weather with some clouds and wind (an occasional rather than regular occurrence in northern Oman, but more frequent higher in the mountains), *jemenitica* maintained the high temperatures required for brood rearing (Figure 5.7); the regression line (Figure 5.8) shows that the small changes in T_B were correlated with changes in T_A.

The *florea* cluster temperature, T_C, remained well above ambient, fluctuating between 22° and 30°C; brood rearing, however, would almost certainly have been impossible under such variable conditions if *florea* brood is at all similar to that of *mellifera* in this respect. *Mellifera* brood is extremely temperature-sensitive and a high incidence of malformed adults and non-emergence has been shown for capped brood (pupae

Figure 5.7 Ambient temperature, relative humidity, temperature of *Apis florea* cluster on comb in experimental hive 9 and brood temperature of *Apis mellifera jemenitica* in a Langstroth hive, at Sayq, Oman on 17 and 18.ii.80 (early spring). Periods of sun, cloud and wind (arrows) are indicated by the symbols just above the time axis.

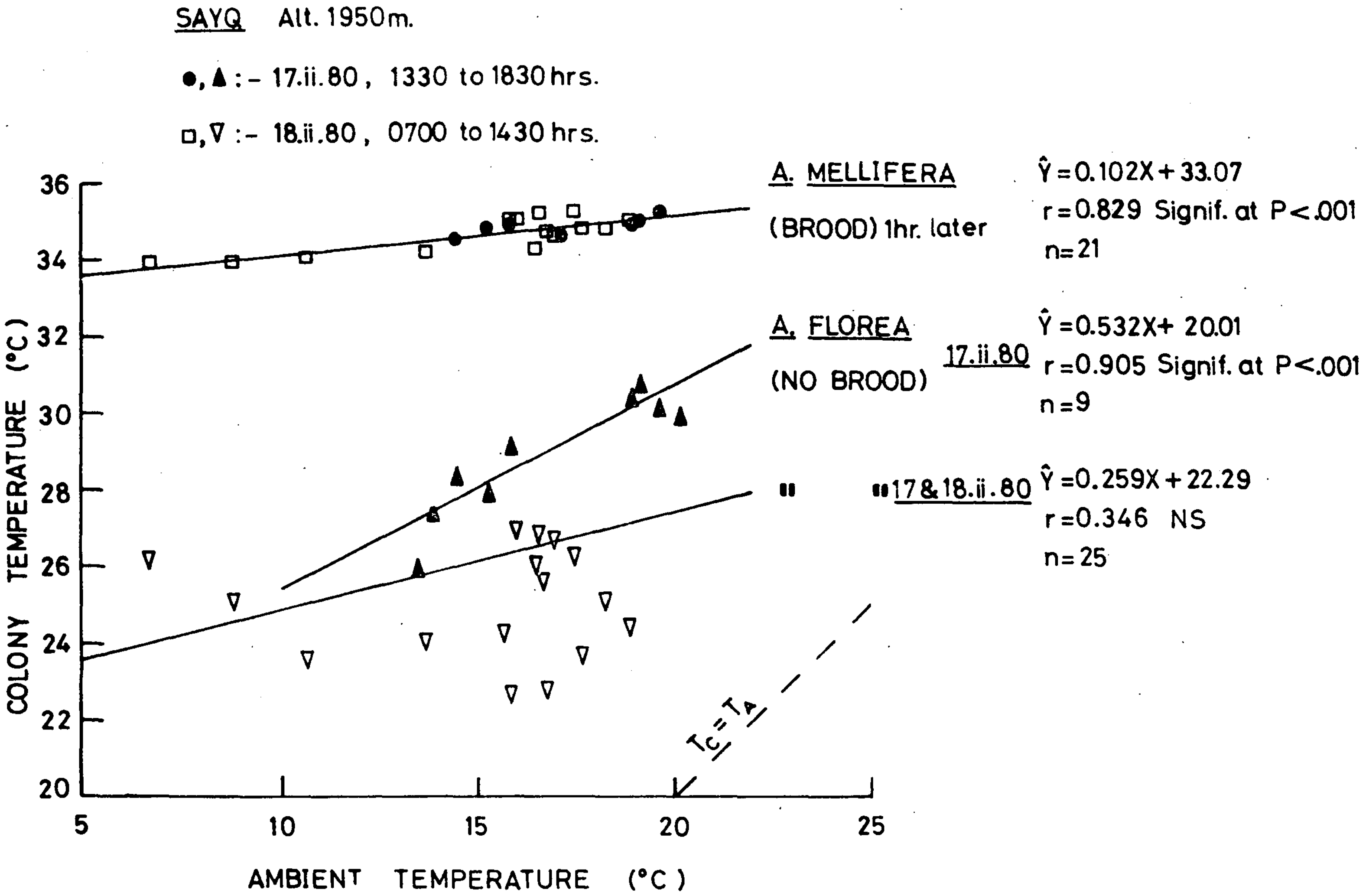
Figure 5.8 Regressions of the temperature of *Apis mellifera jemenitica* brood (in a Langstroth hive) and of an *Apis florea* cluster (on a comb in an experimental hive, no. 9) against ambient temperature at Sayq, Oman in early spring. The line $T_C = T_A$ indicates the relationship when colony (brood or cluster) temperatures equal ambient temperatures.

SAYQ Alt.1950m. FIG 5.7



□, △, ▽, × :- 18.ii.80 ■, ▲, ▼, + :- 17.ii.80

FIG. 5.8


SAYQ Alt. 1950m.
●, ▲ :- 17.ii.80, 1330 to 1830 hrs.
□, ∇ :- 18.ii.80, 0700 to 1430 hrs.
A. MELLIFERA
(BROOD) 1hr. later
$\hat{Y} = 0.102X + 33.07$
r = 0.829 Signif. at P<.001
n = 21
A. FLOREA
(NO BROOD)
17.ii.80
$\hat{Y} = 0.532X + 20.01$
r = 0.905 Signif. at P<.001
n = 9
"
" 17 & 18.ii.80
$\hat{Y} = 0.259X + 22.29$
r = 0.346 NS
n = 25
$T_C = T_A$
COLONY TEMPERATURE (°C)
36
34
32
30
28
26
24
22
20
5
10
15
20
25
AMBIENT TEMPERATURE (°C)

and late-stage larvae) kept between 26° and 30°C (Seeley & Heinrich 1981). The *florea* T_C recorded were similar to those maintained by broodless winter clusters of *mellifera* workers which also fluctuate widely (Free 1977; Seeley & Heinrich 1981). Individual *mellifera* foragers enter a chill coma at approximately 7°- 10°C, younger bees at higher temperatures (12°C) (Allen 1959; Free & Spencer-Booth 1960), so the near-freezing night-time temperatures at Sayq would necessitate clustering and raising of body temperature by *florea* workers, as their chill-coma temperature is likely to be higher than that for *mellifera* workers. The *florea* workers indeed appeared to be clustering tightly on their comb in the hive but no investigations were made to ascertain the degree of clustering or the presence/absence of a separate inner core and outer shell of bees as has been observed for *mellifera* (Seeley & Heinrich 1981).

On 17.ii.80 there was a significant correlation between *florea* cluster temperature and ambient (Figure 5.8), but on 18.ii.80 the cluster did not appear to be responding to or compensating for the variable meteorological conditions. Whether this behaviour was due to (i) inability to cope with such a temperature regime or (ii) it simply being unnecessary to maintain a stable, high temperature (because brood rearing was not being attempted) was not obvious. Forage was available (see p. 218) but maybe the energy costs of gathering it and of brood rearing at these low T_A were just too high. Whatever the cause (i or ii) it was evident that this *florea* colony was not thermoregulating precisely nor rearing brood like the colony of *jemenitica*; though generating heat to keep T_C well above ambient and thus able to survive, the *florea* seemed less well adapted to the relatively cold conditions.

(c) Rustaq, early spring (12-13.ii.79)

Recordings of *florea* and *jemenitica* colony temperatures at Rustaq on 12-13.ii.79 were in general consistent with the different standards of temperature control demonstrated for the two species at both Khabura (a) and Ṣayq (b); graphs and full details are therefore not presented, just a few key figures.

With a daily T_A range of 10.5° - 26°C, both species were rearing brood. However, between 09.30h and 17.00h on 12.ii.79 *florea* did not maintain its T_B (33.0° - 34.0°C) within quite such precise limits as *jemenitica* (33.6° - 34.2°C) when T_A ranged from 22.5° - 26°C. On 13.ii.79 when recordings were started earlier in the day, 08.00h, the *florea* T_B apparently ranged from 28.6° - 34.5°C (T_A, 16.0° - 23.0°C), but I believe this wide range was due to the thermometer not being fully inserted in the comb. However, it was interesting to note that the highest "T_B" was reached at 10.00h before maximum T_A (see Figure 5.13), when the sun was shining directly on the hive and only 2 hours after the 28.6°C "T_B" low; "T_B" dropped again as the direct sun moved off the hive. This again demonstrated the significant influence (potentially harmful or beneficial) that insolation can have on *florea* colony thermoregulation and is further indication of the important role that appropriate nest site selection (Chapter II) can play in the ecology of this honeybee.

Additional evidence as to the sensitive nature of *florea* colony thermoregulation was a temporary drop in "T_B" to 32.1°C, after the 34.5°C peak, when a small but significant proportion (at least 100, possibly more than 1,000) of the workers left the comb to fly around the hive at c. 13.00h. It was assumed these were young bees on orientation flights as they returned to the colony whose temperature quickly rose again to 33.2°C and a little later to 33.6°C. Thus at Rustaq too, it appeared that *jemenitica* were able to maintain brood nest temperatures at a more stable level than *florea*.

2. Foraging activity

2.1 Diurnal foraging patterns of *jemenitica* and *florea*

(a) Khabura (10m), early summer (8-9.v.80)

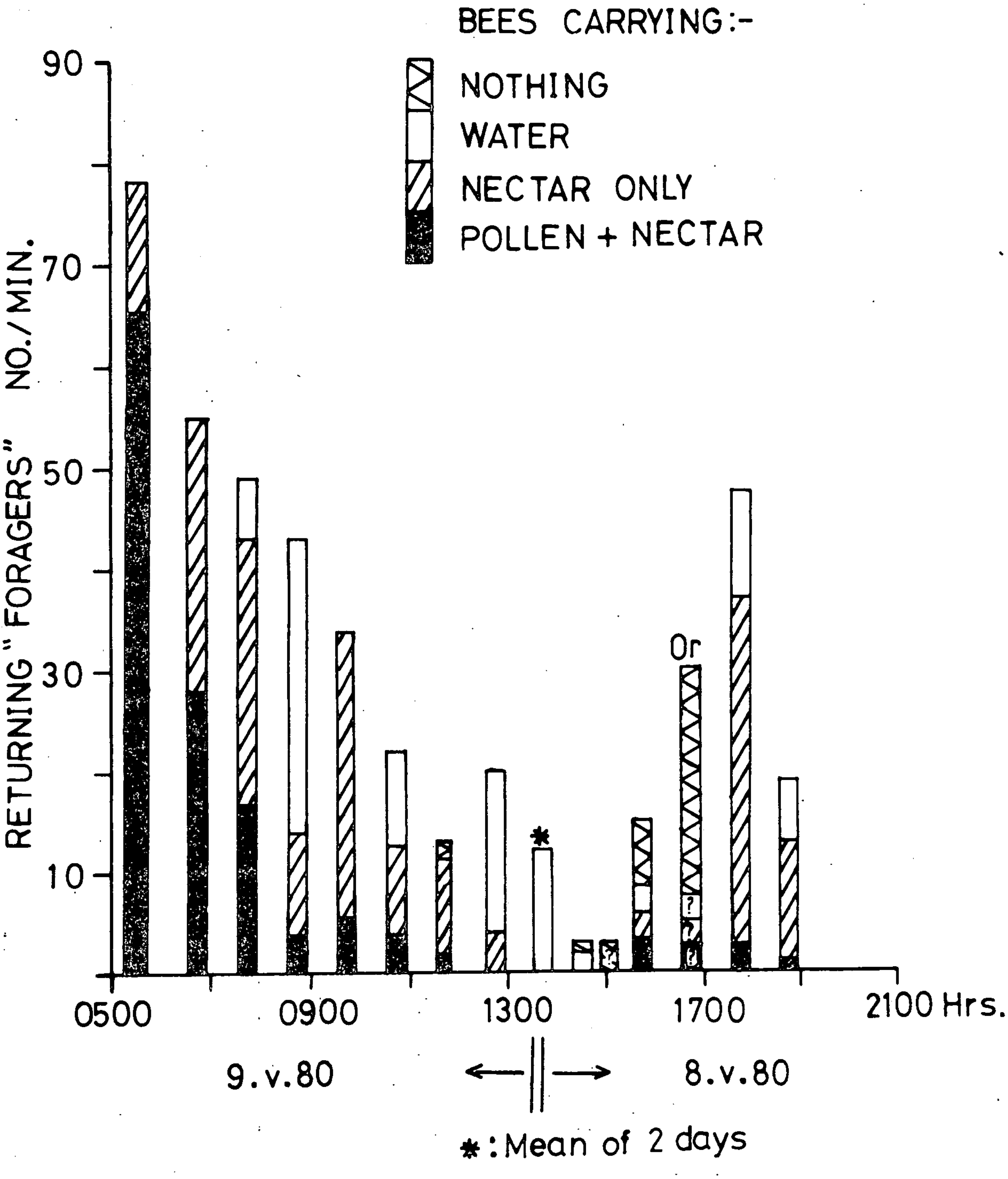
The diurnal pattern of flight activity of *jemenitica* in Oman in summer, as exemplified by the observations at Khabura (Figure 5.9) was markedly different from that usually observed in summer in temperate climates (eg Lundie 1925; Lewis & Taylor 1964; Szabo 1980). On 9.v.80 the bees started foraging at 05.00h (approximately Civil Twilight 05.07h and well before sunrise 05.32h, Oman Standard Time and calculated from the Nautical Almanac), presumably leaving the hive as soon as there was sufficient daylight for them to see to forage efficiently. The daily peak of foraging activity was reached almost immediately and then declined as it became hotter during the morning. They foraged little at the hottest part of the day, collecting mostly water, but there was a secondary peak of activity just before dusk, as it became cooler again. A similar pattern of foraging, however, with intense activity at dawn and dusk (even when there was insufficient light to permit accurate observations) was recorded by Gary (1967) for *mellifera* in California during summer, when temperatures were high (mean daily maximum 46°C) and relative humidities low. In contrast, in Canada during July/August (Szabo 1980), in the U.K. during summer (Lewis & Taylor 1964) and at Sayq in early spring (Figure 5.11, next section) foraging by *mellifera* did not usually start till long after dawn, reached a peak near the middle of the day and then declined in the afternoon and evening before dusk.

Figure 5.9 Daily pattern of *Apis mellifera jemenitica* foraging activity at Khabura, Oman in early summer (8 and 9.v.80) as indicated by numbers of returning foragers/min to a Langstroth hive. Foraging had stopped by 18.55h, just after sunset. Or: Some bees on orientation flights.

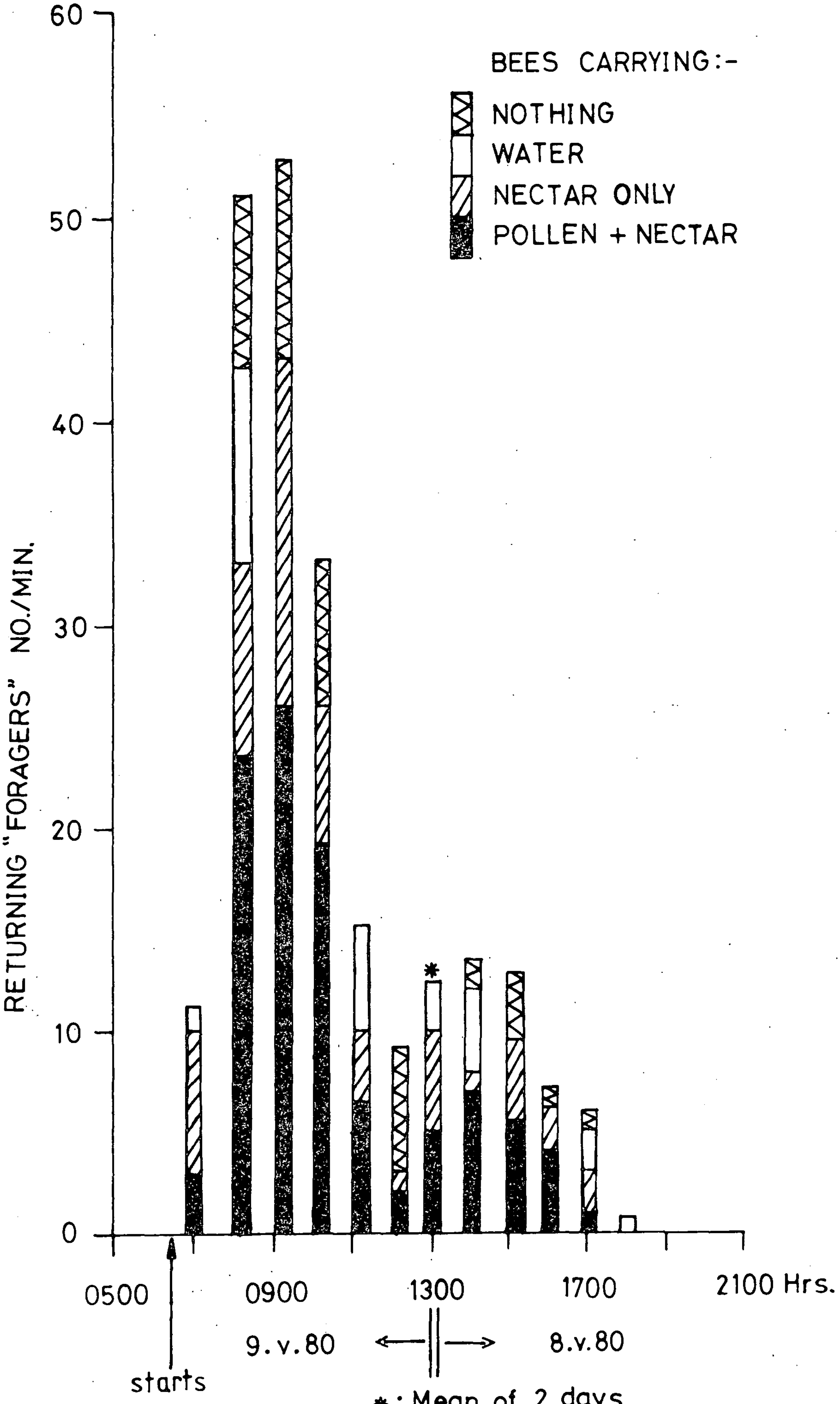
Figure 5.10 Daily pattern of *Apis florea* foraging activity at Khabura, Oman in early summer (8 and 9.v.80) as indicated by numbers of returning foragers/min to an experimental hive (No. 2).

Figures 5.9 and 5.10 To even out short term variations, actual counts were usually made for periods of more than 2 mins, depending on the level of activity. The proportions with different loads were calculated from the relative numbers seen returning with and without pollen and from dissections of samples of approximately 10 bees at each period; they should be considered as reliable estimates rather than absolute - see text for further details. Sunrise: 05.32h Sunset : 18.45h Civil Twilight : 05.07h 19.10h (Oman Standard Time).

APIS MELLIFERA KHABURA Alt. 10m. FIG. 5.9



APIS FLOREA KHABURA Alt. 10m. FIG: 5.10



* : Mean of 2 days

The *florea* in Hive 2 (Figure 5.10) started foraging at c. 06.30h, later in the day than *jemenitica*, as did the natural colony of *florea* FD (between 06.00h and 07.00h though the exact time was not observed). *Florea* 2 reached a peak of foraging activity approximately 3h after *jemenitica* and their foraging continued for much of the rest of the day, at a rather lower rate than the peak, but without the pronounced midday trough and rise in activity before dusk that *jemenitica* exhibited.

These differences in foraging pattern and times cannot be attributed to the two species of honeybee exploiting different floral sources, producing nectar and pollen at different times of day. Analysis of pollen on returning bees (those with pollen loads and those gathering nectar only) showed that *florea* and *jemenitica* were both visiting *Acacia tortilis* and *Prosopis cineraria* almost exclusively. From the proportion of the honeybee samples with each type of pollen, at different times of day, it was estimated that most floral visits (70 - 90%) of *jemenitica* were to *Prosopis* between 05.00h and 07.00h, but after that most (90%) were to *Acacia tortilis* until c. 15.00 - 16.00h when *Prosopis* again became the main source. From c. 06.30h to c. 09.30h *florea* foraged on both *Acacia* and *Prosopis*, but rather more (70%) on the *Acacia*; from c. 10.00h till they stopped (18.00 - 18.15h) they foraged almost entirely (90%) on *Prosopis*. (These percentages exclude visits to unidentified nectar sources - see below.) Thus at times *Prosopis* and *Acacia* were used simultaneously by *florea* and *jemenitica*, but there was some suggestion that the two sources of forage were on the whole being exploited by each species of honeybee at different times of day.

The floral source for 25% of the *jemenitica* foragers, all nectar gatherers, could not be identified (because no pollen type predominated on their bodies; some bees may even have been visiting banana flowers which can produce copious nectar but, in cultivated varieties, rarely any pollen). It was calculated that of the remaining 75% of *jemenitica* foragers (including some gatherers of nectar only), overall 43% had visited *Prosopis* and 32% *Acacia*. Similarly for *florea* 26% of all the foragers were "nectar only" gatherers from unidentified floral sources; of the 74% of foragers whose floral source was identified, 48% had visited *Prosopis* and 26% *Acacia*. Thus the two honeybee species showed a similar preference for *Prosopis* over *Acacia* (and/or more *Prosopis* was available in the locality) and it can be concluded that their differences in foraging times cannot be attributed to differential preferences for or availability of these two trees. (The quoted percentages were determined from calculations based on the total numbers of returning foragers at the different times of day and the proportions carrying *Prosopis* pollen, *Prosopis* nectar, *Acacia* pollen and so on at each time; because the number of bees sampled at each time was small, in the order of 10, the percentages should not be regarded as absolute but I believe they are sufficiently accurate for the above conclusion to be reliable.)

(b) Sayq (1950m), early spring (17-18.ii.80)

The foraging pattern exhibited by *jemenitica* (Figure 5.11) at this locality and season, starting at c. 08.00h and finishing at c. 17.00h with a peak around midday, is typical of the activity pattern of *mellifera* in other areas of temperate climate in spring and summer (Lundie 1925; Lewis & Taylor 1964; Szabo 1980); the continuation of foraging till c. 21.00h in Canada (Szabo 1980) is attributable to the long July evenings.

Excluding water gatherers, it was determined that 91% of the returning *jemenitica* foragers with nectar and/or pollen had been visiting *Prunus* spp. (peach *P. amygdalus* the most abundant fruit tree in the area

Figure 5.11 Daily pattern of *Apis mellifera jemenitica* foraging activity at Sayq, Oman in early spring (17-18.ii.80) as indicated by numbers of returning foragers/min to a Langstroth hive. Most of the workers with "nothing" at 11.00h, from their pilosity and lack of pollen, were probably young bees on orientation flights.

Figure 5.12 Daily pattern of *Apis florea* foraging activity at Sayq, Oman in early spring (17-18.ii.80) as indicated by numbers of returning foragers/min to an experimental hive (No. 9); the bees were not rearing brood though the queen was ovipositing.

Figures 5.11 and 5.12 To even out short term variations, actual counts were usually made for periods of more than 2 mins, depending on the level of activity. The proportions with different loads were calculated from the relative numbers seen returning with and without pollen and from dissections of samples of approximately 10 *mellifera* and 5 *florea* at each period; they should be considered as reliable estimates rather than absolute - see text for further details.

Sunrise: 06.42h Sunset: 18.06h Civil Twilight: 06.20h and 18.29h (Oman Standard Time)

APIS MELLIFERA SAYQ Alt. 1950 m. FIG. 5.11

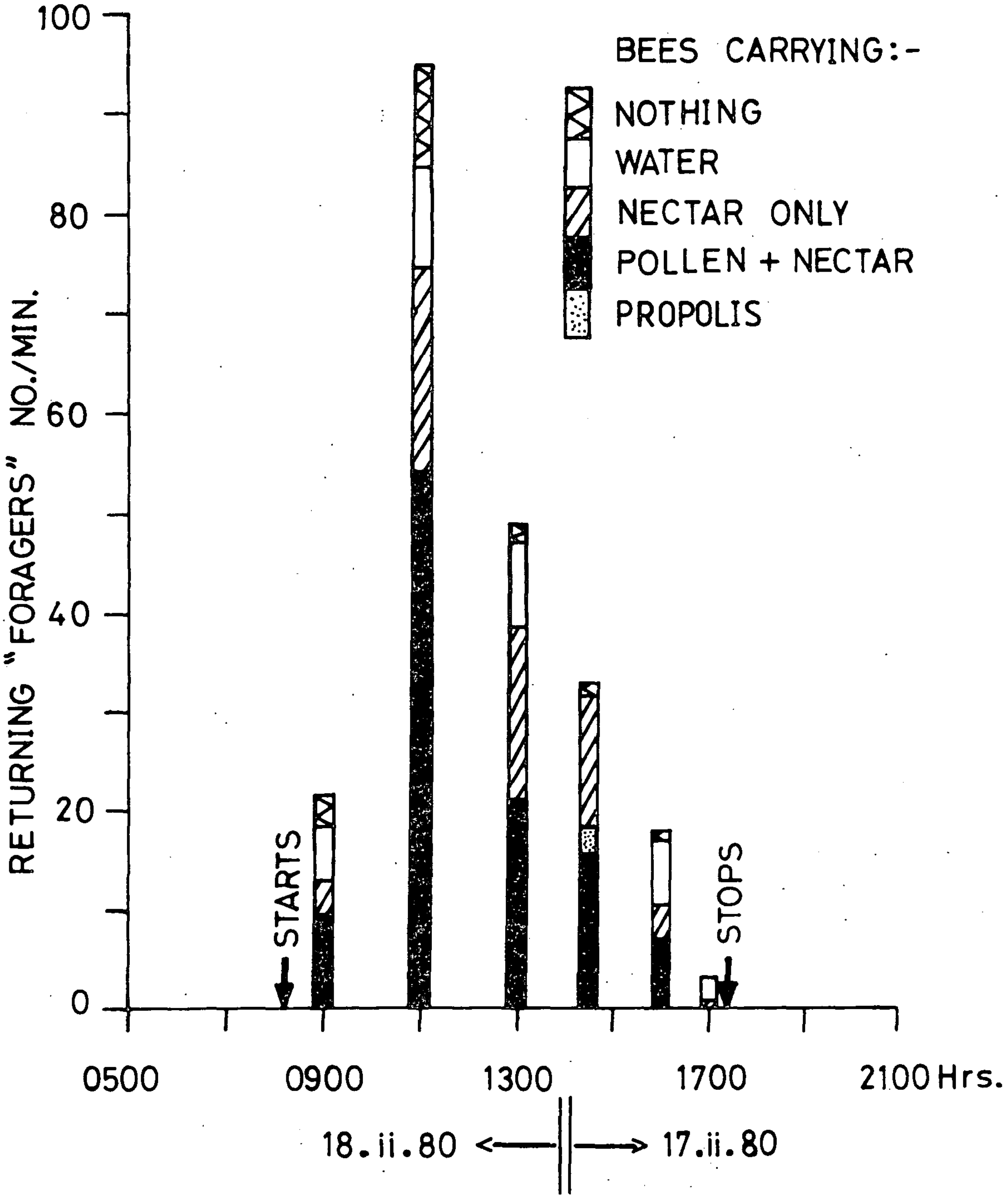
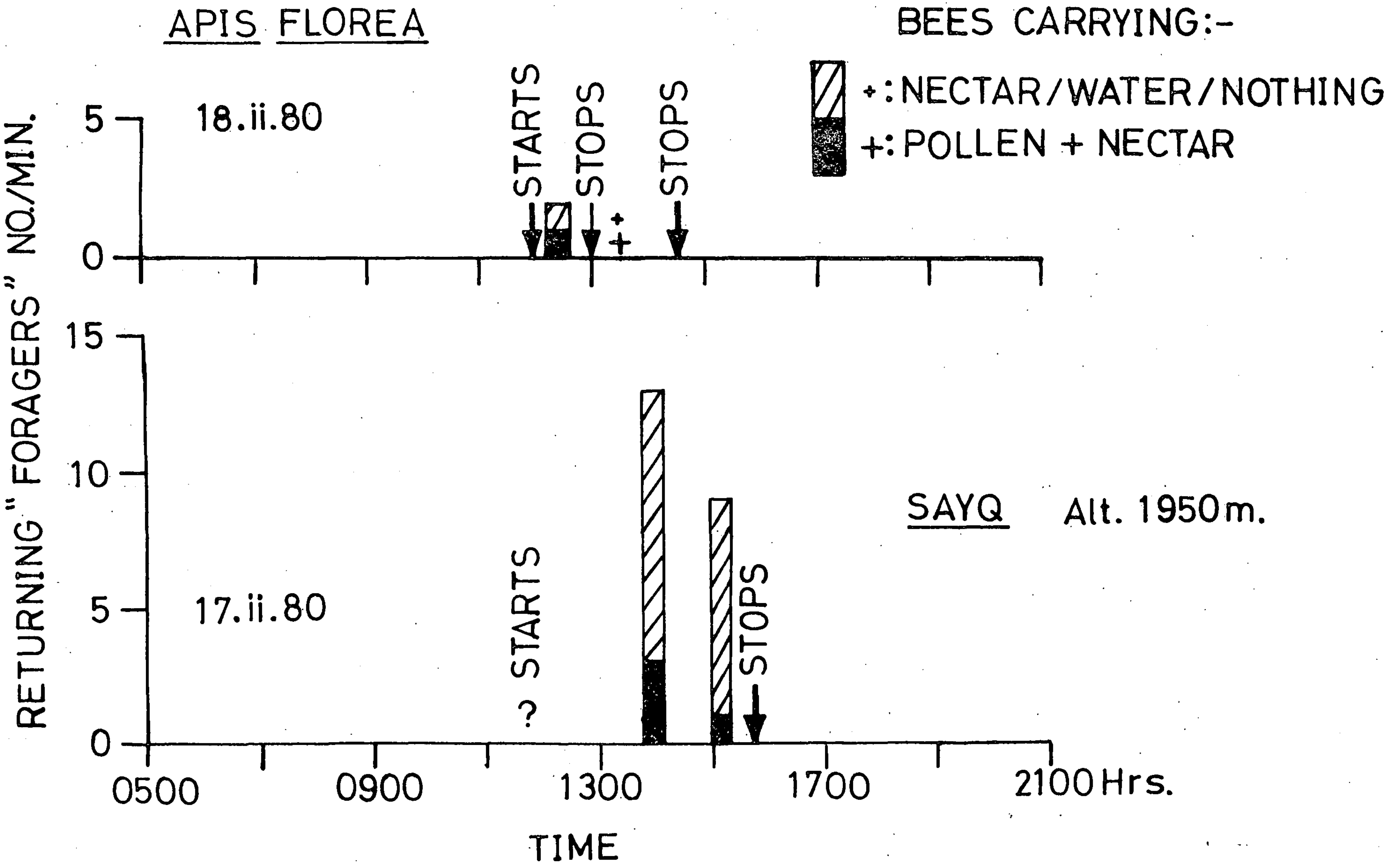


FIG. 5.12


APIS FLOREA
BEES CARRYING:-
+: NECTAR/WATER/NOTHING
+: POLLEN + NECTAR
18.ii.80
STARTS
STOPS
STOPS
17.ii.80
? STARTS
STOPS
SAYQ
Alt. 1950m.
RETURNING "FORAGERS" NO./MIN.
0
5
10
15
0500
0900
1300
1700
2100 Hrs.
TIME

was thought to be the main source, but its pollen could not be distinguished from that of almond *P. armeniaca*, plum *P. domestica* and apricot *P. dulcis* which also occurred); 5% had been visiting *Sisymbrium erysimoides* and 4% *Silene apetala*. 34% of the *Prunus* visitors had collected nectar only, 66% nectar and pollen or pollen only, though a number of the pollen loads were quite small.

In contrast, *florea* (Figure 5.12) could hardly manage to forage at all over the range of ambient temperatures prevailing (6.7^{o} - 20.2^{o}C, Figure 5.7). Pollens of *Prunus* spp., *Euphorbia* sp. and apparently *Citrus* sp. (no such trees were noticed in the vicinity but the winter temperatures were probably just high enough for them to be grown) were identified on samples of those few bees that were foraging. Therefore, given the abundance of nectar and pollen that the *jemenitica* were harvesting from *Prunus* for much of the day, lack of forage cannot have been responsible for the observed inactivity of *florea*. Temperature was the obvious limiting factor and it was apparent that some of those workers that did forage had difficulty in maintaining their flight when returning to their hive. They did not always land on the colony directly, but on nearby vegetation and after a short period (presumably of "warm-up" by microcontractions of their thoracic muscles and in opposition, to prevent flight) would make another attempt to enter the hive, hovering uncertainly before landing. Ambient temperatures of 18^{o}C, particularly when there is little sunshine to warm the bees directly, must be the approximate lower limit for *florea* flight activity and the unusual flight behaviour above I attribute to temperatures too low for normal flight.

(c) Rustaq (300m), early spring (12-13.ii.79)

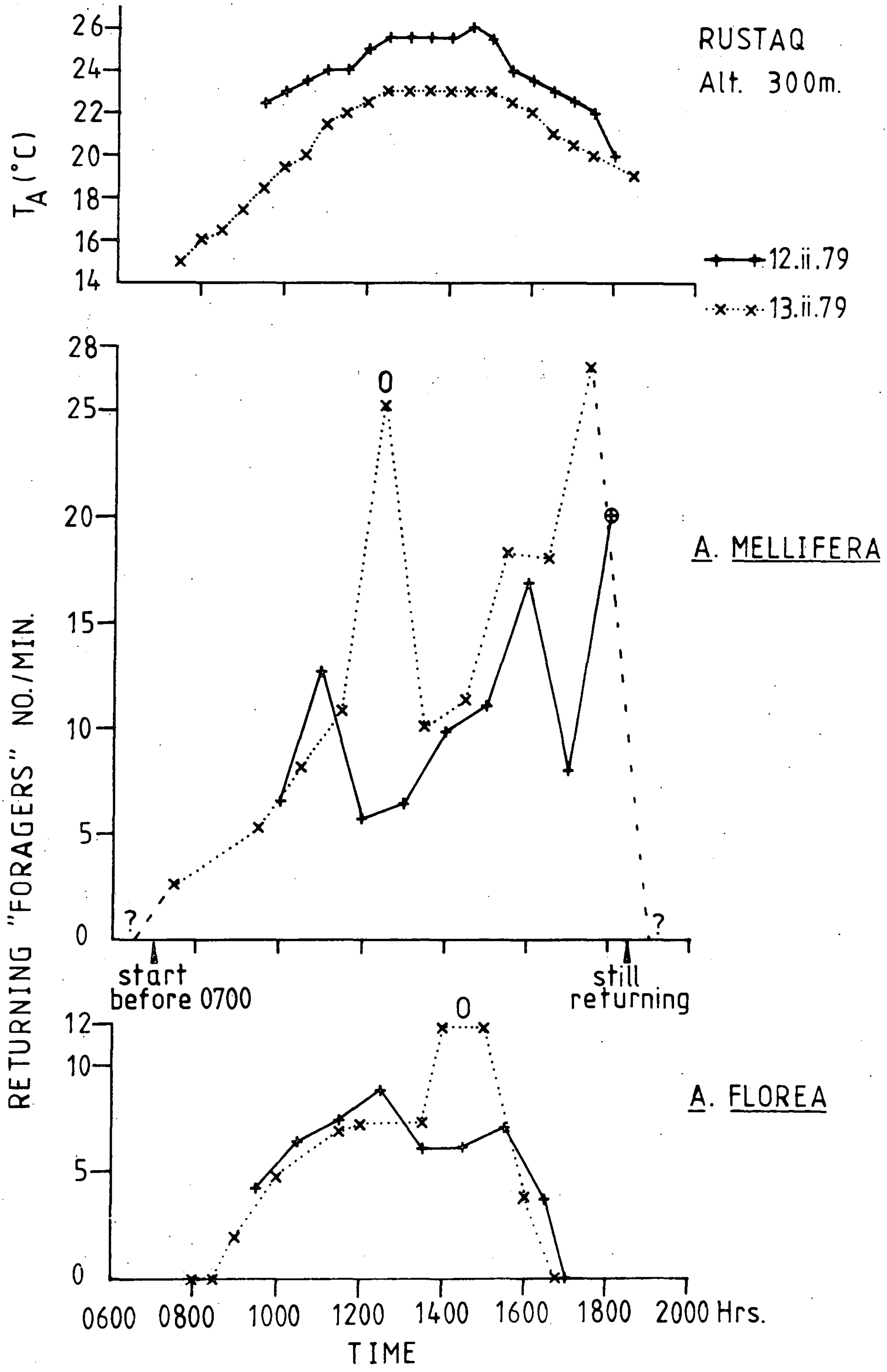
Here the principal difference between the foraging patterns of *jemenitica* and *florea* was in the overall period of activity (Figure 5.13). *Jemenitica* started foraging before 07.00h but *florea* only at 08.30h. *Jemenitica* foragers continued returning until after sunset (18.05h) and until at least 18.20h when light levels were already too low for counts to be possible. *Florea* had stopped foraging by 17.00h, about an hour before sunset.

On the warmer day (12.ii.79, maximum 26°C), peak flight activity by *florea* was around 12.30h, but on 13.ii.79 when it was rather cooler (maximum 23°C) the peak appeared to be a little later (around 14.00h) and was probably over-accentuated by the orientation flights of young workers. On both days, the colony of *jemenitica* reached its peak of foraging activity a little before the *florea* colony. There was a drop in *jemenitica* activity in the early afternoon, the hottest part of the day, but this was not as marked as the corresponding trough at Khabura (Figure 5.9) when T_A were considerably higher. As at Khabura in summer, *jemenitica* exhibited another peak of activity in the late afternoon as it became cooler but, as at Khabura also (Figure 5.10), a distinct second foraging peak did not occur with the colony of *florea*.

Thus, as at Khabura and Sayq, the diurnal foraging patterns of *jemenitica* and *florea* seemed to be markedly different, the former starting foraging and reaching a peak of activity at lower T_A than the latter, and appearing less active during the hottest periods. As at the other sites such differences could not be attributed to the exploitation, by the two honeybee species, of different plants. Though samples of pollen were not taken at regular intervals from returning foragers as at Khabura and Sayq, analysis of pollen loads gathered between 8 and

Figure 5.13 Ambient temperatures (T_A) and patterns of *Apis mellifera jemenitica* (in a Langstroth hive) and *Apis florea* (in an experimental hive, C) activity, as indicated by numbers of returning foragers/min, at Rustaq, Oman in early spring; both colonies were rearing brood. To even out short term variations, actual counts were usually made for periods of more than 2 mins, depending on the level of activity. From the behaviour of some bees that circled in flight around the hives, some of the peaks (O) were exaggerated by workers on orientation flights. The point ⊕ on the *jemenitica* graph was an estimate as poor light made an accurate count impossible. The minimum T_A on 14.ii.79 was 10.5°C giving an indication of the lower range of T_A experienced.

Sunrise: 06.44h Sunset: 18.05h Civil Twilight: 06.21h and 18.28h (Oman Standard Time).


RUSTAQ
Alt. 300m.
T_A (°C)
26
24
22
20
18
16
14
12.ii.79
13.ii.79
RETURNING "FORAGERS" NO./MIN.
28
25
20
15
10
5
0
0
?
?
⊕
A. MELLIFERA
start
before 0700
still
returning
12
10
5
0
0
A. FLOREA
0600
0800
1000
1200
1400
1600
1800
2000 Hrs.
TIME

14.ii.79 showed that *Citrus* spp., *Ocimum* spp., *Phoenix dactylifera, Vicia faba* and *Asphodelus fistulosus* were the main sources of forage for both species of honeybee. Most of the samples analysed were from *florea* and as a result additional floral sources were revealed for this species, including members of the Compositae (probably *Launaea* sp., *Vernonia cinerea, Flaveria trinerva*), Cruciferae (probably *Diplotaxis harra* and/or *Physorrhynchus chamaerapistum)* and Euphorbiaceae. Therefore there were no data to suggest that the reduced periods of activity of *florea* in the early morning and late afternoon were attributable to absence of forage. Indeed it was evident that most of the bees contributing to the *jemenitica* foraging peak before dusk were visiting a crop of *Vicia faba* near to the hive and that *florea* had also been visiting this earlier in the afternoon; therefore *florea* foraging must have ceased when there was still ample nectar and/or pollen available. No interference competition between *florea* and *mellifera* on flowers was observed in Oman and in general this is dismissed as an explanation for the early cessation of foraging by *florea* and certainly in the above situation when forage was obviously in good supply.

Finally, the performance of these flight activity experiments at Sayq and Rustaq at almost exactly the same season (17-18 February and 12-13 February respectively, albeit in different years and with different forage available) when the times of twilight, sunrise and sunset and so on were almost identical, means that light levels and set diurnal rhythms can be ruled out as major factors determining flight times and activity levels, ie barring cloudy periods, light levels will have been the same at each locality during the course of a day but the activity patterns at the two sites were completely different for both species.

2.2 Relationship between foraging activity and ambient temperature

(a) Khabura, early summer (8-9.v.80)

Under the conditions at Khabura in early summer, regression plots of *jemenitica* activity against T_A showed that there was an inverse relationship between the two, whether activity was considered in terms of numbers of bees leaving (Figure 5.14) or returning (Figure 5.15), and that the negative correlations were significant. For both species at all 3 sites the numbers leaving and returning were generally similar to each other over a short period, though slightly out of phase for obvious reasons. Therefore, apart from Figure 5.14 only one set of activity data are presented for each species at the 3 sites and that is numbers returning since it was for this category that the proportions of bees gathering water, nectar and so on was known.

At Khabura there was a negative correlation for *florea* activity at $T_A \geqslant 32^{\circ}C$ (Figure 5.16), comparable to that for *jemenitica* at a slightly lower range of T_A. However, the graph does suggest also that *florea* activity <u>increases</u> from low levels at $25.5^{\circ}C$ to a peak near $32^{\circ}C$ (but the T_A increase over this range during the morning of 9.v.80 was so rapid that only one recording of activity was made during this period). In contrast, *jemenitica* activity generally decreased over the whole range $22.5^{\circ}C - 37.5^{\circ}C$. Overall the data suggest there is a close link between honeybee activity and T_A, but that the optimal range of T_A is not the same for the two species.

(b) Sayq, early spring (17-18.ii.80)

The few points on the flight activity - T_A plot for *jemenitica* at Sayq (Figure 5.17) suggest there may be a good positive correlation between the two from $12^{\circ}-20^{\circ}C$ if pre-13.00h activity alone or post 13.00h

Figure 5.14 Regression of *Apis mellifera jemenitica* (in a Langstroth hive) activity, as indicated by number of workers leaving/min, on ambient temperature at Khabura, Oman in early summer. Recordings correspond to those in Figure 5.9 and Figure 5.15. The dusk and orientation values were excluded from the calculations.

Figure 5.15 Regression of *Apis mellifera jemenitica* (in a Langstroth hive) activity, as indicated by number of workers returning/min, on ambient temperature at Khabura, Oman in early summer. Data as in Figure 5.9 and corresponds to that in Figure 5.14. The dusk and orientation values were excluded from the calculations.

Figure 5.16 Regression of *Apis florea* (in an experimental hive, No.2) activity on ambient temperature at Khabura, Oman in early summer, as indicated by the numbers of bees returning/min. Data as in Figure 5.10. The point at 27°C, when activity is increasing, is excluded from the calculations which refer to the temperature range over which foraging decreased; the final value when it is believed the bees were anticipating dusk is also excluded.

KHABURA Alt. 10m. APIS MELLIFERA

FIG. 5.14

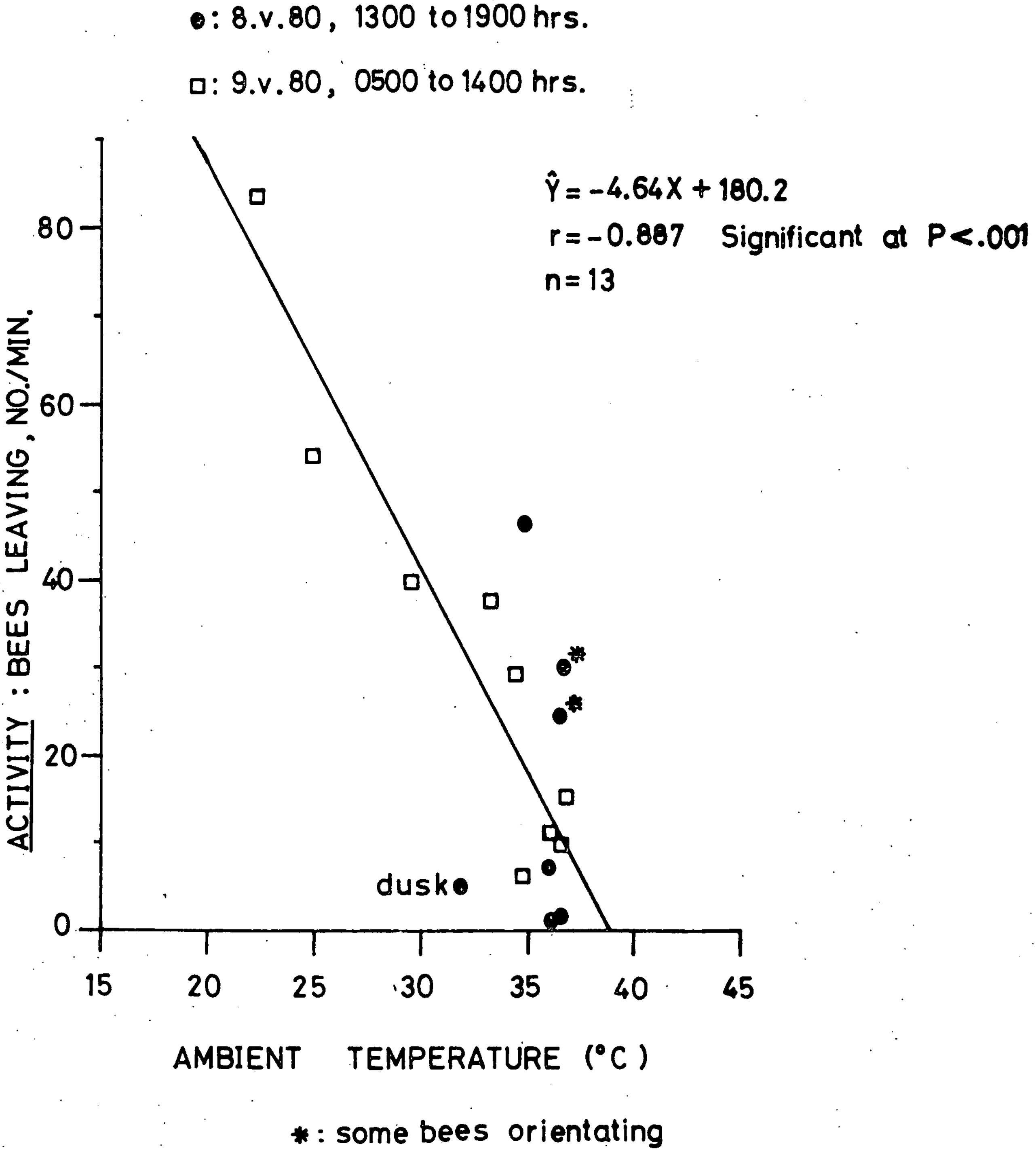


FIG. 5.15

KHABURA Alt. 10m. <u>APIS MELLIFERA</u>

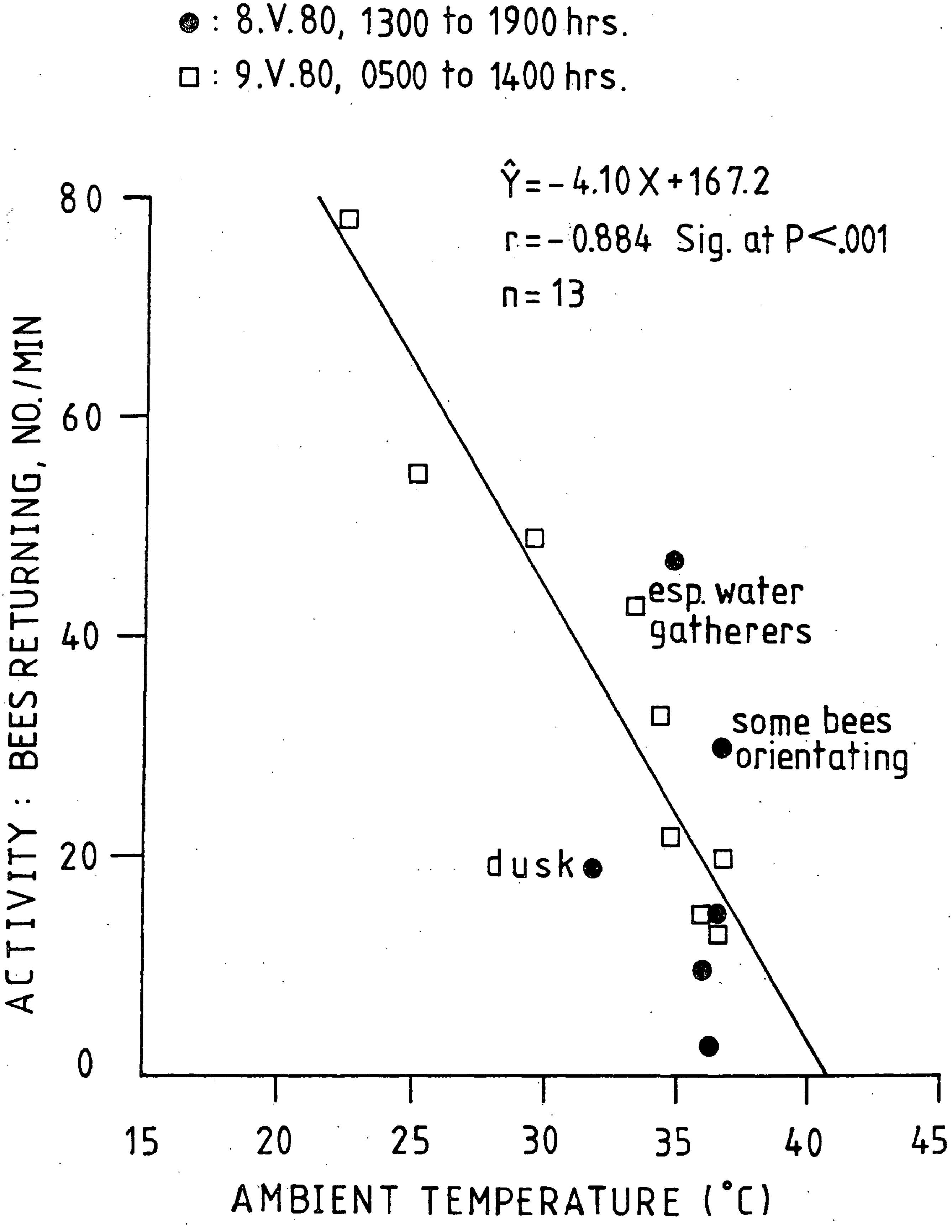


FIG. 5.16

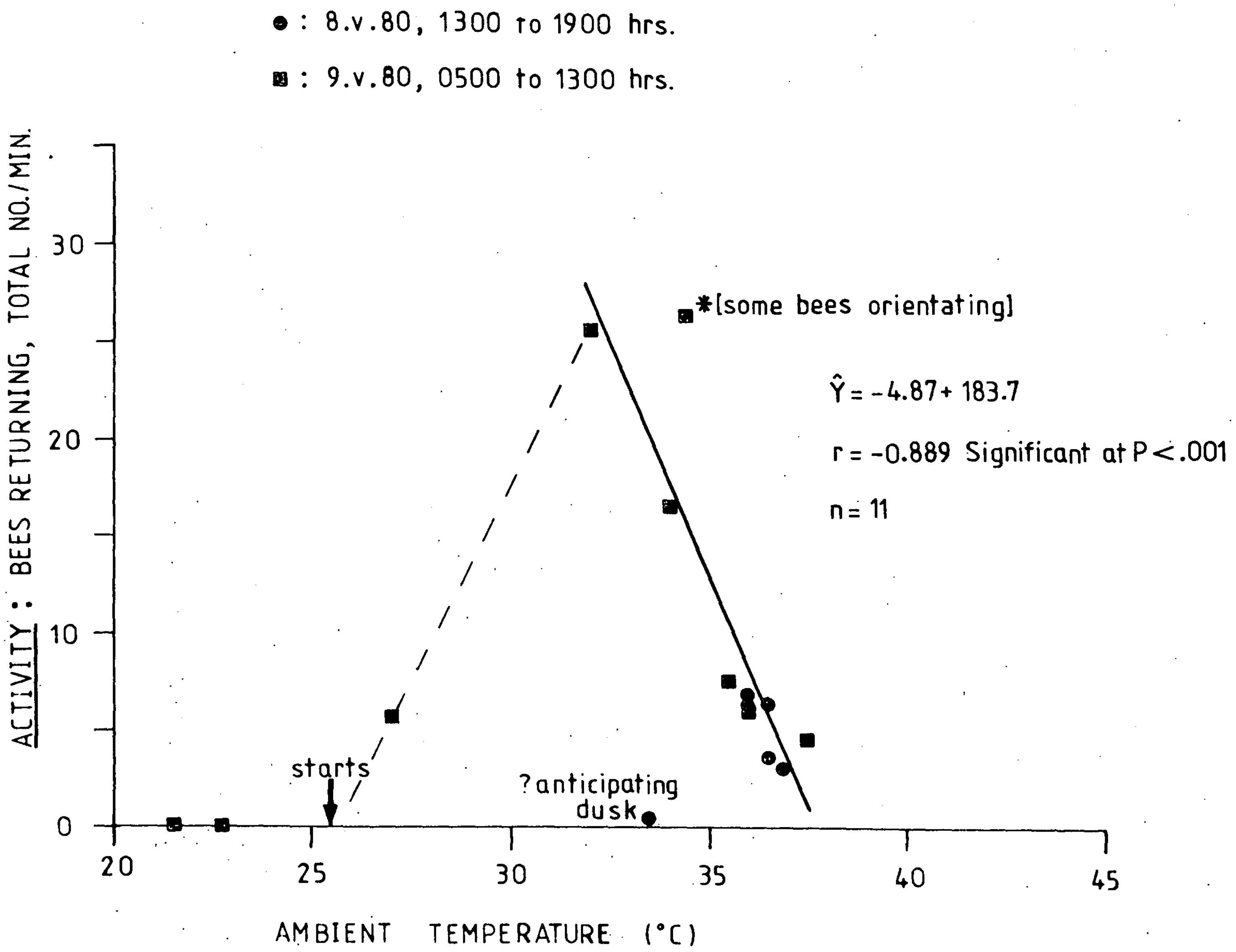

● : 8.v.80, 1300 to 1900 hrs.
▨ : 9.v.80, 0500 to 1300 hrs.
ACTIVITY : BEES RETURNING, TOTAL NO./MIN.
0
10
20
30
20
25
30
35
40
45
AMBIENT TEMPERATURE (°C)
*[some bees orientating]
Ŷ = -4.87+ 183.7
r = -0.889 Significant at P < .001
n = 11
starts
? anticipating dusk

Figure 5.17 Regression of *Apis mellifera jemenitica* (in a Langstroth hive) foraging activity, as indicated by numbers of returning foragers/min, on ambient temperature, at Sayq, Oman in early spring. Data as in Figure 5.11.

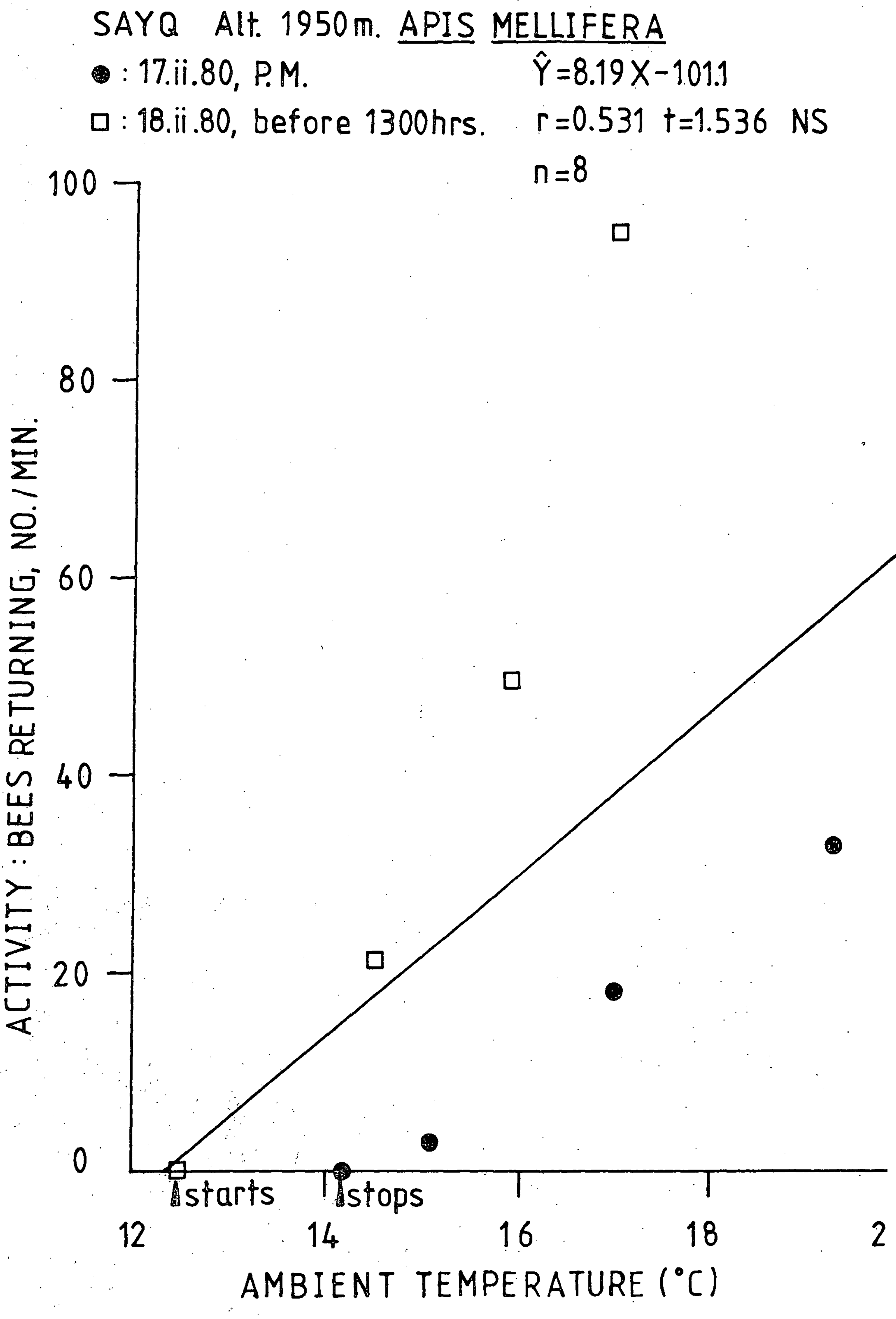

SAYQ Alt. 1950m. APIS MELLIFERA
● : 17.ii.80, P.M.
□ : 18.ii.80, before 1300hrs.
$\hat{Y}=8.19X-101.1$
r=0.531 t=1.536 NS
n=8
ACTIVITY : BEES RETURNING, NO./MIN.
100
80
60
40
20
0
starts
stops
12
14
16
18
2
AMBIENT TEMPERATURE (°C)

Figure 5.18 Regressions of *Apis mellifera jemenitica* (in a Langstroth hive) foraging activity on ambient temperature (T_A), as indicated by numbers of returning foragers/min, at Rustaq, Oman in early spring. 4 different regression equations were calculated and lines drawn by analysing separately the data from each day, T_A being higher overall on 12.ii.79 (2) than on 13.ii.79 (1), and the data for T_A's above (3) and below (4) 22°C separately. No significant correlations, however, were obtained. Data as in Figure 5.13, Or indicating some of the bees were on orientation flights and ●? that the figure was an estimate only, because of poor light levels.

STATISTICS

	r	t	Sig.	n
(1) $y = 1.58x - 19.51$	0.495	1.613	NS	10
(2) $y = -1.63x + 49.69$	-0.603	2.00	NS	9
(3) $y = -1.9x + 57.1$	-0.399	-1.375	NS	12
(4) $y = 2.09x - 27.53$	0.534	1.41	NS	7

Figure 5.19 Regressions of *Apis florea* (in an experimental hive, C) foraging activity on ambient temperature (T_A) as indicated by numbers of returning foragers/min, at Rustaq, Oman in early spring. 3 different regression equations were calculated and lines drawn, by analysing the data from the two days (12 and 13.ii.79) separately (1) and (2) and together (3); there was a significant correlation between activity and T_A in each case. * represents 2 points, both high because bees returning after orientation flights are included.

STATISTICS

	r	t	Sig.	n
(1) $y = 1.32x - 26.3$	0.731	2.835	$p<0.5$	9
(2) $y = 1.39x - 23.6$	0.774	3.456	$p< .01$	10
(3) $y = 0.83x - 12.98$	0.589	3.005	$p< .01$	19

activity alone were considered. Over the whole day, however, there was no significant correlation between activity and T_A. Perhaps the nectar secretion and/or pollen presentation levels of the *Prunus* spp. being exploited had dropped in the afternoon and/or some of the standing crop of nectar and pollen that may have been available in the morning could have been depleted, so the rewards of foraging and thus the numbers of bees active later in the day were lower. Though not providing any explanation, Szabo (1980) also recorded lower levels of flight activity in the afternoon than in the morning at equivalent temperatures and Hambleton (1925) recorded that foragers did not desert the field in the evening for lack of nectar and that foraging ceased at T_As higher than those at which it started in the morning. In a flight room Nelson & Jay (1968) recorded a bimodal pattern in daily flight activity, the afternoon peak being lower. Thus honeybee flight activity cannot solely be determined by T_A, but must be influenced by other factors such as forage availability, colony requirements (for nectar, pollen and water) and even a diurnal rhythm.

Insufficient *florea* flight activity occurred at Sayq for a graph or statistical analysis of its relationship with T_A. However, examination of Figures 5.7 and 5.12 indicates that activity was greatest between 13.30h and 15.30h on 17.ii.80 when T_A were highest (18°-20°C) and was effectively zero at lower T_A. The observations were therefore consistent with a hypothesis that *florea* activity is positively correlated with T_A from 18° to perhaps 30°C or more. Yet at Khabura no foraging activity was recorded from *florea* 2 until T_A was 25.5°C. This suggests either that foraging at "low" T_A (18° - 25°C) is suboptimal and only occurred at Sayq to compensate for dwindling food reserves and/or that some acclimatisation occurs to different temperature regimes, with corresponding adjustment in foraging activity responses ie colonies kept in a cold environment start and stop foraging at lower T_A than colonies kept in hot environments.

It has been shown (Free & Spencer-Booth 1960, 1961) that acclimatisation to lower temperatures of worker honeybees (*cerana* and *mellifera*) reduces their chill-coma temperature and that survival of individual *mellifera* workers around their upper lethal temperature (c. 47°C) is greater after acclimatisation to 35°C than to 20°C (Free & Spencer-Booth 1962). Verma & Edwards (1971) have also shown for *mellifera* and *cerana* that tolerance of high and low temperatures are altered by acclimatisation. Thus acclimatisation may also change the range of T_A over which foraging activity occurs, though with consistently high brood nest temperatures how such acclimatisation by individual foragers might occur is not immediately apparent. However, *mellifera* foragers tend to keep away from the brood nest when inside the hive, particularly at night (Free 1960), so are subject to lower temperatures than young bees (Free & Spencer-Booth 1960); therefore the temperatures foragers experience may indeed be influenced by those external to the hive, thus resulting in a degree of acclimatisation to the T_A regime prevailing at a site. This is even more likely to be the case for *florea* foragers as Seeley *et al* (1982) have shown that when not foraging (night-times, rainy days and so on) these workers form the outermost layer of a colony's protective curtain where exposure to T_A will be the greatest.

Hence with *florea* T_C at Sayq (Figure 5.7) falling at least 7°C below the usual T_B (Figure 5.6) it is easy to see that acclimatisation could explain the initiation of foraging at Sayq at T_A 7°C below that observed at Khabura. Indeed the exposure of the nest and foragers of *florea* and the less stable thermoregulation than *mellifera* (Figure 5.6) may well mean that the flight activity of *florea* foragers is influenced by acclimatisation to a greater extent than that of *mellifera* foragers.

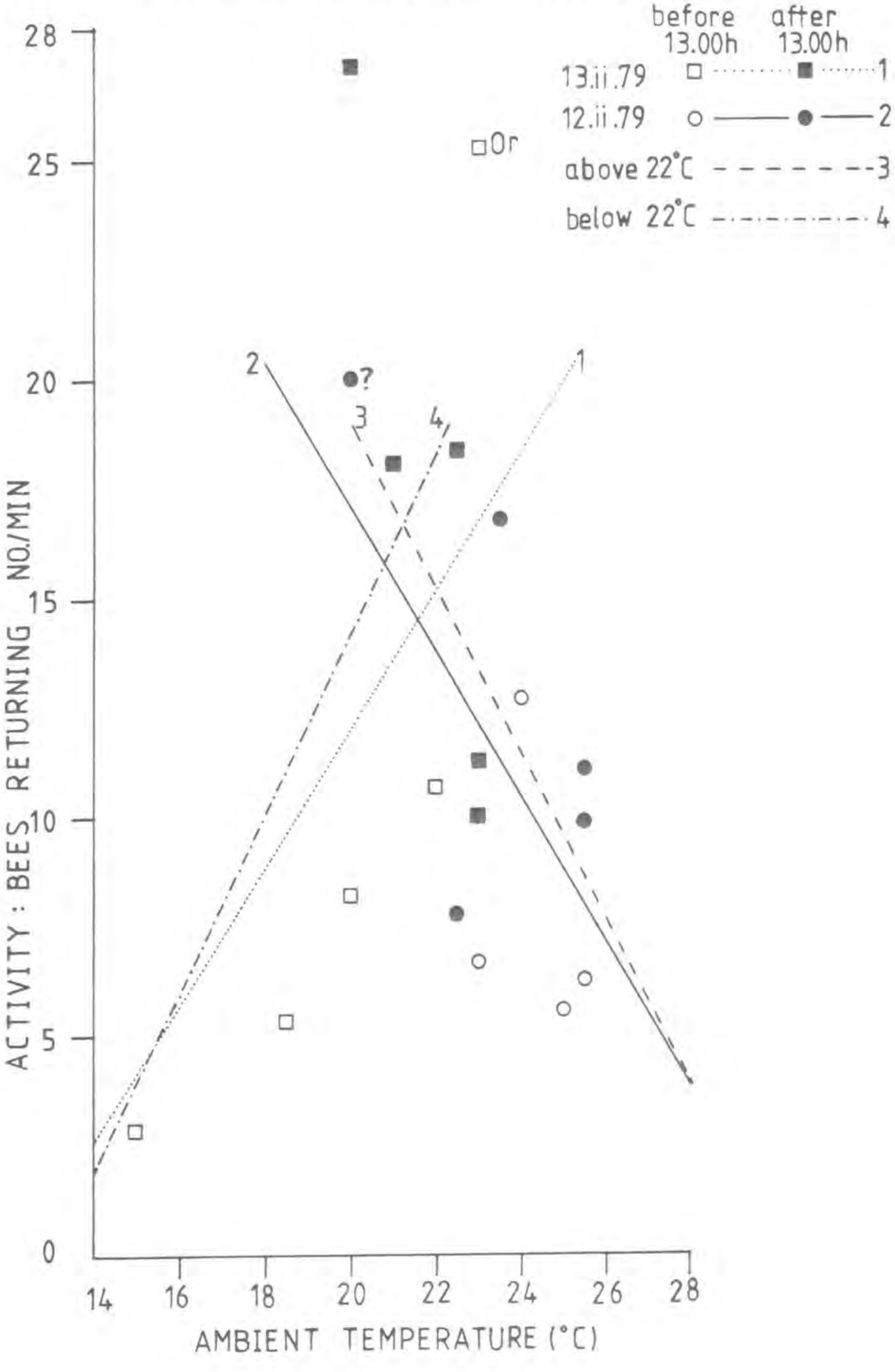
(c) Rustaq, early spring (12-13.ii.79)

Although Figure 5.13 might have given the impression that *jemenitica* flight activity at Rustaq was related to T_A, regression analyses of plots of activity against T_A (Figure 5.18) were not significant. This was the case when recordings from each day were considered separately (12.ii.79 being generally hotter than 13.ii.79) and also when activity levels at T_A above and below 22°C (a possible optimum temperature) were analysed separately. Despite their statistical insignificance, the positions of the regression lines did hint that foraging activity increased from 15-22°C and started to drop above 23°C. Therefore, though significant temperature - activity relationships may exist and be clearly evident under some conditions (eg Khabura, early summer, Figure 5.14), other factors such as forage availability, humidity, wind, light levels and radiant energy, and colony strength and requirements, are likely to obscure the influence of ambient temperature; this may be particularly so around the optimum T_A for a species, as here at Rustaq for *jemenitica*.

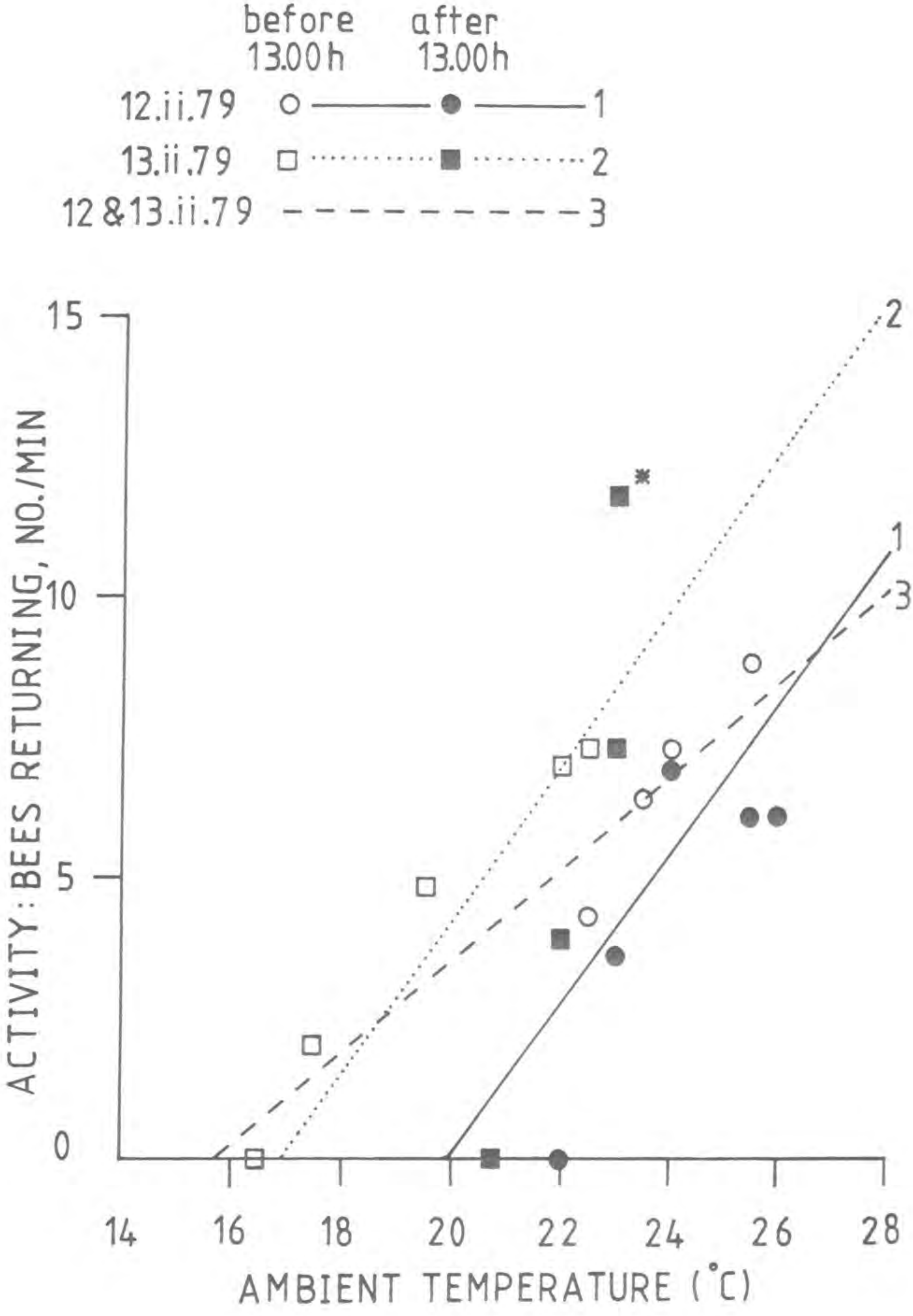
Measurements of as many appropriate variables as possible, followed by multiple regression analysis, would be needed to elucidate the relative roles of these other factors that influence flight activity. With meteorological and soil conditions affecting nectar secretion and pollen presentation as well (see Introduction 2.1), it is unlikely that the results of analyses at one site would ever allow really accurate prediction of levels of foraging activity at another. Nevertheless, with the influence of T_A seeming to be of particular importance it should be possible to forecast general activity trends and approximate light and temperature thresholds for *mellifera* and the other *Apis* species.

RUSTAQ Alt. 300m. APIS MELLIFERA

FIG. 5.18



RUSTAQ Alt. 300 m. <u>APIS</u> <u>FLOREA</u> FIG.5.19



For *florea* at Rustaq a significant positive correlation between flight activity and T_A was recorded, whether 12 and 13.ii.79 were considered separately or together; thus over a range of 17° - 26°C, as was predicted from the results at Khabura and Sayq, foraging activity increased with T_A. It seemed that a higher T_A was required on 12.ii.79 (the warmer day) to produce levels of activity corresponding to those on the cooler day (13.ii.79), but the shift in the position of the regression line was possibly exaggerated by the absence of recordings early in the morning of 12.ii.79 when the lowest activity levels would have occurred. Nevertheless acclimatisation, as discussed in the previous section, during a cold night between 12 and 13.iii.79, might have been partially responsible for the greater activity at lower temperatures on 13.ii.79. Alternatively Figure 5.13 could be interpreted as showing an element of diurnal rhythm in the foraging activity of *florea*, that was independent of T_A. The correlation between activity and T_A might thus be attributed to T_A changes co-incidentally following the same diurnal pattern as *florea* activity. However, as already mentioned in 2.1 (c), the fact that *florea* at another, colder site showed a completely different activity pattern at the same time of year is contrary to a fixed diurnal rhythm explanation and the direct role of climatic factors, especially of T_A is indicated.

Overall then, the explanation of foraging activity at Rustaq mainly in terms of T_A appears to be satisfactory for both *florea* and *mellifera*, but it must be stressed that this was evidently not the only determining parameter involved. Furthermore, the temperature relationship was consistent with the results from Khabura and Sayq with little foraging at 18°-20°C (none at Khabura) but activity then increasing up to temperatures of 32°C (Khabura, Figure 5.16), before falling to low levels again between 32° and 37.5°C. It should be mentioned, though, that similar recordings conducted on colonies at a site in the Wadi Hawasina from 15-17.v.80, but not presented here, showed that both *mellifera* (*jemenitica* x "Australian" hybrid) and *florea* workers would continue to forage when T_A was even higher (42^o-43^oC); nectar as well as water was being gathered by each species.

DISCUSSION

1. Colony thermoregulation

The evidence presented on thermoregulation confirms the earlier reports (Lindauer 1957; Akratanakul 1977; Free & Williams 1979) that *florea*, like the other *Apis* species (Seeley & Heinrich 1981) and some stingless bees (Fletcher & Crewe 1981), maintains a relatively high brood nest temperature over a wide range of T_A. However, particularly at low T_A, the *florea* colonies were not able to maintain such precise control as *jemenitica* which thermoregulated effectively and reared brood at T_A from 7^o to 37^oC and above. The difference is of considerable ecological significance but perhaps not surprising when one considers that *florea* has a small, exposed, single-combed nest and *mellifera* a larger, enclosed, multiple-combed nest providing much more insulation for the brood. With forage available at Sayq in early spring, I am certain that the high energy cost of thermoregulation (and of foraging) at low T_A for this species with an exposed nesting habit, was responsible for the absence of brood in the *florea* colony kept there. Conversely, the exposed nesting habit may be advantageous to *florea* in facilitating ventilation and evaporative cooling at high T_A and Figure 5.6 indicates there is little difference in the T_B of *florea* and *jemenitica* at T_A above 35^oC. Further studies are required to see if *florea* needs to devote a smaller proportion of its worker force to cooling activities than *mellifera* at high T_A.

Whether as a result of this poorer temperature control *florea* brood is less susceptible than *mellifera* brood to damage at temperatures below c. 30°C and/or higher than c. 36°C also needs investigation (T.D. Seeley, pers. comm.). The results here and others not presented, however, have shown that *florea* is like *mellifera* (Lensky 1964a; Seeley & Heinrich 1981) in that it exerts relatively little thermoregulatory control over areas of honeycomb, but does maintain some control over the temperature of non-brood rearing clusters (eg in winter); the latter not within narrow limits like T_B but allowing fluctuations with T_A, presumably to reduce the rate of fuel utilization.

Finally, these conclusions on the poorer thermoregulatory abilities of *florea* concur well (i) with those on nest site selection (especially Chapter II) that colonies, except perhaps in summer, are seeking sites which provide a degree of warming insolation, particularly in the morning and (ii) with those on the annual cycle (Chapter VI) showing that brood rearing is reduced or absent in a greater proportion of colonies in the cooler months than at any other time of year, even though more forage appears to be available in winter than in summer (Chapter VII).

2. Foraging activity

In brief, the results have shown that at a given locality and season, *florea* did not forage at such low T_A as *jemenitica*, reached a peak of activity at a higher T_A (c. 30°-32°C compared to c. 22°C) and had a larger proportion of foragers remaining active at even higher T_A (eg 34°C) when *jemenitica* foragers were relatively few and mainly water gatherers. The evidence on foraging/flight activity therefore also concurs with the results on colony thermoregulation in that they suggest that *florea* is less well adapted than *jemenitica* to low T_A, but are well adapted to cope with a high range of T_A.

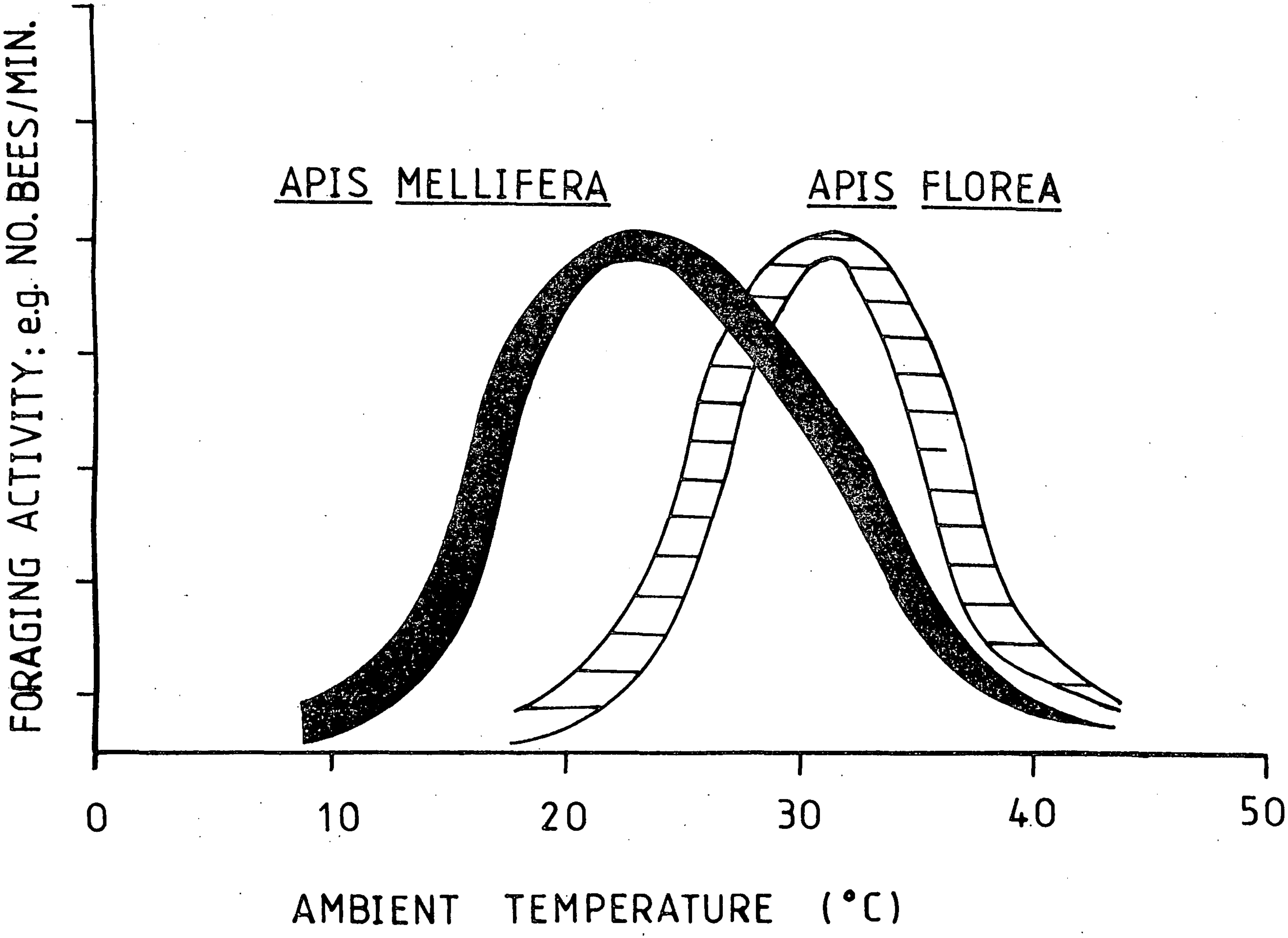
Field observations on foraging, pollen analyses throughout northern Oman (Chapter VII) and the pollen analyses associated with these particular recordings have shown that the 2 species of honeybee in general and during these experiments used at least some of the same plant species for nectar and pollen; indeed the major plants during the recordings at Khabura, Sayq and Rustaq were the same for *florea* and *jemenitica*. The knowledge that *florea* and various *mellifera* races (Lensky 1964a; Gary 1967; Whitcombe 1980, unpublished recordings in the Wadi Hawasina, Oman p. 226) are able to fly at T_A over 40°C indicates that *jemenitica* were opting to reduce their foraging activity at the higher T_As at Khabura, in spite of some forage being available at such times, sufficient at any rate for *florea*.

Though the literature discussed in the introduction to this chapter and the results for *jemenitica* from Sayq and Rustaq demonstrate that the level of foraging activity cannot be explained in terms of T_A alone, the results from Khabura and of investigations such as those of Nelson & Jay (1967), Szabo (1980) and Burrill & Dietz (1981) indicate that a close correlation can exist between the two. However, the regression of *mellifera* flight activity against T_A at Khabura in summer showed that there was a significant negative relationship, while the results in the literature quoted all show a positive relationship. These latter data were obtained under temperate conditions and comparison of my data with those of Szabo (1980) shows that the range of T_A over which the recordings were made barely overlapped; Szabo's maximum T_A was 22°C, the minimum T_A for the Khabura recordings. Approximately 22°C is in fact the T_A at which maximum foraging activity was recorded both in Canada and at Khabura. I believe this is not a coincidence and that a T_A near 22°C represents a rough optimum for the species as a whole, though minor differences between races may exist.

If the evidence from these two sets of data and other sources are combined to give the near total range of T_A that colonies of *mellifera* experience at all seasons and bee-keeping latitudes, a graph of the pattern presented in Figure 5.20 might be expected. These data and patterns for honeybees are in part contrary to the hypothesis of Taylor (1963) that insects have upper and lower temperature thresholds for flight and that between them the proportion of insects in flight may be independent of T_A. Thresholds do appear to exist (c. 9°C and over 46°C with water available according to Heinrich 1979b and 1980b), but levels of activity between them definitely vary with T_A.

Though Figure 5.20 may demonstrate the influence of T_A alone fairly satisfactorily it is an oversimplification of the situation in nature where levels of radiation (for vision and direct warming of workers), hunidity, wind, nectar and pollen availability and so on will also determine the actual levels of foraging. The width of the curve is intended to demonstrate the variability of the temperature response as a result of these other factors and acclimatization, but clearly cannot cover all eventualities eg foraging will be zero, whatever T_A, in conditions of complete darkness and/or high wind and rainfall. Thus, as was exemplified at Khabura, low visible (to the honeybee) light levels appeared to restrict the activity of *jemenitica* early in the morning and late in the evening in summer, when T_A was several degrees above the threshold (c. 12°C at Sayq) for flight activity. However, observations of night-time foraging by African *mellifera* (Fletcher & Tribe 1977) and of *jemenitica* in northern Oman (M. Manley, pers. comm.) indicate that under certain environmental conditions (perhaps in hot months with low day-time forage availability, but high forage demand from the colony) little light is required when foraging is essential.

Figure 5.20 Sketch indicating the possible overall relationship between foraging activity and ambient temperature (T_A) for *Apis mellifera* and *Apis florea*. The width of the curves demonstrates that a range of activity levels will occur at any one T_A for each species because of acclimatization and the influence of other factors such as forage availability, light levels, wind and so on, as discussed in the text. The full range will be greater than these widths indicate, but it is hypothesized that this type of relationship between activity and T_A should hold when these other variables are constant.


APIS MELLIFERA
APIS FLOREA
FORAGING ACTIVITY: e.g. NO. BEES/MIN.
0
10
20
30
40
50
AMBIENT TEMPERATURE (°C)

For foraging bees that are partially ectothermic, the warming effect of direct radiation is probably of far greater importance than is visible light in determining the level of activity, once the lower light threshold is passed. Insolation and ambient temperature are themselves interrelated and I believe the overall heating effect of sunshine was the reason that Szabo (1980) in Canada found light intensity, as well as air temperature, had a significant positive correlation with flight activity. Butler & Finney (1942) also showed there was an association between variations in honeybee activity and clear light, but found there was insufficient T_A variation to determine whether flight activity was determined by the diurnal T_A cycle or equivalent diurnal rhythms.

Any diurnal rhythm component of activity that does operate is presumably adapted to coincide with suitable meteorological and forage conditions and would not be totally fixed in this group of organisms that have evolved to be active for much of the year in order to exploit flexibly an ever-changing diverse pattern of floral resources. Indeed, Kefuss & Nye (1970) considered that the rhythms detected in *mellifera* were overshadowed by exogenous factors. However, the drop in *florea* activity at Rustaq at the end of the afternoon (Figure 5.19), when T_A was still 2°-3°C above that at which foraging started in the morning, may be an expression of a rhythm that anticipates the pending low T_A and/or low light levels that would make flight and return to the colony difficult. In this case, the afternoon drop in activity was unlikely to have reflected dwindling supplies of forage (see Results 2.1 (c)), nor was this the case with *mellifera* in the U.S. according to Hambleton (1925). However, the fact that *jemenitica* in Oman showed completely different flight activity patterns (diametrically opposite at Khabura and Sayq) with different temperature regimes shows that a standard rhythm is far from paramount. Endogenous rhythms do exist (Renner 1960) but these are adjusted to exogenous factors such as time of dawn in only a temporary way, and act primarily as cues to the likely timing of suitable environmental conditions eg of forage and temperature.

A hypothetical activity-T_A curve for *florea*, similar in shape to that for *mellifera* and based on data from Khabura and Rustaq is also presented (Figure 5.20) as the principles discussed above should apply equally to both species. The optimum T_A for *florea* lies between 26° and 32°C, probably closer to the latter. However, as discussed in Results 2.2(b), some acclimatization may occur that is related to the prevailing T_A regime. Thus foraging by *florea* at Sayq, and also Rustaq (Figure 5.19), in early spring, started at c. 18°C, approximately 7°C lower than at Khabura in early summer and acclimatization is likely to be the explanation for such a <u>large</u> discrepancy. <u>Small</u> differences in foraging periods at one site (and thus T_A at which it is initiated and stopped) also occur and these can best be attributed to differences between colonies in terms of size, level of brood rearing, honey stores, exposure to insolation and so on. For instance, though *florea* 2 and FD at Khabura both started foraging near to 06.30h, T_A 25.5°C, on 9.v.80 (p. 216), as did a third colony present (IC), a fourth colony (12) started foraging at 05.55h when T_A was 23°C. All these *florea* still started foraging considerably later than the Khabura *jemenitica*, but not at such low T_A as the *florea* at Sayq and Rustaq. So the inter-colony differences do not appear to be as marked as the inter-specific differences nor as important as the effects of acclimatization.

It seemed unlikely that bees from the 4 *florea* colonies at Khabura were "choosing" not to fly at T_A less than 23°C, since the pollen analysis had shown that forage was available (Results 2.1(a)), so acclimatization and secondarily "colony circumstances" must have been responsible for the observed intra-specific variations in flight activity at the 3 study sites. Recordings of the times at which foraging starts in 20 to 30 colonies at <u>one</u> location and of their condition and exact siting, especially with respect to shade/exposure to insolation, should help to identify the critical "colony circumstances". The apiary of Nāsr Ahmad al-Ghaythi (Chapter IV) would be excellent for such an investigation on *florea*.

In Oman, as opposed to temperate climates, there did not appear to be marked changes in the physiological state of honeybees between winter and summer, but Nelson & Jay (1968) have demonstrated differences between "winter" and "summer" bees in their levels of flight activity at different ambient temperatures; more "winter" bees than "summer" bees flew at low T_A, but fewer at high T_A. Despite all these variations, I believe that further data on *florea* and *jemenitica* under a range of conditions should in general be consistent with the hypothetical foraging patterns indicated in Figure 5.20, with the curves changing shape a little and/or being shifted to left or right according to temperature regime, colony strength, foraging opportunities and other local conditions. However, as for *jemenitica* at Sayq and Rustaq, the pattern is liable to become less clear and more subject to the influence of factors other than T_A, around the optima and differences will still remain between the levels of morning and afternoon foraging (by and large attributable to the anticipation of night-fall, and to surpluses of nectar and pollen produced overnight being more abundant in the morning but exhausted in the afternoon). Also, extreme conditions could induce responses distinct from the typical foraging patterns for nectar and pollen; for instance high T_A (34^{o}-39^{o}C) at the hive may necessitate water-gathering and produce a second activity peak (Bodenheimer & Ben-Nerya 1937).

Why do honeybees have optimal temperatures for foraging with reduced levels of activity on either side, instead of their activity being constant between upper and lower thresholds for flight, and why is there such a difference between *florea* and *mellifera* in their preferred temperature ranges for foraging? The work of Heinrich (1979b and c; 1980a and b), in particular, indicates the answers. Between 15° and 25°C T_A, Heinrich (1979b) found that honeybees, *mellifera*, in uninterrupted free flight generated on average T_{TH} (thoracic temperatures) 15°C in excess of ambient, so that when flying at even higher T_A they may generate so much heat in their thoracic muscles that, unless the heat is dissipated, the bee's own temperature will rise above the lethal level of approximately 48°C.

Heinrich (1979c; 1980a and b) showed that the bees must achieve this heat dissipation by regurgitating and evaporating fluid (nectar or water) from the head, which is capable of cooling three times faster than the thorax and so acts as a heat sink for the thorax. Therefore, unless quantities of nectar or water are carried, there are considerable problems (potentially lethal) for honeybees flying at high T_A. The need to carry quantities of fluid when leaving the hive must diminish the rewards of foraging so, unless the demand for nectar/water/pollen is particularly great or large quantities of forage are readily available nearby, it is not surprising that foraging activity decreases at high T_A.

At T_A of 22°C, the optimum for *mellifera* foraging activity according to this study, T_{TH} of a worker in flight will be approximately 37°C, according to Heinrich (1979b). I believe it is no coincidence that this is close to T_B for *mellifera* colonies and that it reflects an optimum temperature for the metabolism of active honeybees.

Allen (1959) found that the respiration rates of individual workers had a minimum near 32°C, indicating low levels of energy consumption for thermoregulation and thus also suggesting that temperatures of this order were optimal.

A T_{TH} of 27° - 28°C is the lower limit for level flight for *A. m. mellifera,* and foraging *A. m. adansonii* have T_{TH} above 30°C (Heinrich 1979b). At lower T_{TH}, power output is presumably insufficient for flight. Thus at low T_A (8° - 15°C), time and energy must be spent on pre-flight warm-up (or flight may even have to be interrupted for bouts of "warm-up") to increase T_{TH} to the required level; this is a necessary consequence of evolving biochemical machinery to operate at higher than prevailing T_A (Heinrich 1981a, p.269). Foraging at low T_A may therefore be costly in time and energy, "but it is not known if the reluctance of most bees to forage at low T_A is due to few flowers offering nectar at these temperatures, to energetic costs that would minimize profits, or to individual differences among the bees of any one hive" (Heinrich 1979). If the *florea* at Khabura (8-9.v.80) are considered, it was found they did not forage till T_A reached approximately 25°C, even though *Acacia* and *Prosopis* nectar and pollen were available (they were being gathered by *jemenitica*); I therefore conclude in their case that the reluctance to forage at lower T_A was to minimize the energetic costs, with acclimatization to higher T_A making it more difficult. As the T_A and "profits" rise it is worth such a colony devoting a larger proportion of its workers to foraging. The principle should apply to both *mellifera* and *florea*. Nevertheless, observations indicate that, especially with some metabolic acclimatization and if the floral rewards ("profits") are good, both species will forage at T_A well below their optima. Thus with disadvantages in foraging at low and high T_A and an optimum T_A in between, a satisfactory energetic/thermoregulatory explanation for the hypothetical activity patterns (Figure 5.20) exists, and it supports the causative nature of the correlation between T_A and flight activity.

Why then the differences between *florea* and *mellifera*? The mass of *florea* flight muscles must be smaller than that of *mellifera* and the body surface area to volume (or mass) ratio considerably greater, so assuming similar metabolic rates less heat will be generated in the *florea* thorax and the rate of passive cooling, directly or through the head, must necessarily be greater. I would therefore predict that the number of degrees to which T_{TH} of *florea* workers in flight is raised above T_A, is much less than the 15°C rise for *mellifera*. This is consistent with Heinrich's (1981a, p. 266) generalization that the larger the insect the higher its body/thoracic temperature during flight, at least until the high temperature ceiling of 45° - 46°C is reached. Assuming then that *florea* like *mellifera* (Heinrich 1979b) needs T_{TH} greater than 30°C for flight (and the approximately equal raised brood nest temperatures, 33° - 36°C, suggests the metabolisms of the 2 species are essentially similar in their temperature requirements), the consequence of a relatively small rise of T_{TH} above T_A in *florea* would be the situation observed ie a higher T_A before foraging starts, but flight activity continuing at higher T_A than for *mellifera*. The need to take the unprofitable step of carrying extra fluid to prevent overheating presumably occurs at a higher T_A for *florea*.

It is tempting to conclude that Bergmann's rule is applicable in this situation, comparing *florea* to the larger *mellifera*, and *A. m. jemenitica* (the smallest race of the species and occurring in a very hot climate) to other races of *A. mellifera*. Bergmann's rule that "the smaller-sized geographic <u>races</u> of a species are found in the warmer parts of the range, the larger-sized <u>races</u> in the cooler districts" can be applicable to poikilotherms as well as homiotherms (Ray 1960) (honeybees falling somewhere between the two), but if applied strictly should not concern different species, even of the same genus. Thus as Ruttner (pers. comm.) has pointed out, the much larger *dorsata*, which is restricted to tropical regions like *florea*, goes against the rule as applied to the genus *Apis*, presumably because of differences in biochemistry, physiology and behaviour. Even applying Bergmann's rule to races of *mellifera* is not really satisfactory as *A.m. sahariensis* lives in similar climatic conditions to *A.m.jemenitica*, but is distinctly larger; the former belongs to a group of Mediterranean races which include larger bees in general, while *A.m.jemenitica* belongs to the races of tropical Africa which are all small (Ruttner, pers. comm.). Indeed Heinrich (1979b) has shown that though *A.m.adansonii* have a lower thoracic mass than *A.m.mellifera* and must have a greater passive cooling rate, their active foragers did not show a correspondingly lower T_{TH} and they are known to be more willing to fly at lower T_A (eg 9°C). He thus inferred that the African bees had a higher metabolic rate than the European. Similarly, the hot climate *Xylocopa californica* is tolerant of high T_{TH} (48°C) and can fly over a much higher range of T_A than temperate *Bombus* species of equivalent size, a high thermal conductance (possibly because of few hairs) aiding heat dissipation (Chappell 1982).

Therefore the different *Apis* species, as well as races, must have some physiological/biochemical differences affecting their thermoregulation, and divergent foraging times though associated with T_A cannot be entirely attributed to size differences. Nevertheless, it is interesting to note that where the *Apis* species do overlap in their range, some of the observations on foraging times indicate that the order in which this activity starts in the morning is *dorsata*, *cerana/mellifera*, *florea*, that peaks of activity occur in this order too and that foraging ceases in the reverse order (Morse & Laigo 1969; Murrell & Nash 1981; Swaminathan & Bhardwaj 1982; these observations).

What are the consequences of the differences between *florea* and *jemenitica* in their optimal temperatures for flight activity and thus in their daily foraging times? Where they are utilizing the same sources of forage, which is frequently the case (this chapter and Chapter VII), it suggests that competition for food might to some extent be avoided. There is little information on diurnal patterns of nectar secretion and pollen presentation in hot, arid areas such as Oman. However, my impression from honeybee pollen and crop content analyses was that their availability from plants in general, being under the influence of meteorological factors such as T_A and humidity, was high in the morning, dropped during the hottest part of the day and increased again in the late afternoon. (In the cooler months a more temperate pattern might prevail, cf Corbet 1978 and Corbet *et al* 1979). In Buenos Aires, Nunez (1977) found that the rate of flow of *Eucalyptus melliodora* decreased during the hours of day having maximal temperature and minimal humidity and in Bangladesh the volume of nectar available in toria was most between 08.00h and 09.00h (Murrell & Nash 1981). With the investigations presented in this chapter the floral rewards of *Prosopis cineraria* and *Acacia tortilis* appeared to be highest fairly early in the morning and those of *Vicia faba* at Rustaq greatest a little before dusk. Furthermore, Cruden *et al* (1983) conclude that a typical flower begins to secrete nectar prior to the activity of its pollinators and that, with exceptions, maximum nectar accumulation also occurs prior to or shortly after initiation of pollinator activity.

Therefore, assuming such a pattern of nectar and pollen availability in Oman and that forage is to some extent a limited resource (not unreasonable given the generally arid conditions and low yields of honey in Oman), *jemenitica* by being active before *florea* may be able to take advantage of this early abundance of forage, leaving less for the little bee workers that usually arrive at least an hour later. Similarly, in the Mojave desert where pollen from *Oenothera* is greatly reduced in dry seasons, Linsley *et al* (1955) concluded that competitive pressure favoured the species of *Melandrena* able to fly slightly earlier in the morning and collect the pollen rapidly. In areas where *jemenitica* are completely absent, the nectar produced by flowers earlier in the day would still be available an hour or so later to *florea* when they start foraging - assuming that resorption by the nectaries and the numbers of other insect visitors are low. So even though there is separation of foraging times and *florea* is more willing to exploit floral resources at higher T_A than *jemenitica*, those resources available to *florea* may be reduced by the presence of colonies of *jemenitica*. With some overlap in activity periods *florea* may reduce the forage available to *jemenitica*, but to a lesser extent, so I suggest that this difference in foraging times could be responsible for exploitative competition to the detriment of *florea*.

Roubik (1978, 1982) has demonstrated competitive interactions between stingless bees and Africanized honeybees in South America, with the former becoming less abundant on flowers and artificial feeders or harvesting less resources as visitation by Africanized honeybees increased. He concluded that such shifts in resource use by native Neotropical pollinators could lead to declines in their population. No population figures are available for numbers of *florea* colonies in areas of Oman with and without *jemenitica*; but in the dry period 1978-80 my impression, and that of some beekeepers, was that the density of wild and kept *florea* in the central Jabal Akhdār (where *jemenitica* occurs) was less than in regions such as Ibri and Zāhib (Chapter IV) where *jemenitica* did not occur. Nevertheless, *florea* appeared to fare better than *jemenitica* in these dry years (Chapter VII, p.356-8) perhaps because their forage requirements were less.

E. CONCLUSIONS AND IMPLICATIONS FOR BEEKEEPING

(a) Especially at low T_A, colonies of *jemenitica* were able to maintain the high temperature required by their brood more effectively than colonies of *florea*. They were able to rear brood in Oman during the winter, even at altitudes of 2,000m, when sufficient forage was available. *Florea* did not rear brood at this altitude during winter and even at lower altitudes it was reduced (Chapter VI). Correspondingly, with their single-combed, exposed nest, *florea* <u>may</u> be able to cope better with high T_A. These findings endorse one practice employed by certain keepers of *florea*, namely that of "migrating" colonies to or siting them in sunny and shady positions during winter and summer respectively (Chapters III and IV). Such a procedure, if performed carefully, is to be encouraged and sites which provide sunshine early in the morning to warm up the colony, including foragers, should be selected.

(b) The stress, in terms of temperature regulation and water gathering, which the high summer T_A in Oman put on both species of honeybee should be minimized. The pressure on workers to fan their wings and fly long distances to collect water will divert bees from other colony duties such as tending the brood and foraging for nectar and pollen. It may also lead to early "ageing" of the bees concerned, since research has indicated that individual *mellifera* workers exhaust their energy supplying mechanism after a certain total flight performance (Neukirch 1982). Therefore every attempt should be made to provide adequate shade and water for the bees at all apiaries. Any modern hives should be painted white, the roof included, as is already the practice of the bee-keeping project in Oman, since this has been shown to have a marked effect in reducing hive temperatures (Lensky 1958, 1964b; Smith 1964). These authors also recommend siting the hives on grass and off the ground, with the provision of a small, low entrance and top ventilation to aid the bees in their thermoregulation.

(c) *Florea* workers were unable to forage at T_A below approximately 18°C and were most active at T_A of approximately 30°C. *Jemenitica* workers were active at T_A as low as approximately 12°C and were most active at T_A of approximately 22°C. This resulted in the peak of foraging activity of each species being at a different time of day, though with a certain amount of overlap. Potentially this could have reduced any interference competition between the 2 species, but none was observed and in fact by being active earlier in the day, at lower T_A, *jemenitica* is likely to reduce the amount of pollen and nectar available to *florea* when supplies are limited. Keepers of *florea* should bear this in mind if they are planning to keep colonies of *jemenitica* as well. Keeping both species might, however, lead to increased crop pollination and more complete exploitation of floral resources; whether this would result in greater yields of honey overall, or diminish yields because the strength of colonies of one or both species is reduced, is not known. *Mellifera* might do better in the lower T_A of winter and *florea* in periods with higher T_A.

(d) Where both *jemenitica* and *florea* are present, the timing of any pesticide applications is particularly crucial as some bees will be active at nearly all periods of the day. Before spraying is undertaken, flowering crops should be examined to see at what time the least number of bees are present. As a general rule, dusk, and the later the better, is probably the best time of day for spraying from the honeybees' and therefore the bee-keeper's point of view.

Thus the findings that *florea* and *jemenitica* are adapted to different ranges of T_A, both in terms of brood nest thermoregulation and foraging activity is of practical importance to bee-keeping in the hot, arid Oman climate. The suggestion that competition for forage detrimental to *florea* may take place because of the presence of *jemenitica* and as a result of these different temperature adaptations, should be borne in mind whenever plans are considered to introduce *mellifera* to areas where the 3 Asian *Apis* occur. Further comparative investigations of the temperature relations of the 4 *Apis* species are recommended and in Oman comparisons between *jemenitica* and the introduced races of *mellifera*. The influence of colony condition, especially population size, on the ability of *florea* to thermoregulate and rear brood also deserves closer examination. Finally, the actual thoracic temperatures of active and inactive workers and the sensitivity of *florea* brood to high and low temperatures, needs to be determined too.

CHAPTER VI

SEASONAL CYCLE OF *APIS FLOREA* AND ABSCONDING

A. INTRODUCTION

1. Seasonal cycle

To my knowledge, apart from Sandhu & Singh (1960) as outlined below, no proper study of the seasonal cycle of *Apis florea* has been carried out in any part of its range. Even the detailed investigations of Akratanakul (1977) and Seeley *et al* (1982) did not cover this topic as fieldwork was not undertaken throughout the year. Various studies in India and SE Asia (Douglas 1886; Franssen 1932; Mehta 1948; Ghatge 1949; Muttoo 1956; Sakagami & Yoshikawa 1973; Kshirsagar *et al* 1980) have mentioned or described worker and drone brood, honey and queen cells, but give little information as to their occurrence or frequency in different months of the year. Tirgari (1971) observed the growth of a colony in Iran and that its population began to increase in April, peaking in May with the initiation of queen rearing while Dutton & Free (1979) and Williams (1979) outlined the annual cycle in Oman as indicated by a local bee-keeper. None of these papers presented actual data on the monthly status of brood, adult drones, queen cells, pollen, honey etc, for given numbers of *florea* colonies. Nor have any papers outlined the developmental history of individual colonies from establishment through swarming to absconding.

However, at Ludhiana (Punjab) in India, Sandhu & Singh (1960) did investigate brood rearing in *florea* for 16 consecutive months from April 1958 to July 1959, but examining only 2 to 4 colonies in each month. Their results indicated that brood rearing continued throughout most of the year, but not in the cooler months of December and January nor, in

1958 only, in July. They associated the resumption of brood rearing in February with the "warming up of the season" but presented no conclusions as to the influence of other factors, such as forage availability, in determining the annual cycle.

There are more studies on the annual cycle of *Apis mellifera*, detailed research in temperate climates going back a long way (Nolan 1925; Allen & Jeffree 1956). In the warmer climate of Palestine, Bodenheimer & Ben-Nerya (1937) have shown that egg production and brood rearing can continue throughout the year but at a much lower level in winter, before rapidly reaching a peak around March. In wet tropical areas where periods of severe rainfall with reduced forage availability, not periods of low temperature, are equivalent to "winter conditions", brood rearing is continuous throughout the year, though at a reduced level during the height of the wet season (Winston 1980a).

Being of importance to bee-keepers, the seasonal cycle of queen cell production and swarming (Simpson 1959; Burgett & Morse 1974; Fell *et al* 1977) and the mechanisms by which swarming is induced (Simpson 1958; reviewed by Simpson 1972; Butler 1974; Brian 1979) have come under particular attention. More recently, following the accidental release and spread of an African race of honeybee *Apis mellifera scutellata* in South America (Winston 1977), there has been some intense research on the ecology of *mellifera* in the tropics and on the differences between the temperate and African races, especially in their swarming and absconding behaviour (Otis *et al* 1981; Otis 1982; Winston 1979a; Winston 1980a; Winston 1980b; Winston & Taylor 1980; Winston *et al* 1981 and reviewed by Winston *et al* 1983).

Both in Africa (Ruttner 1975; Chandler 1976; Fletcher & Tribe 1977; Fletcher 1978) and in South America (Winston 1979a, 1980a and b; Winston *et al* 1980; Otis 1982) the reproductive rate of tropical *mellifera* through swarming is greater than that of European races, whether the latter are in temperate latitudes (Seeley 1978) or have been introduced to tropical regions. This research therefore suggests that differences between races in their annual cycles of brood rearing, swarming etc are partly genetic and they are not wholly a direct response to immediate environmental conditions such as temperature and forage availability. Work by Avitabile (1978) and Kefuss (1978) has shown that the brood rearing activities of temperate *mellifera* can respond to increasing and decreasing photoperiods (with the rearing of more and less brood respectively). Furthermore, by transferring colonies and queens between regions in France, Louveaux *et al* (1966), Louveaux (1969, 1973) and Cornuet & Louveaux (1981) have demonstrated that local populations of *mellifera* show bioclimatic adaptations of a genetic nature to their own environments ie are ecotypes.

Seeley & Visscher (unpublished, quoted in Seeley 1983) have shown that *mellifera* swarms produced early in the season have a greater chance of surviving to the next spring, in a temperate climate, and Seeley (1983) has pointed out that this may explain why colonies that have stopped brood rearing in October resume it again, before spring forage is available, shoftly after the winter solstice (Jeffree 1956; Avitabile 1978) by using their stores of honey and pollen. Therefore, by genetic adaptations to respond to cues such as photoperiod, honeybees have been selected that start annual development before maximum forage is available, thus "anticipating" the optimal swarming season.

As with *florea*, literature on the annual cycle of brood rearing, swarming, honey storage etc for *Apis dorsata* is negligible; this will in part be due to its aggression ("There is no question that *dorsata* is the most ferocious stinging insect on earth", Morse & Laigo 1969), but also in some areas such as Sri Lanka (Koeniger & Koeniger 1980) to its long distance migratory behaviour which make observations at one locality impossible. Studies on the annual cycle of *Apis cerana* in the Indian sub-continent indicate similarities to that of tropical races of *mellifera* with brood rearing continuing throughout the year in most areas, though it is at a reduced level during periods of floral dearth (Kapil 1957; Reddy 1980) and is almost completely suspended in winter at higher altitudes (Hameed & Adlakha 1973). Like tropical races of *mellifera*, *cerana* is also characterized by high rates of reproductive swarming (Ruttner *et al* 1972; Koeniger 1976).

It was important that a knowledge of the seasonal cycle of *florea* in Oman and of the factors controlling it were obtained to ensure that traditional and modern management practices and their timing were appropriate. Laboratory experiments to test the brood rearing response of this species to photoperiod were not possible, but with a knowledge of the annual temperature regime (Appendix II) and floral cycle (Chapter VII) in Oman and of the cycles of other *Apis* species as discussed, it was hoped an understanding of the annual cycle of *florea* would emerge.

2. Absconding

Absconding, the desertion of one nest site by all the adult bees of a colony and their movement to a new nest site, appears to be a characteristic of the 3 Asian species of *Apis* (Lindauer 1957) and of tropical but not temperate races of *mellifera* (Martin 1963; Ruttner 1975; Woyke 1977). It seems that the absconding rate of *mellifera* when moved to the tropics usually remains low (eg Otis & Taylor 1979) but in some cases increases to higher levels as in Colombia with 200 out of 900 colonies absconding in a season (Robinson 1982).

It has been calculated that reproductive and absconding swarms of Africanized *mellifera* may travel up to 64km and 131km respectively

(Otis *et al* 1981) and possibly further if in transit foraging takes place. Such foraging would probably be necessary to explain the observed expansion of Africanized honeybees in South America (Taylor 1977). Koeniger & Koeniger (1980) have provided strong evidence that migrating *dorsata* swarms also travel considerable distances of the same order.

It has been reported that *florea* changes its nest site 2 or 3 times a year and that it is migratory (Douglas 1886; Rahman & Singh 1940; Mehta 1948; Muttoo 1956; Sandhu & Singh 1960; Thakar & Tonapi 1962; Pandey 1974; Dutton & Free 1979; Williams 1979; Free 1981; Nash & Murrell 1981). In some cases movement over long distances was implicated, but neither direct evidence nor figures have ever been presented to support these claims. Pandey (1974) states that *cerana* is less migratory than *dorsata* and *florea*, but this and other papers referring to absconding by *cerana* (Ruttner *et al* 1972; Woyke 1976; Raj & ChannaBasavanna 1980) do not indicate whether absconding or reproductive swarms of this species move long distances.

As with aspects of the seasonal cycle, absconding by *mellifera* has been investigated in greater detail than for the other *Apis* species (Martin 1963; Fletcher 1975, 1976, 1978; Fletcher & Tribe 1977; Winston *et al* 1979; Winston 1980a; Otis *et al* 1981; Otis 1982). Various reasons for absconding have been proposed in these papers, with different authors emphasising different causes. Thus Winston *et al* (1979) considered there were two basic types of absconding (i) disturbance-induced and (ii) seasonal absconding. In addition to pests and predators and manipulation by bee-keepers, they included inferior nesting sites in the disturbance category, while in the other category they included dearth of resources and other seasonal factors such as rainfall and high temperatures. Fletcher (1978) recognized many causes of absconding (predation, overheating, lack of water, inadequate nest size and others) but did not draw such clear-cut distinctions between types. He gave evidence that migratory swarms were not necessarily seasonal and that they sometimes exploited temporarily resource-rich areas in an opportunistic fashion. Fletcher (1975, 1976) also pointed out that absconding bees at particular seasons have been called "starvation" swarms when in fact some such colonies abscond when nectar is not in short supply and even abandon substantial food stores.

In discussing the 3 Asian species of honeybee, Seeley *et al* (1982) and Seeley (1983), though not eliminating excess insolation as a possible stimulus to colony movement, considered that absconding by *florea* had evolved primarily in response to predation pressure. They also noted that all abandoned *cerana* nests had been destroyed by predators. However, for *dorsata*, they observed there was a seasonal migration right out of their study area. In Iran, Tirgari *et al* (1969) and Tirgari (1971) considered that *florea* moved short distances (5 to 400m) to change their nest sites between winter and summer for microclimatic reasons.

In Thailand, Akratanakul (1977) thought the main two causes of *florea* absconding were lack of food and disturbance from enemies. As has been considered in Chapter II (p. 53-56) a view of the sky for *florea*'s communication dances appears to be important and Koeniger *et al* (1982) found that *florea* brought to locations from which the sky was not visible showed a strong tendency to abscond. In his review of *florea*, Free (1981) thought that diminution of the supply of forage was probably the main factor that caused absconding but that temperature changes were also important and invasion by enemies such as wax moth and ants were other causes. In Bangladesh, Nash & Murrell (1981) claimed dearth periods and predation by man caused frequent migration to other locations.

Thus there was no consensus of opinion as to the main functions of absconding for *florea* or the other *Apis* species and the several causes advanced have been grouped in different ways and attributed different degrees of importance. It may well be that the causes of absconding vary according to the region concerned, with differences in climate, flora and levels of predation, and that the causes should not be ranked in the same order of importance for each species. Investigations of the causes and seasonality of absconding by *florea* in Oman should be of help to local bee-keepers and might shed light on the problem in general, but are not necessarily directly applicable to *florea* elsewhere in its range or to other *Apis* species.

B. METHODS

1. Seasonal cycle

1.1 General

The data in this section is derived from "spot" inspections of 102 naturally established colonies of *florea*, between December 1977 and August 1980; the colonies were found as described in Chapter II, Methods, B.1. Though there is likely to be some variation in the development cycles of colonies from different nest sites, habitats and regions (eg mountain caves as opposed to bushes in date gardens) due to differences in microclimate and forage availability, the main brood rearing and swarming seasons appeared to be approximately the same in most parts of northern Oman. There were insufficient records to investigate any such variation, so the data from all nest site types and localities were combined. Similarly, there were not enough records to consider differences in brood rearing between years (due to variations in rainfall and thus forage availability) so the results from different years were grouped according to calendar month. Despite this grouping, some months had only a few records; however, further grouping of data into 2 month periods was considered undesirable, as substantial colony growth can take place within a single month and finer details of seasonal colony development would then have been obscured.

1.2 Colony attributes recorded

Colonies were inspected and measured for the attributes listed below; this usually entailed approaching the colony closely and brushing the bees in the protective curtain aside (with a paint brush, twig or hand) in various places to examine the comb underneath. Unless the colony had been disturbed by vibrations and movement caused by climbing the tree or clearing surrounding twigs, the inspection did not usually induce an aggressive response if undertaken gently.

(i) Presence or absence of worker brood: larvae and/or sealed cells (pupae)

(ii) Presence or absence of worker eggs

(iii) The percentage of the comb covered by the protective curtain of bees; usually a visual estimate was made, sometimes backed up by measurements and photographs. The values were considered to be accurate to approximately ± 5%.

(iv) Presence or absence of drone brood; eggs, larvae and/or pupae. Colonies with old, empty drone comb were put in the "absent" category.

(v) Presence or absence of adult drones. If a close inspection of the protective curtain on both sides of a colony was not possible and only a few drones were present they may occasionally have been missed; in such cases their numbers would have been dwindling anyway so the negative record would not be inappropriate.

(vi) Indications of swarming. The presence or absence of new queen cells (with or without eggs, larvae or pupae) showed that swarming would soon occur, or had recently occurred if the number of adult bees appeared depleted. Also, colonies known to be newly established and which contained relatively large numbers of drones were assumed to be swarms ie their parent colony had just reproduced.

(vii) Empty queen cells, being a sign of colony reproduction in a previous month. In the cases of colonies on which inspections were made in more than one month, empty queen cells were recorded as present only on the first occasion that they were encountered - not on subsequent visits, even though the cells were still present. Similarly for the 2 colonies seen to produce new queen cells in one month and which were then inspected in subsequent months, the queen cells were recorded as old in the following month only.

(viii) Honey. An assessment was made of the size of each honeycomb relative to the size of the comb as a whole, and of the quantity of honey each contained. These assessments were allocated to 3 broad categories - Substantial Quantity, Medium Quantity and Negligible Quantity of honey. However, only colonies of a fair size were included in the "Substantial Quantity" category; thus small, newly established colonies that had a considerable amount of honey relative to the size of their comb, but in which the absolute quantity of honey was small, would be put in the "Medium Quantity" category.

(ix) Pollen. As for honey, the amount of pollen stored was assessed, relative to comb size, and put in 3 broad categories - Substantial, Medium and Negligible Quantities.

(x) Colony width and height. The width and height (including honeycomb) of each colony was measured with a tape measure, in positions where the dimensions were at a maximum. These measurements usually included the bees that enveloped the combs at the edges, but in colonies which did not have 100% cover of bees it was sometimes just the <u>comb</u> height or width that was measured. With colonies recently established, that had a small comb relative to the size of the cluster of bees, measurements of both comb and cluster size were made where possible. With large colonies rearing drones, the drone comb was included in the measurements.

(xi) Colony size. As described in Chapter IV, Methods, a Colony Cover Index (C.C.I.) was derived for each colony by multiplying the Colony Area Index (C.A.I. : maximum height x maximum width) by the % Cover of bees. This was a guide to the active or functional size of the colonies. With some diurnal contraction and expansion of the cluster of bees around the comb, the values obtained will partly have depended on the time of day measurements were made. However, the greatest expansion seemed to take place in the early morning and most measurements were made after this time, so errors due to this were probably small.

In addition, quantitative assessments of the area of eggs, brood etc were sometimes made as, particularly in winter and summer, brood rearing was not always carried on in the whole brood comb; these finer details were excluded from the analyses but helped to indicate prevailing trends. Photographs were used to supplement and confirm some of the observations and measurements, while with a few inaccessible colonies estimates of the dimensions with respect to objects of known size had to suffice.

1.3 Problems

Most colonies (86) provided data on the various attributes for one month only, either because they were in places I did not visit again or because the colony had been removed/damaged when return visits were made in subsequent months. 16 colonies, however, provided data in 2 or more months; with one exception (colony IC mentioned below) there was no obvious imbalance in the strength of these 16 colonies that would have biased the results. They covered a representative range of sizes, some being small and some large, but they were all colonies which had been left undisturbed, as far as I could tell, between visits. Altogether a total of 136 colony inspections were made on the 102 colonies. However, data on each of the colony attributes under investigation usually came from only c. 70-75% of the colony inspections. The remaining 25-30% of the colony inspections usually yielded information on only one or two attributes because of the sort of problems outlined below.

With certain inaccessible colonies , eg in dense thorn trees, it was possible to assess only the % cover of bees around the comb and not the comb underneath. A few colony "inspections" consisted of honeycombs, brought to me for help with honey extraction, still attached to their supporting stick, having just been removed from a wild colony; the quantity of honey could be assessed, but no other colony attributes. As mentioned in Chapter II, B.1 cursory inspections of some colonies were performed when they were first located, but no further data obtained because the colonies had disappeared before the return visit was made for a proper inspection.

Some of the data omissions were due to failings on my part. Thus with a few colonies examined early in the study, in the winter of 1977-78, the <u>absence</u> of eg drones was not always specifically recorded, as the significance of such negative information was not appreciated at the time. As hardly any colonies were rearing drones or queens at this season anyway, a few records being excluded rather than added to the absent totals would affect the results (percentages) little. In one or two cases certain records were omitted by mistake because my attention was distracted by onlookers (the owner, children etc) or because the bees were becoming aggressive.

With some of these omissions the missing colony attributes could be deduced or interpolated. For instance, if a colony had sealed drone cells in the second half of one month, the presence of adult drones would be certain at the following month's inspection even if their presence/absence was accidentally not recorded. Similarly, the absence of drones (brood and adults) and queen cells in a colony in February was certain if they were recorded as absent in both January and March. However, with colonies inspected only once, extrapolations to their state in the previous or succeeding months were not made, though it would have been simple for certain attributes.

Three queenless colonies and 2 recently abandoned combs were included, but these provided minimal information eg on the presence of old queen cells. It would have been misleading to have recorded a queenless colony as not rearing brood, so such data had to be excluded for these colonies. All data from colonies being managed by Omanis, eg kept on a "zoora" or in a cave, and by myself, eg in hives, were excluded from these analyses, but they are referred to where there are gaps in the record. However, records from one colony, designated IC, that was moved from Seeb to Khabura (both on the Batina Coast) but left undisturbed on its original support , were used. It was, though, a colony with an exceptionally wide comb (35.5cm high by c.74cm wide and thus probably the largest comb of *florea* on record) of which the bees were occupying only about 50% of the total area while I had it under observation. Therefore its exceptional width dimension was excluded from the monthly averages.

Colonies, which I knew from marked queens, to have swarmed or absconded from an earlier, known site at which records had been obtained, were included and treated as separate, new colonies, not as continuations of the previous ones.

2. Absconding

Data on absconding was available from three sources:- (i) *florea* colonies managed by Omanis in some of the traditional ways described in Chapter III, (ii) colonies put in my experimental hives or managed in some other way by myself, (iii) wild colonies. Ideally (iii), regular observations on a large number of wild colonies undisturbed by man would have revealed any natural, seasonal absconding pattern, the proportion of colonies involved and typical colony longevity. However, such data was almost non-existent as the Omanis who owned the gardens where I found the wild *florea* usually wanted to take their honey as soon as the combs reached an adequate size, so "natural" absconding was rarely achieved by these colonies under observation.

Apart from the more detailed investigations on the *florea* at Zāhib managed by Nāsr Ahmad al Ghaythi, considered separately (Chapter IV), only a little data (approximately 13 colonies) on absconding was derived from other traditionally managed colonies; it was not possible to make frequent enough visits to determine accurately the dates on which colonies were established, on which honey was taken and on which the bees absconded. Therefore the bulk of the data, on approximately 69 colonies, comes from colonies in category (ii) that I had under more regular inspection, mainly in the Khabura region.

During the period December 1977 to August 1980, several different hive types with and without mesh as a queen "encloser" were experimented with (see Chapter VIII for detailed examples). However, insufficient colonies were tried in each hive type for valid comparisons to be made, as to their relative suitability or tendency to reduce or provoke absconding. In fact, because of the different situations in which nests were found, no two colonies were ever "hived" in exactly comparable circumstances. Some were kept in hives in close proximity to their original nest site, while some were moved to more distant sites in the same garden and yet others to a shelter especially constructed on the Durham University Khabura Development Project farm. Sometimes the whole colony would be put in a sack, in the evening after all the foragers had returned, still attached to its branch and would not be installed in a hive at its new site till the following day. Other colonies would be installed in a hive at their original site during the daytime and then the whole hive plus bees would be moved to a new site one or more days later, depending on how the bees settled. Some colonies were left with all or some of their honey, while it had to be removed from other colonies at the request of the owner.

"Hiving" in a few cases was little more than taking the colony, on its supporting branch, and resting it inside one of my hives, but more usually the brood comb was cut away from the branch and fixed into a frame in the hive. Sometimes a colony's queen could be found and caged temporarily, on other occasions it could not. Sometimes ants gained access to a hive, sometimes they were deterred. These factors must all have affected the inclination of the colonies to stay or abscond, but in almost every case of "hiving" a colony experienced a considerable upheaval.

The purpose of this section being to look at the seasonal cycle of *florea*, these detailed factors and variations have had to be ignored, and only the response to the overall disturbance (in terms of absconding or not) has been considered, according to the months of the year in which the hiving/absconding occurred. As all the colonies were handled as gently as possible, with steps being taken to prevent absconding by keeping ants off the hives, by providing what was thought to be an appropriate amount of shade/insolation, keeping the disturbance to a minimum and so on, it was hoped that any seasonal trends in absconding tendency would emerge above these variations. Nevertheless, colonies were liable to be tampered with when left in their owner's gardens and on some occasions did experience particularly severe treatment, eg being knocked over by a strong gust of wind, which would probably have been sufficient to induce absconding at <u>any</u> time of year.

From the records on each colony, the date on which it was hived, the months in which it was present and the date on which it absconded were extracted, and the length of time each colony stayed before absconding was calculated. When inspections were not frequent enough (daily) to determine the exact date of absconding, information from garden owners and various other signs were used to estimate this date. For instance, the cessation of brood rearing at the last inspection indicated that the colony had probably absconded just a few days later, while the presence of bees gathering honey and wax from a deserted comb indicated the bees had absconded within the previous 2 or 3 days.

The colonies were split into two groups, those that absconded soon after hiving (≤ 15 days, unsuccessful hivings) and those that became established (> 15 days, successful hivings). 15 days was taken as the dividing line, as it gave time for any sealed brood to emerge (as adults) from those colonies preparing to abscond after hiving and for brood rearing to be under way in those colonies intending to stay. Seeley *et al* (1982) found that a deliberately exposed colony did not abscond immediately but waited 13 days, long enough for the sealed brood to emerge, and most colonies in Oman appeared to fall satisfactorily into these 2 categories.

Some colonies provided more than one set of data; for instance, the colony put in Hive 2 (see Chapter VIII, Part I) and which absconded with the queen to a nearby bush, was counted first as an absconding colony but second as one colony successfully hived because, when the queen was enclosed in the hive again, the colony eventually became established. Similarly, on the few occasions when attempts were made to divide large colonies, one half could be counted as a new colony. In one or two instances the adult bees from newly-gathered colonies, when released at their new hive, chose to join instead an established colony nearby. Such large colonies were either split up again or left as they were, and whether or not such behaviour constituted another absconding record depended on the eventual outcome.

The details of all such unusual "hivings" cannot be recorded here, but each was assessed and scored on its own merits, or excluded. Some colonies providing 2 records, others joining together and so on is the reason why the number of colonies furnishing data was given as approximately 69. Queenless colonies were excluded except in a few cases where a new queen had been introduced.

A small proportion of the 69 hivings were performed by Hamoud Ali Sālim, to whom I had given several hives for trial purposes, and which he kept at sites in and around Qusabiyat 6-7km from Khabura, where I was able to keep an eye on them. He too had some successes and some failures and, having hived several colonies with him, I was confident his handling techniques were similar to mine. The absconding data on the c. 13 traditionally managed colonies did not appear to differ from mine and Hamoud's, so was combined with this main bulk of the data to give a total of approximately 82 colony records.

Finally, the new sites of some colonies that had absconded or sent off swarms were located, either by following the swarms or by searching for new colonies in the area and checking their identity by the presence of queens and/or workers marked with paint. The distances the colonies or swarms had moved were measured either in the field and/or from aerial photographs of Khabura. As for *mellifera* (Taylor 1977) and social wasps (West-Eberhard 1982), tracking swarms to obtain this information proved difficult and only a small proportion were found again.

C. RESULTS AND DISCUSSION

1. Seasonal Cycle

1.1 Number of colonies found

Table 6.1 gives the total number of wild colonies studied according to the calendar month in which they were first found and the number of colony inspections made in each calendar month. These indicate the potential maximum number of observations per month for all of the colony attributes, but as explained in the Methods the actual number of records obtained was usually less. If the figures for number of colonies found/month were an index of the seasonal fluctuations in numbers of *florea* colonies in a given area, reflecting the balance between colony mortality and the production of new colonies (swarms), they would be a useful measure. Unfortunately this was not the case as the colony records were not derived from regular censusing of a single area, and the figures were in part determined by the searching intensity in each month. In the months indicated (underlined) on Table 6.1, the search intensity for *florea* was comparatively low because of other responsibilities, illness and my absence from northern Oman

Table 6.1 Numbers of wild *Apis florea* colonies found in each month between December 1977 and August 1980 (numbers from different years combined) and the number of colony inspections made in each calendar month in this period, that provided the data on colony development in northern Oman. Months underlined are those in which the amount of time spent searching for new colonies was comparatively small.

Calendar Month	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	Total
No. of Colonies Found	12	4	12	13	7	9	12	1	3	2	17	10	102
No. of Colony Inspections	16	6	15	19	10	10	15	8	4	3	18	12	136

(necessitated by visits to Dhofar, the U.K. and India). Also the search intensity was probably rather greater in the cooler months, and particularly in one November (1979).

Trying to take this variation into consideration, most new colonies were found in April and November, but very few in February; even though the search intensity in August, September and October was low, the number of new colonies found in these months was still relatively small compared to, say, May. Therefore, the overall picture appeared to be one of new colonies, from swarming and/or absconding, arising in April and November, but fewer in the latter parts of the winter and summer.

Bearing in mind the way in which the figures were gathered, however, not too much emphasis should be put on this interpretation. The records of more detailed aspects of colony development which follow, though based on small sample sizes, are far more reliable as guides to the seasonal cycle of *florea* in northern Oman. They should be interpreted in conjunction with Chapter VII (flowering seasons) and Appendix II (meteorological conditions, especially temperature).

1.2 Worker brood and % cover of adult bees

March, April and May were evidently the most active months with all of the colonies examined rearing worker brood (Figure 6.1a). This coincides with the spring flowering of various crops and wild plants, culminating in the blossoming of *Prosopis cineraria* and *Acacia tortilis*. In autumn there was a second peak corresponding to the flowering of "sidr", *Ziziphus spina-christi*. However, the sample sizes were small in September and October and the real values might have been a little under 100% of the colonies rearing brood, especially at the beginning of September before the "sidr" started to flower.

The percentages of colonies <u>not</u> rearing brood in certain months are possibly the best guide to the other critical points in the annual cycle. Only a small percentage of the colonies (8 to 17%) were not rearing brood in the summer months of June, July and August but in the 2 coldest months, January and December, 45 - 50% of the colonies were not rearing brood. This indicates that the summer months were more favourable to *florea* than the winter months. Compared to the summer, either the forage availability must be particularly low in winter, or the temperature stress greater, or both.

Nevertheless, it was clear that brood could be reared at all seasons, though the histogram gives no indication of the level of brood rearing within those colonies which were active in this way.

Figures 6.1a - 6.5c

Annual cycle, month by month, of naturally established colonies of *Apis florea* in the Sultanate of Oman as indicated by various features of colony development. The data were gathered between December 1977 and August 1980 and, except for a few colonies under regular observation, came from "spot" inspections in a range of habitats. Any variation that might have existed in the state of a colony between the beginning and end of a month was not taken into account. The records for the different attributes on the whole come from the same colonies, but a small number of colony inspections provided records of a few attributes only. Monthly data from different years have been amalgamated. Where appropriate, the annual mean of the monthly percentages (of colonies with each attribute) has been indicated by a dashed line. It does not represent the true mean percentage over a whole year, as monthly sample sizes were not equal, but will be a close estimate and serves to highlight periods of above and below average brood rearing, swarming and so on. Numbers, n, above the histograms and confidence limits give the monthly sample size.

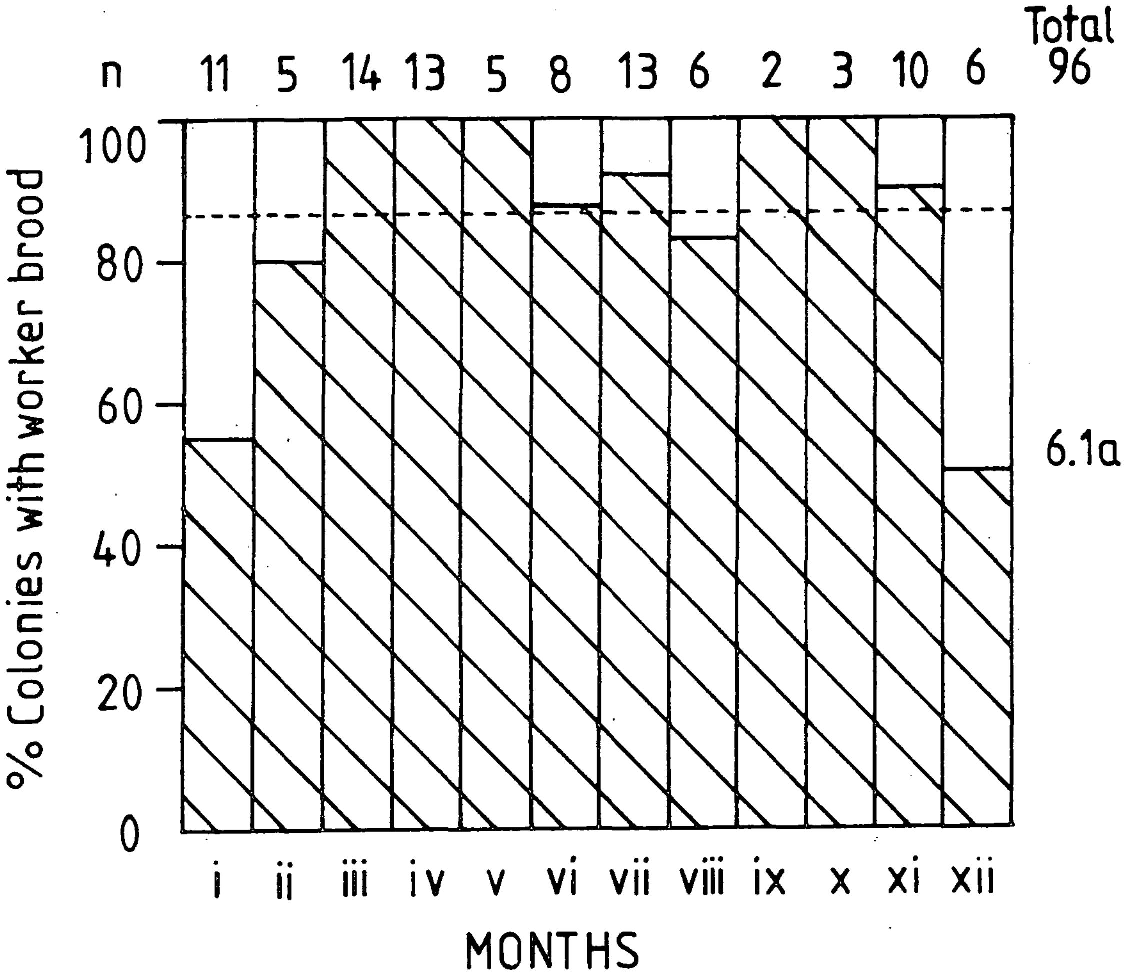
6.1a Percentage of colonies rearing worker brood
6.1b Percentage of colonies with protective curtain of bees covering $\geqslant$ 90% of the comb

6.2a Percentage of colonies rearing drone brood
6.2b Percentage of colonies with adult drones

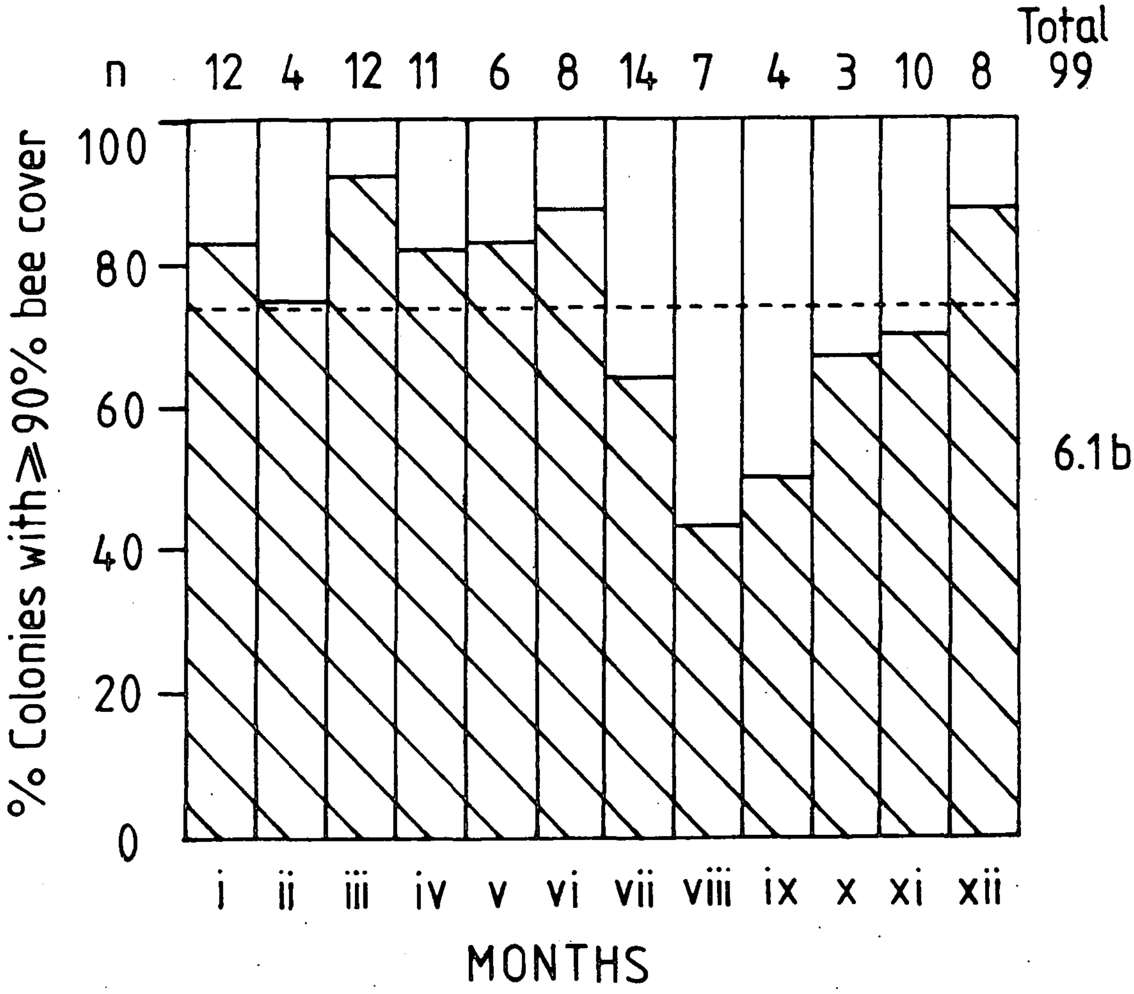
6.3a Percentage of colonies with new queen cells and colonies which are recent reproductive swarms
6.3b Percentage of colonies with old queen cells
Hatching indicates swarm queen cells, cross-hatching re-queening cells

6.4a Percentage of colonies with substantial (black), medium (hatched) and negligible (blank) quantities of stored pollen
6.4b Percentage of colonies with substantial (black), medium (hatched) and negligible (blank) quantities of stored honey or nectar

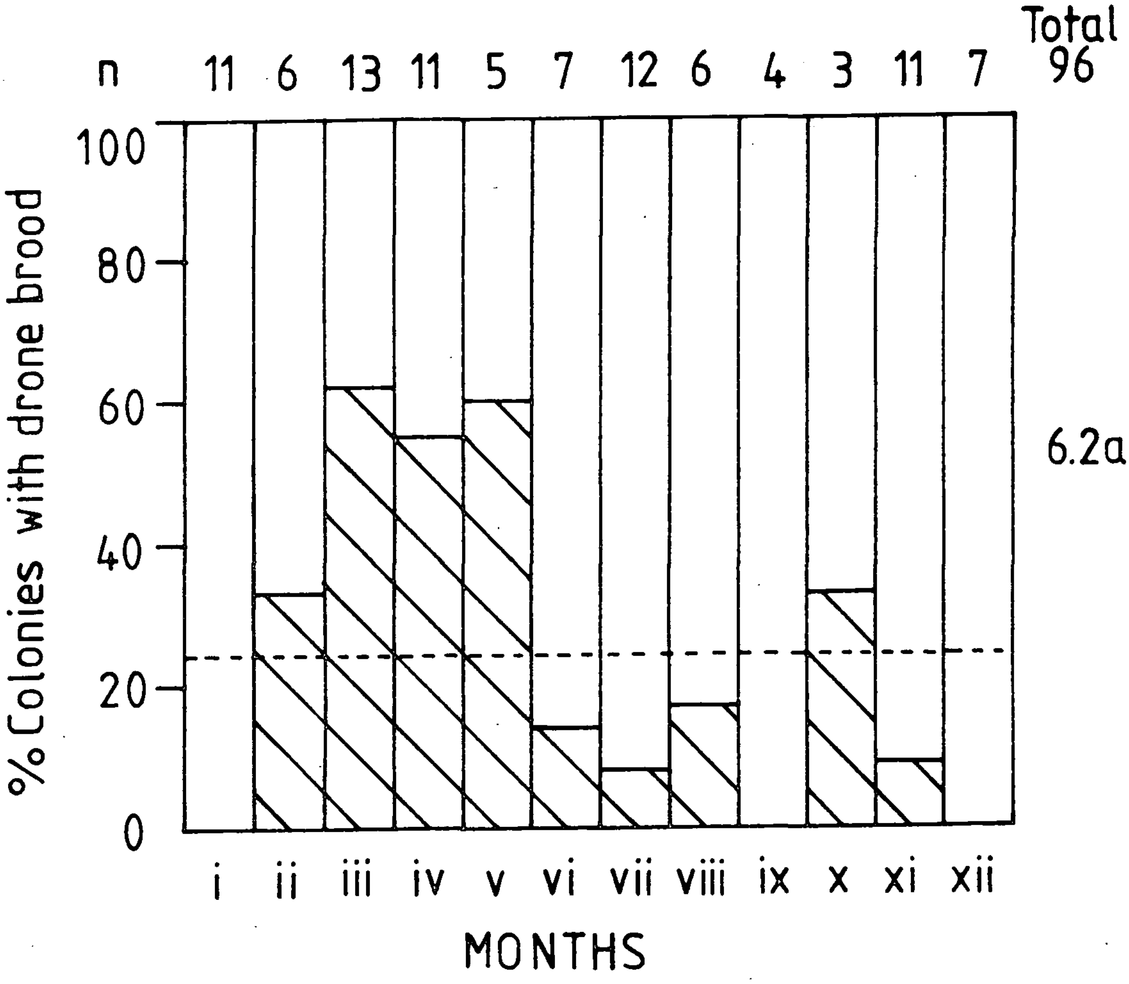
6.5a Mean colony width (cm) plus 95% confidence intervals
6.5b Mean colony height (cm), plus 95% confidence intervals
6.5c Mean colony size (cm^2), as measured by Colony Cover Index (C.C.I. see Methods, p. 251), plus 95% confidence intervals


n 11 5 14 13 5 8 13 6 2 3 10 6
Total 96
% Colonies with worker brood
0
20
40
60
80
100
i ii iii iv v vi vii viii ix x xi xii
MONTHS

6.1a

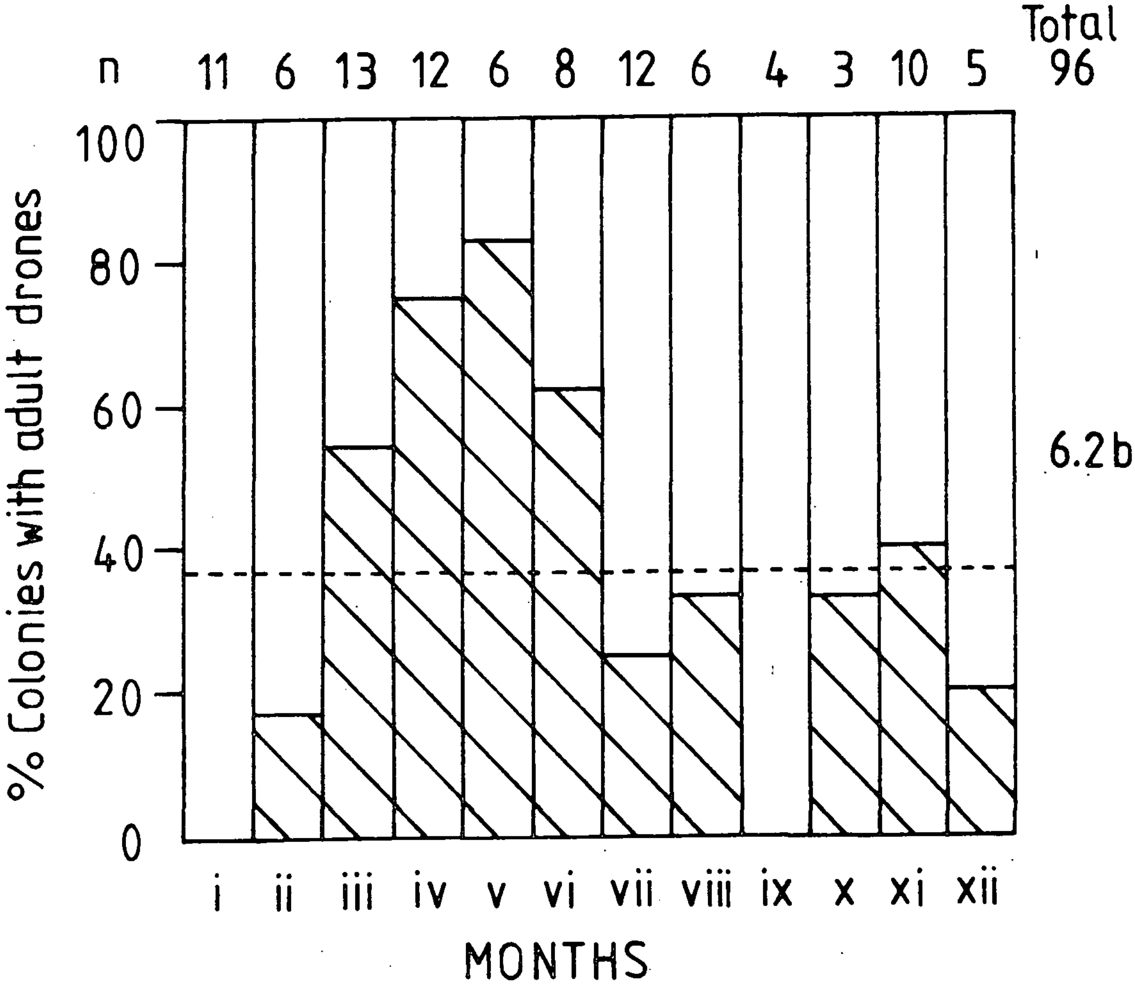

n 12 4 12 11 6 8 14 7 4 3 10 8
Total 99
% Colonies with ⩾90% bee cover
0
20
40
60
80
100
i ii iii iv v vi vii viii ix x xi xii
MONTHS

6.1b



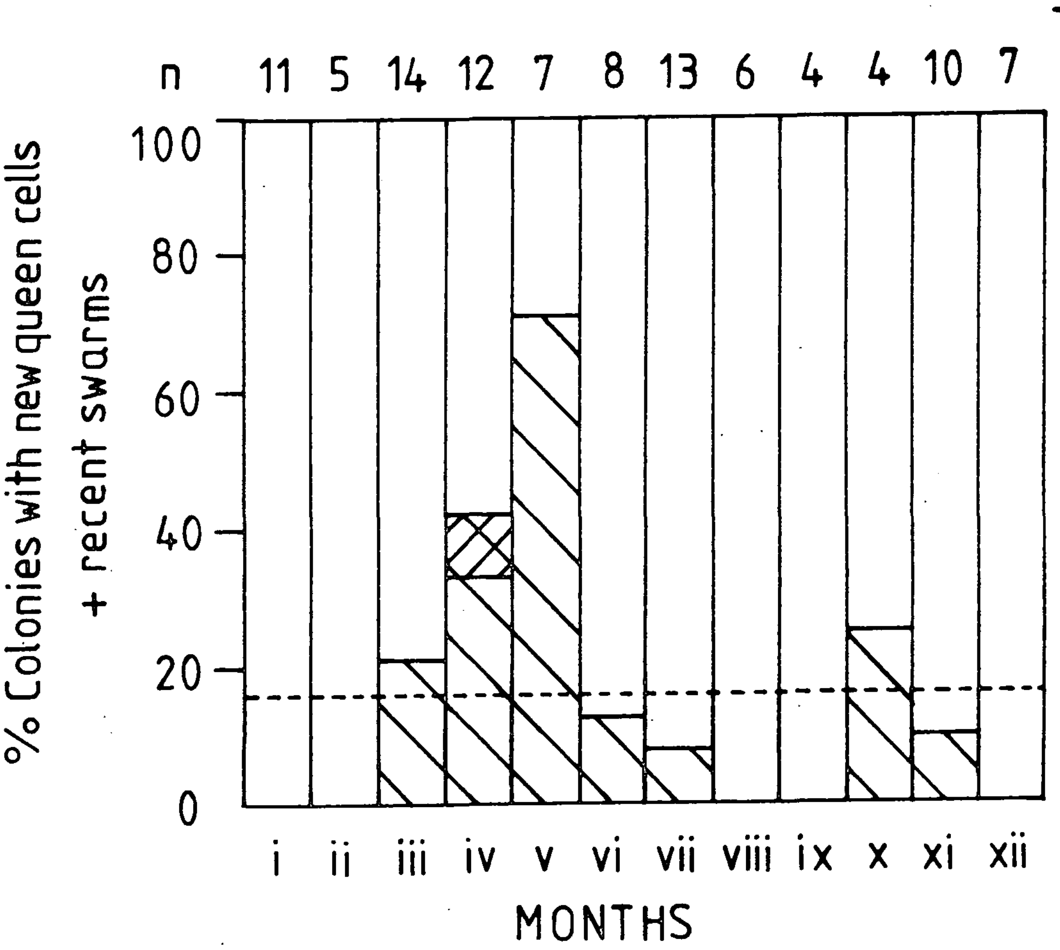
n
11
6
13
11
5
7
12
6
4
3
11
7
Total
96
100
80
60
40
20
0
% Colonies with drone brood
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

6.2a



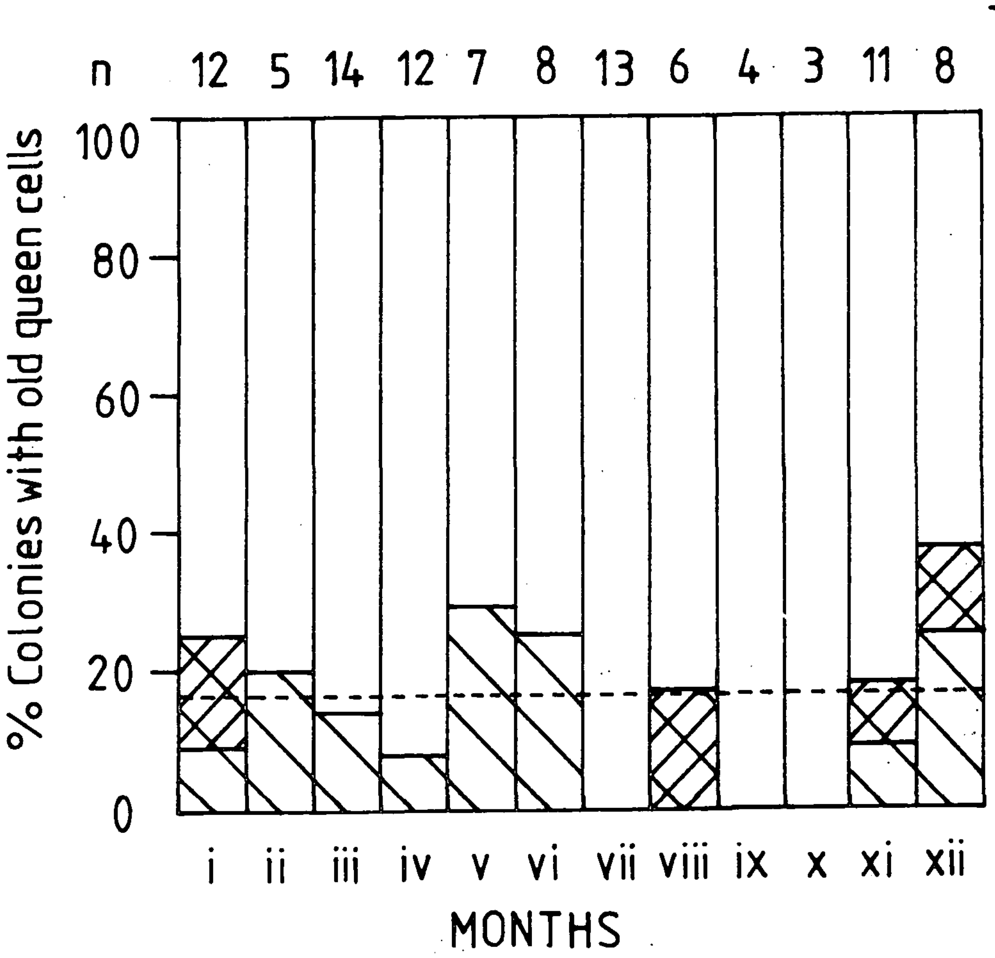
n
11
6
13
12
6
8
12
6
4
3
10
5
Total
96
100
80
60
40
20
0
% Colonies with adult drones
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

6.2b



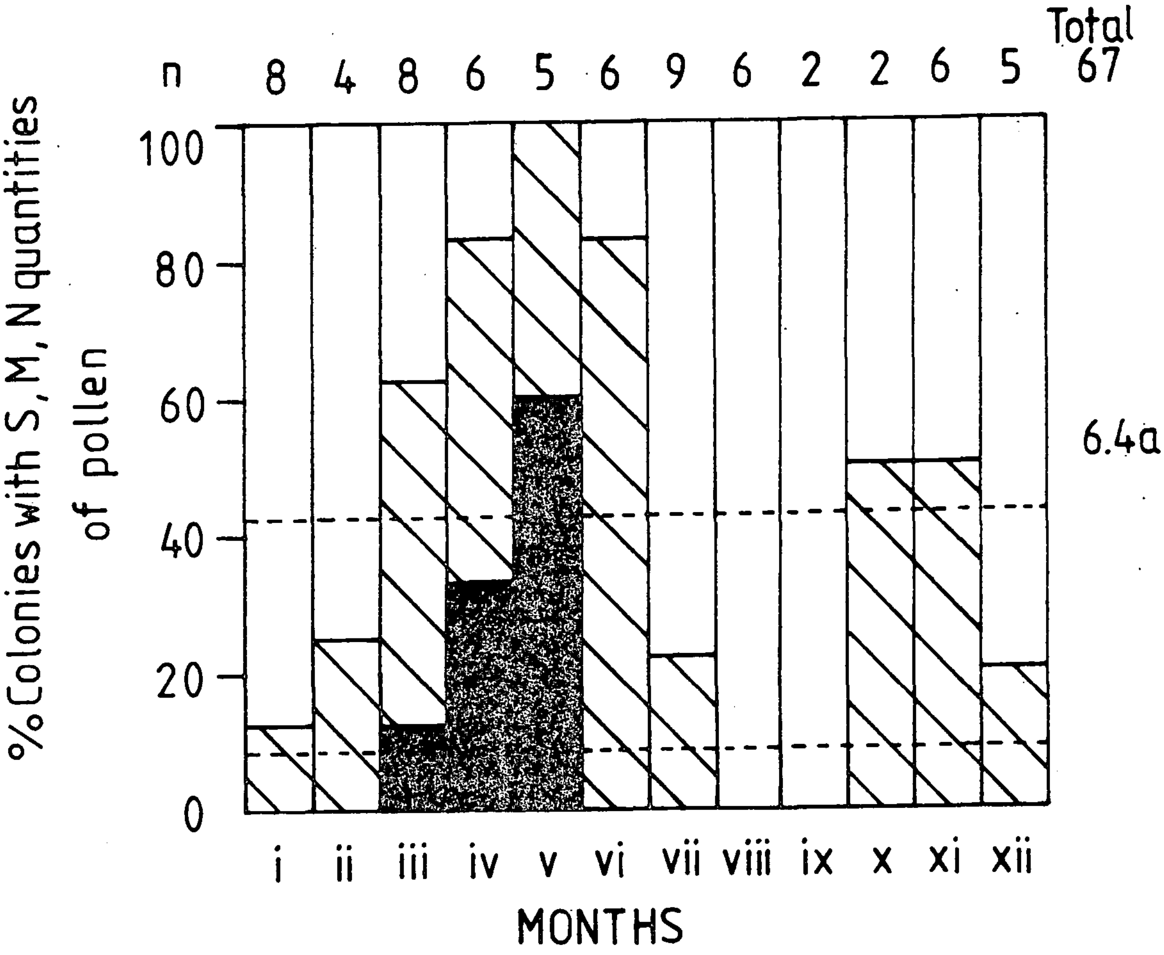
n
11
5
14
12
7
8
13
6
4
4
10
7
Total 101
% Colonies with new queen cells + recent swarms
100
80
60
40
20
0
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

6.3a



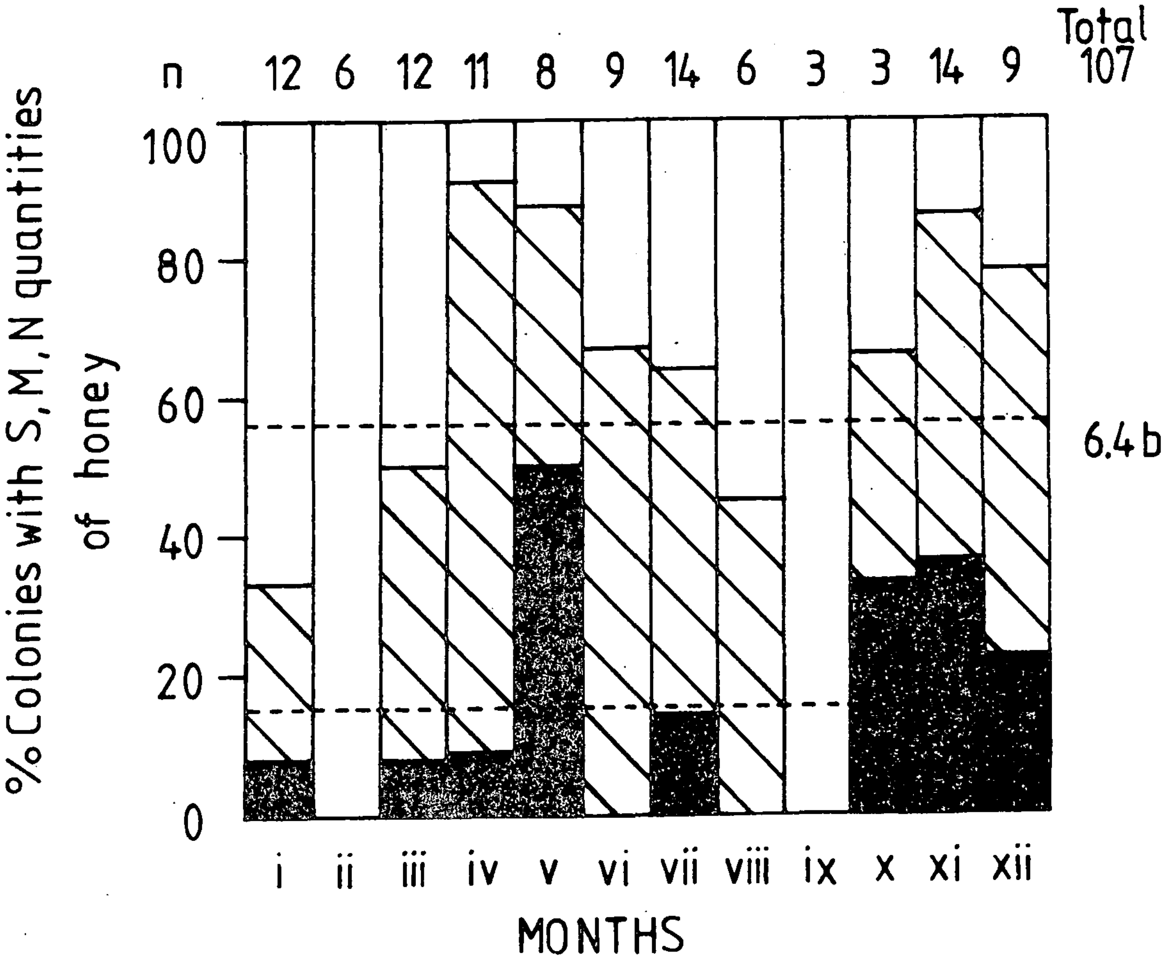
n
12
5
14
12
7
8
13
6
4
3
11
8
Total 103
% Colonies with old queen cells
100
80
60
40
20
0
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

6.3b



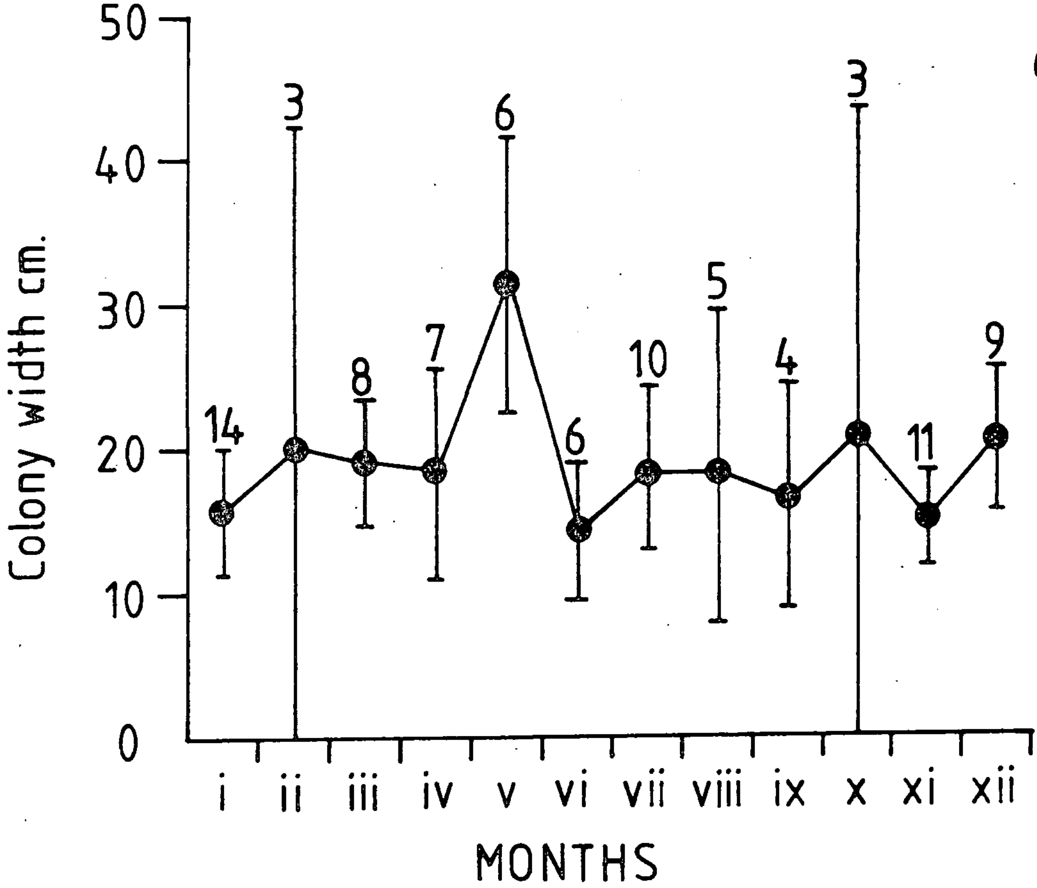
n
8
4
8
6
5
6
9
6
2
2
6
5
Total
67
100
80
60
40
20
0
% Colonies with S, M, N quantities of pollen
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

6.4a

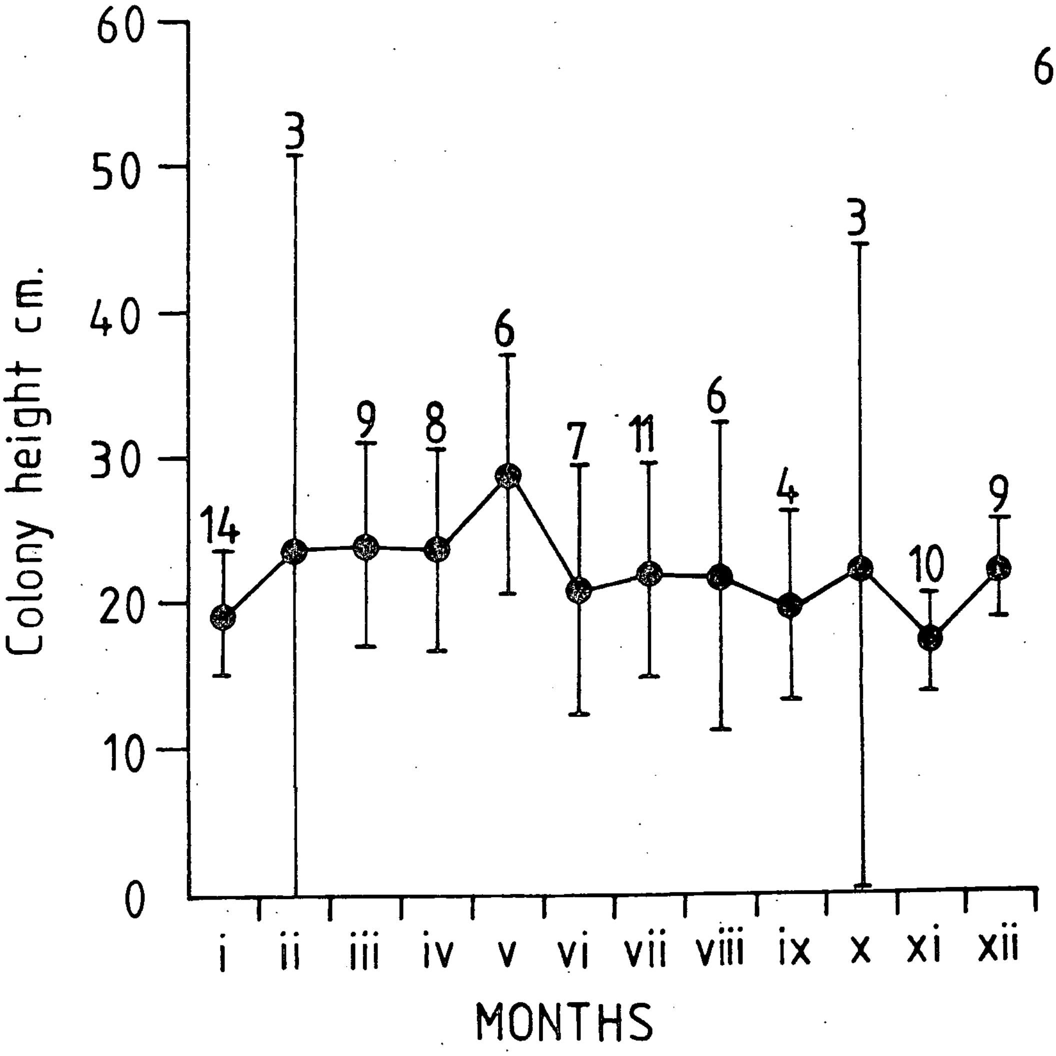


n
12
6
12
11
8
9
14
6
3
3
14
9
Total
107
100
80
60
40
20
0
% Colonies with S, M, N quantities of honey
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

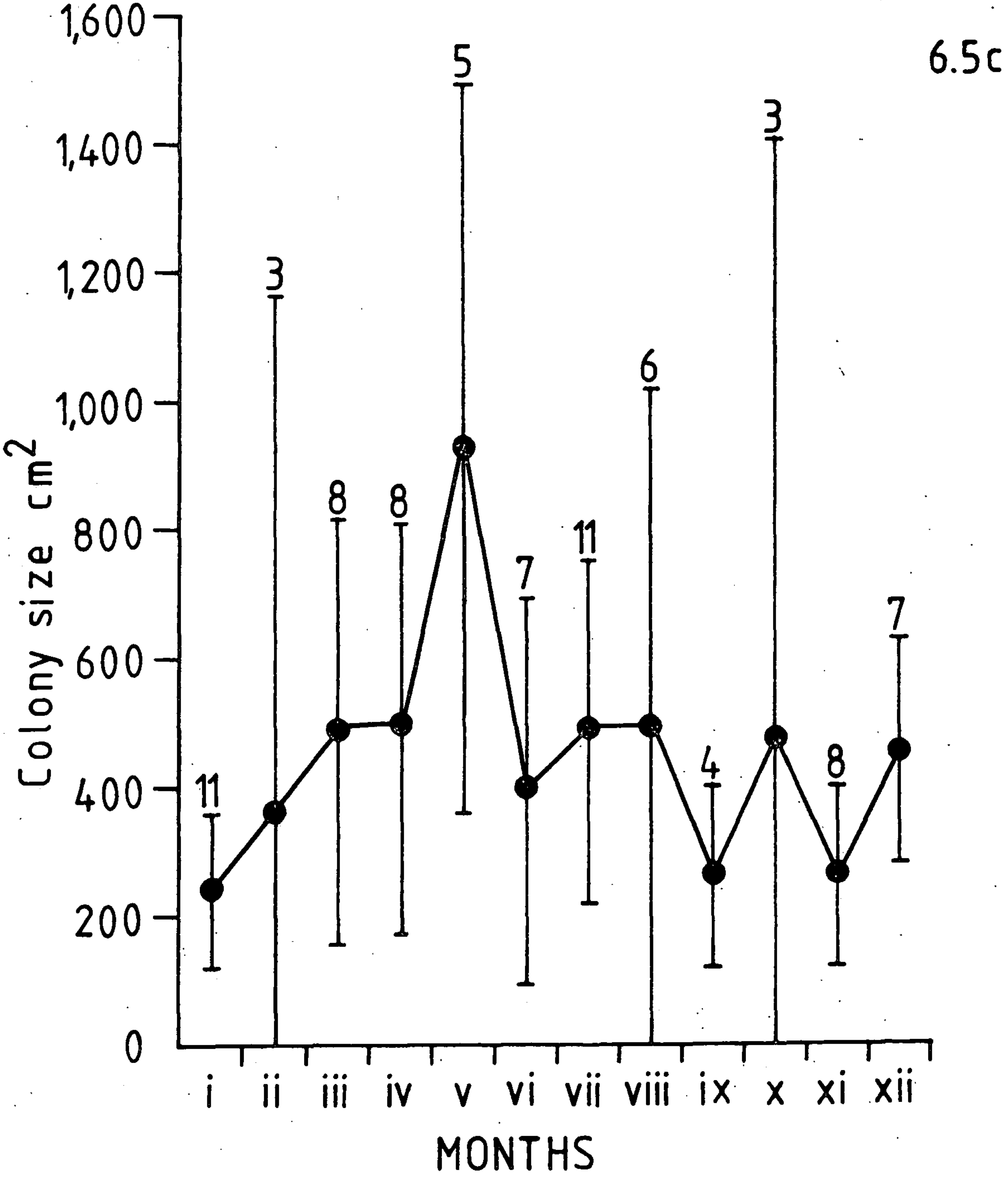
6.4b


Colony width cm.
0
10
20
30
40
50
14
3
8
7
6
6
10
5
4
3
11
9
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

6.5a


Colony height cm.
0
10
20
30
40
50
60
14
3
9
8
6
7
11
6
4
3
10
9
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

6.5b


6.5c
Colony size cm^2
1,600
1,400
1,200
1,000
800
600
400
200
0
11
3
8
8
5
7
11
6
4
3
8
7
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

The impression gained from the more detailed colony inspections was that in both summer and winter many of the colonies rearing brood were not doing so over the whole area of worker comb, as was usually the case in April and October, but often in the central portion only. So brood rearing at these seasons was reduced in terms of intensity as well as number of colonies. For the summer months, this conclusion is supported by the fact that in July and August 36% and 57%, respectively, of the colonies had less than 90% of their comb area covered by a protective curtain of worker bees (Figure 6.1b). Despite this, 92% and 83%, respectively, of the colonies were still rearing brood, but necessarily in a restricted area of comb for living brood was not left exposed by the "curtain" of bees in normal circumstances.

In contrast to summer, in December and January over 80% of the colonies had their combs completely enveloped by bees, or nearly so ($\geqslant$ 90% cover), but brood rearing was not taking place in 45 to 50% of colonies. This again suggests that the winter months are more of a problem to *florea* colonies than the summer months, in that depleted colonies (< 90% cover) can still rear brood in the summer, while $\geqslant$ 90% cover is not necessarily sufficient for brood rearing in winter.

Is this reduced brood rearing primarily an effect of particularly low forage availability in winter or of smaller colonies being unable to maintain a high enough temperature for brood rearing (or it being energetically uneconomic to do so)? Forage is not abundant in December and January and is even less so in July and August (see Chapter VII), but it is not totally absent and 50% or more of the colonies still find enough nectar and pollen and/or have enough food reserves to continue brood rearing in these winter months. As for colony size, combining the colony data of December and January, the mean colony cover index (C.C.I., measuring functional colony size) of colonies rearing brood was 451.6cm^2 (S.E. = 93.3, n = 7) but of colonies without brood was 208.3cm^2 (S.E. = 47.4, n = 8); these means were significantly different at the 5% level (t_{13} = 2.418). Thus, with the mean C.C.I. of colonies rearing brood being more than twice that of those without brood, the evidence strongly suggests it is the larger colonies that are most able to rear brood when it is cooler.

This phenomenon could partly be explained if the larger colonies had sufficient reserves of honey and pollen that enabled them to continue brood rearing, while the smaller colonies did not. Examination of the data on individual colonies showed that some of the larger colonies rearing brood did indeed have medium to substantial stores of honey and pollen. But there was also a large colony without stores that was rearing brood and a medium-sized colony with stores not rearing brood, so it cannot be the possession of adequate stores alone that leads to brood rearing in *florea* colonies.

With *Apis mellifera* in Scotland, Allen & Jeffree (1956) have shown that both colony size and stored pollen independently influenced brood rearing and suggested that in spring the larger colony can afford more field bees to make a quicker start collecting the pollen essential for rapid development. Being able to thermoregulate more effectively (Chapter V), colony size may not be so important to *mellifera* , in influencing brood rearing activities, as it is to *florea*. However, Allen & Jeffree's study does indicate that large colony size, as well as aiding thermoregulation, may be advantageous to *florea* in terms of a more satisfactory division of labour between nurse and field bees.

With more data, multi-variate analysis might elucidate the relative importance of honey and pollen stores, colony size, forage availability and temperature for brood rearing, but the present data does indicate that low temperatures are an important factor in reducing brood rearing in smaller colonies in winter. On the other hand, in summer most colonies, including small ones, were able to rear at least some brood despite forage and stores being even scarcer than in winter, presumably because the bees can cope with high temperatures better than low ones. In fact, in June, July and August, though the mean colony sizes were rather larger than in winter, there were so few colonies without any brood that a test on any association between brood rearing and colony size could not be performed. Also in May, the month when temperatures were usually at their highest, all colonies were rearing brood. It appears then that fewer bees are needed to maintain an appropriate colony temperature in summer than are needed in winter, and even colonies which did not have enough adult bees to cover the comb completely could do so, albeit at a reduced rate because of low forage availability.

It was interesting to note that the smallest colony rearing brood in December and January (winter) was found in the SW sector of an *Acacia tortilis* tree, away from shady date gardens, in a position where it was exposed to a certain amount of warming insolation (60 - 75% shade). It only had a very small brood comb with unsealed cells, so brood rearing was at a low, initial level, but it concurred with Nāsr Ahmad al Ghaythi's practice of putting colonies in the "sayḥ" in winter for warmth and is further evidence that *florea* colonies benefit from nest sites that facilitate thermoregulation.

Considering other aspects of the annual cycle of % cover of colonies (Figure 6.1b), the values were not 100% in March, April and May because large colonies which had swarmed and lost in the order of half their adult bees were included. Such parent colonies probably return to > 90% cover very quickly as sealed brood, derived from the old queen, emerges. The percentages here are probably biased on the low side by the extremely large colony IC (see Methods) which never occupied as much as 90% of its total comb area while under my observation, even when its population of bees was very high and it was producing queen cells prior to swarming.

The percentage of colonies with ≥ 90% cover decreases from June to August, presumably as the colony populations diminish in response to dwindling food stores and sources of forage. In autumn there was then a build up in the proportion of colonies with ≥ 90% cover, with the flowering of *Ziziphus spina-christi* and most combs remained well-covered over winter.

1.3 Worker eggs

The seasonal pattern of presence of eggs in *florea* colonies, as might be expected, was exactly the same as that for brood (larvae and pupae) apart from the 2 cases mentioned below, so the full figures are not presented. Woyke (1977) observed with colonies of *A.m.adansonii* that during a dearth of nectar and pollen, the queens would continue to lay but the workers ate all the larvae and no brood was reared, and that absconding colonies often left viable eggs in the combs. This appeared to be the case with *florea* in Oman, so those colonies with only a few eggs present and for which it was evident that they were not being reared to the adult stage, were scored as zero. Such colonies account for the few differences that were recorded between the presence of eggs and of larvae/pupae and these were as follows.

(i) In mid-March, one colony (out of 14 observed, ie 7%) that had just reached the end of a swarming cycle had newly emerged workers (indicating that brood rearing had been taking place from eggs laid at the end of the previous month) but no larvae and only a few eggs. An attempt was made to hive the remaining bees, but had they been left undisturbed, normal oviposition and brood rearing would soon have taken place on the old combs, if they had chosen to stay, or at a new site. Therefore, the presence of very few eggs, scored as zero, was temporary and a consequence of reproductive swarming/ deserting of an old nest, not of forage scarcity, inability to thermoregulate or other reason.

(ii) One very small colony, which had both eggs, larvae and pupae in June, and was therefore coping with high temperatures, had dwindled by the end of July, probably as a result of predation of adult bees by the toad, *Bufo orientalis*. It then contained some sealed pupae, but just 2 larvae, and no eggs could be seen. By the middle of August there was still a little sealed and also unsealed brood, but only 3 eggs could be seen (scored as zero), and there were even fewer adult bees, covering barely 20% of the comb. The colony was clearly in the process of dying out and though a little brood had been reared sporadically and there was some honey present, there was virtually no pollen and the colony must have gone below a critical size limit. It appeared that most of the few eggs being laid were being eaten by the workers. Thus, because of this one colony, in both July and August the number of colonies recorded with eggs was one less than the number with larvae and pupae.

In a number of colonies, both in summer and winter, many cells, especially round the periphery of combs, contained no eggs. Presumably either reduced oviposition by the queen and/or increased consumption of eggs/young larvae by the workers were the mechanisms by which brood rearing intensity was reduced in unfavourable seasons. With the colonies not rearing brood at all in these seasons, in most cases no eggs at all could be seen in the brood comb. This to me suggested that the queens had stopped ovipositing altogether, as can occur with *mellifera* in the fall (Gary 1975), rather than that workers ate all the eggs as happens sometimes with *mellifera* at the end of winter when the queens lay for several weeks before brood is actually reared (Free 1977). Closer observations are needed to determine more exactly the processes involved in reduction of oviposition and brood rearing.

1.4 Drone brood and adult drones

Both drone brood (Figure 6.2a) and adult drones (Figure 6.2b) were recorded in at least one colony in the months from February through to August and also in October and November. Adult drones were recorded in December too, but not drone brood.

Adult drones have occurred in an extra month because, drones starting as eggs and brood at the beginning of one month, here November, will still be present circa 40 days later as adults in the following month, here December. (The development period from egg to adult of *florea* drones is 22.5 days according to Sandhu & Singh (1960) and the mean longevity of adult drones is probably in the order of 20 days, since *mellifera* drones' mean longevity is 21.2 days (Witherell 1972)). For the same reason, when drone rearing starts in February, fewer colonies (18%) had adult drones than had adult drone brood (36%). The sample size was small (6) and it was only one colony which made the difference, but it illustrated the point as it had drone brood in February that did not emerge as adults till March. The one colony in February with both drone brood and adult drones was inspected on the last day of the month, so the adults were probably derived from eggs laid early in February, rather than the colony being an unusual case in having drone rearing starting very early in the year in January.

More colonies were recorded overall with adult drones (39.6%) than with drone brood (25%) as a glance at the histograms will indicate. The main reason for this was that adult drones were often recorded from new colonies that had no drone brood or drone comb at all. These colonies were derived, as reproductive or absconding swarms, from parent colonies that contained drones. One large colony with drone brood and adult drones was capable of dividing to produce several colonies each of which had adult drones for a period, but no drone brood. Two other minor reasons which may have contributed to adult drones being recorded more often than drone brood were that (i) with 1 or 2 inaccessible colonies adult drones were visible from the ground, but closer inspection for drone brood was not possible (ie no record) and (ii) with 1 or 2 combs from which bees had just absconded, drone brood could be scored as absent, but adult drones would be scored as "no record".

Overall the records show that maximum drone rearing coincides with the peak periods of worker brood production in March, April and May, with a shorter, smaller episode in the autumn (October and November) when worker brood production reaches a second peak. Thus in spring it appears that drone rearing is initiated in most colonies before *Acacia tortilis*, the tree which Omanis claim provides the main honey flow, comes into flower around the end of the first week in April. Therefore the nectar and pollen for this development must come from earlier floral sources. In autumn, the secondary episode of drone production coincides with the flowering of *Ziziphus spina-christi*.

In spring/early summer it can be seen (Figure 6.2a) that c. 60% of colonies were rearing drones at any one time while in the autumn the figure is only c. 30%. Therefore, most colonies already established at the beginning of spring probably reach a drone rearing phase at some stage in the following few months. Some large colonies, eg FD (see later, Table 6.3) even go through 2 phases of drone rearing, with different queens, in the one spring/summer season. It is these colonies and those established later in spring that account for the small percentage of colonies rearing drones in June, July and August. A few colonies, for instance those which have been robbed of honey and forced to abscond to a new site and those in sites with a locally poor forage supply, probably never reach drone rearing/swarming strength at this season.

In contrast, during autumn the limited episode of drone rearing that is apparent must be restricted to the colonies which were strongest at the end of summer, presumably those which swarmed early in spring/summer (but not twice) and which were able to accumulate adequate stores before the late summer dearth.

The mean C.C.I. (Colony Cover Index) of those colonies rearing drone brood and for which the necessary dimensions were measured was 828.9cm^2 (S.E. = 116.7cm^2, n = 12). The mean C.C.I. of colonies not rearing drone brood in equivalent months (ie excluding January, September and December when drone brood was not being reared at all) was 377.9cm^2 (S.E. = 73.8, n = 38), which was significantly different, $t_{48} = 3.035$, $p < .01$). Therefore, on average, the colonies rearing drone brood were over twice as large as those not rearing drones. Ideally the size measurements of those colonies with drone brood would have been made just as the drone cells were being started, but in fact most of the C.C.I. values given included the areas of drone cells already present; their inclusion is however justifiable on the grounds that they are part of the active colony.

Thus, though some of the colonies not rearing drone brood (particularly those which had reared drones earlier, swarmed and then stopped) were larger than the smallest colonies that were rearing drone brood, it was clear that drone rearing was entered on primarily by the larger colonies - and not by all colonies in a certain season (eg the "samur" season), irrespective of colony strength.

All the colonies measured in January, September and December (none of which were rearing drones) had C.C.I.s below the mean C.C.I. of the drone rearing colonies. However, there was some overlap in size of the largest winter colonies with the smaller drone rearing colonies, so other factors such as forage availability, stores of honey and pollen and ambient temperatures must play a part in the initiation of drone rearing too. As with worker brood production, multivariate analysis of complete data on a large number of colonies would help to indicate the relative importance of the various factors.

That drone rearing is not primarily under genetic control, with factors such as photoperiod determining its initiation, is also evident from the fact that if observations from colonies under management are considered too, adult drones were recorded in every month of the year. Thus a large colony I had in a hive (No. 9) at Khabura had both drone brood and adult drones present in September 1979, while another large colony kept in a garden at Bisyah, SW of Nizwa, possessed adult drones in January 1978; these drones were probably reared in December as the drone cells on the comb were empty. Thus only in January was drone brood not recorded, but in wetter years, with more forage available, there is little doubt that it is sometimes reared in this month.

According to Brian (1979) in higher bees male production is related to worker number. The findings here on *florea* are consistent with this observation and in general it applies to *mellifera* too in temperate climates (Free & Williams 1975) where drones are reared from April to September with a peak of adults around June (Allen 1958; Free 1967). However, the situation is complicated by various inter-related colony and environmental factors; thus workers will regulate drone production by killing larvae and eggs, especially if a colony is small and the season early (Free & Williams 1975). Also the area of drone comb present has been shown to influence the amount of drone brood reared (Allen 1963). Some of these factors and mechanisms involved in controlling drone brood rearing may be operative in *florea* too; however, in Oman it appeared that drones were reared and subsequent swarming cycles initiated over a less restricted period than in Britain, and primarily in response to a good supply of forage and only by the larger colonies.

1.5 New queen cells and recent swarms

The swarming season, as indicated by % colonies with new queen cells or which were recent swarms (Figure 6.3a), was from March to July, peaking in May, with a separate small episode in October and November. As would be expected, these periods coincided with drone brood production, but over a slightly more restricted period and with a smaller percentage of colony records (16.8% as opposed to 25%). These differences can probably be explained by the facts that (i) the development from egg to adult is quicker for queens (16.5 days) than for drones (22.5 days) according to Sandhu & Singh (1960), so active queen cells will be present for a shorter time than active drone cells, (ii) queen cells were more easily overlooked than drone cells in colony inspections and (iii) Omanis were more likely to "predate" colonies when they were producing queen cells, as they would be at maximum size and probably contain a near maximum amount of honey; therefore not all drone rearing colonies would reach the final swarming phase.

The restriction of queen rearing to a shorter period within that of drone rearing, if real and not due to sampling error or predation, would be advantageous as the alternative, colonies with virgin queens unable to mate because of absence of drones, would be fatal.

It appeared that nearly all swarming colonies produced drone cells before queen cells. (An exception was one colony in a hive, No. 5, which did not produce any drone cells in September/October but did construct c. 15 queen cells while swarming; also re-queening colonies did not usually produce drone cells.) So the criteria, of adequate supplies of nectar and pollen and large colony size, for the initiation of drone rearing (last section) apply equally to queen rearing and swarming.

1.6 Empty queen cells

The percentage of colonies with empty queen cells (Figure 6.3b), which are a sign of queen rearing in the previous month or earlier, shows a pattern with some resemblance to that of active queen cells and swarms. The several records of "old" queen cells in November and December suggested that swarming in this "sidr" season was rather more frequent than the few records of swarms in October and November indicated.

Two other facets of the seasonal cycle of *florea* are hinted at by Figures 6.3a and b. First the incidence of colonies re-queening from October to December (old queen cells November to January) appears to be greater than at other times of year eg the summer. Successful re-queening can only occur during months in which adult drones are available and this was the case in October, November and

December (Figure 6.2b). How long *florea* queens remain fertile is not known, so neither is the frequency with which they need to re-queen. Second that a number of colonies have old queen cells from November through to March but hardly any possess them in the summer, suggests that combs are less frequently abandoned in autumn (after swarming) than are abandoned after spring/early summer swarming. This period of desertion of larger, old combs in early summer coincides with that recorded for the kept colonies of Nāsr Ahmad al-Ghaythi (Chapter IV, Pt II, C. 3) after the *Acacia tortilis* honey flow.

Figures 6.3a and b probably illustrate the typical seasonal pattern of queen cell production in northern Oman but in certain areas with differences in bee flora, or in wetter years, swarming might be expected to occur in the other months too. For instance, a colony that I had in a hive (No. 9) produced drone and queen cells in September and would have swarmed naturally had I not tried to divide it artificially. So further investigations on *florea* in Oman are likely to reveal occasional swarming during the months in which it was not recorded in this study.

1.7 Stores of pollen and honey

Honeybees regulate the amount of brood reared in response to the quantity of forage entering the nest, especially the quantity of pollen which is the sole source of protein for the bees (Allen & Jeffree 1956; Free 1977). Thus though honey/nectar is essential as a source of carbohydrate and a colony can maintain its adult bee population primarily on this diet, the pollen supply is critical for brood rearing. It was apparent that a shortage of pollen was responsible for the decline and demise of many of the 80 colonies of *mellifera* that were imported to the Batina gardens of northern Oman from Australia in March 1979. It was unusual to record an abundance of pollen in the *mellifera* combs and the dead colonies left virtually none behind, only quantities of honey and stored sugar syrup (Whitcombe, unpublished observations).

Pollen shortage did not seem to be quite so severe for *florea* on the Batina, but considering Figure 6.4a and Figure 6.3a it is not surprising to note the close similarity between the occurrence of the "Substantial Quantities" category of pollen and that of new queen cells/swarms. It is at this period in the life cycle of a colony when a maximum of worker brood, drone brood, queen cells and a large population of adult bees has to be supported and that pollen is most needed. Only in March, April and May were colonies recorded as having Substantial Quantities of stored pollen and it is in these months that swarming occurs. Lesser quantities are stored in the preceding and succeeding months but presumably sufficient is available for the build up and maintenance of the worker and drone brood concomitant with swarming.

On the other hand in autumn, October/November, only "Medium Quantities" of pollen were recorded, not "Substantial". This is probably the explanation for the comparatively low frequency of swarming in the "sidr" season, despite the Substantial Quantities of stored honey that were recorded (Figure 6.4b) in October, November and also December. Over the rest of the year the main period of honey storage was April - May, particularly the latter month presumably because worker and drone brood rearing decreases and more of the nectar gathered can be stored. The bulk of this must come from *Acacia tortilis* and to a lesser extent *Prosopis cineraria* (see Chapter VII).

In February, no stored honey was recorded and little stored pollen even though foraging and brood rearing were on the increase;

therefore all the food that was being gathered was being used immediately for brood rearing. By March a little nectar and pollen were being stored but generally insufficient for harvesting, so the bulk was still being used for colony growth. Only in April - May and October - November were the quantities of stored honey large enough for worthwhile harvesting.

Lucerne (*Medicago sativa*) which manages to produce some flowers despite regular cutting, and the sticky exudate of ripe dates ("rutab") are probably major components of the forage from May to July and, in addition to any "samur" honey remaining in the combs, will have contributed to the stores recorded in these months. Apart from these, comparatively little other forage can be available over the summer as the stores in those colonies which survived predation dwindled from June till September when stored honey/nectar was negligible in the 3 colonies inspected. Their maintenance was probably dependent by and large on just a few plants, especially weeds, in flower at that season. Therefore the taking of all the honey from a colony right at the end of May should not be encouraged as it would seriously endanger a colony's chance of survival over the summer.

The same caution applies to the taking of honey at the end of November, though the period of comparative dearth until around February appears to be shorter than the summer dearth. More energy in the form of honey, however, may be needed for thermoregulation in the colder months of December and January. The sample sizes are small, but the winter forage dearth also appeared to be less severe as well as shorter in duration as the proportion of colonies with Substantial and Medium Quantities of stored honey and pollen in December and January are greater overall than in August. However, the nectar and pollen supplies in the two periods could in reality be similar as a smaller proportion of colonies were rearing brood in these winter months than in August, and this may have meant that winter colonies were not using so much nectar and pollen and therefore their stores were greater. In August incoming nectar and pollen may have been used immediately for brood and not stored. Thus colony store data may not always indicate forage availability and should be interpreted carefully. The honey and pollen assessments here reflect the balance between the amount being gathered and that consumed for brood rearing and thermoregulation.

1.8 Colony width, height and overall size

The monthly means of colony width, height and size (as measured by Colony Cover Index) are given in Figures 6.5a, b and c and all follow broadly the same pattern of seasonal change. The confidence limits are on the whole large, but this is <u>not</u> just because the sample sizes are small. The other reason for the large confidence limits is of biological significance and is a result of there being a mixture of large and small colonies in certain months due to swarming and asynchrony. Thus in June and December (Figure 6.5c) the sample sizes are the same (7) and the mean colony sizes similar (c. $400cm^2$) but the 95% confidence limits in June are large (92 - $694cm^2$) because some of the colonies will have started as small swarms in the previous month, while in December the colonies have more uniform C.C.I.s (277 - $625cm^2$), there being comparatively little swarming in November. Similar comparisons can be made between April and October, each with n = 8, and July and January each with n = 11. (See later section 1.11 for an example of asynchrony.)

The main feature of the graphs, particularly clear with that of C.C.I. (Figure 6.5c) where the % cover is taken into account (which it is not with width and height) is the growth of colonies from January to May, with a sudden drop in June. This represents the spring to early summer build up with drone comb being built and a sudden expansion in size from April to May as *Acacia tortilis* and *Prospois cineraria* flower. The size of the confidence limits and the sudden drop of C.C.I. from May to June indicate some swarming in March and April, but a peak in May, and also reflects the predation of the larger colonies by man as the "samur" honey is harvested. Such colonies would have their combs fixed in "zoora", and therefore not be counted again, or the bees would abscond to start again as small colonies.

So a greater proportion of small colonies was present in June. They showed only a little growth in June and July and a probable decline from August to September (based on a very small sample). This concurs with the evidence in the previous section that lucerne and fresh dates provide forage in the former months, but that forage is particularly scarce by the end of the summer.

Similarly in autumn, with the flowering of the "sidr",there appears to be an increase in colony size in October (but again based on a small sample) followed by a drop in November, attributable primarily to the predation of the larger colonies for their honey, but secondarily to swarming. There appears to be some recovery in the latter half of November (maybe through late flowering of *Ziziphus spina-christi* and *Acacia nilotica*) but then a decline from December attributable to lower temperatures and comparative floral dearth.

Only one small difference between the width (Figure 6.5a) and height (Figure 6.5b) graphs is worthy of comment and that is the greater increase of colony width from April to May, than of colony height. As described in the next section with reference to Figure 6.6, colony height is initially greater than colony width but as colonies grow, width increases more rapidly than height so when near maximum sizes are reached, as in May, colony width overtakes colony height. I believe this difference is real but merely reflects changes in comb shape with growth; it may have been exaggerated too, as a result of chance effects due to small samples.

Overall, the data on colony size matches well with the observations on specific aspects of colony development (preceding sections). The former are, nevertheless, based on small samples during what were comparatively dry years. Measurements of greater numbers of colonies in wetter years might indicate larger colonies overall, but I expect the seasonal patterns would still be similar. It would have been informative to have measured the numbers of adult bees in the colonies of *florea* too, as has been done for *mellifera* eg Jeffree (1955), particularly to have elucidated the problem of nest thermoregulation in winter with respect to colony size and brood rearing. However, measurements would have been difficult on natural colonies attached to fixed supports without sacrificing them.

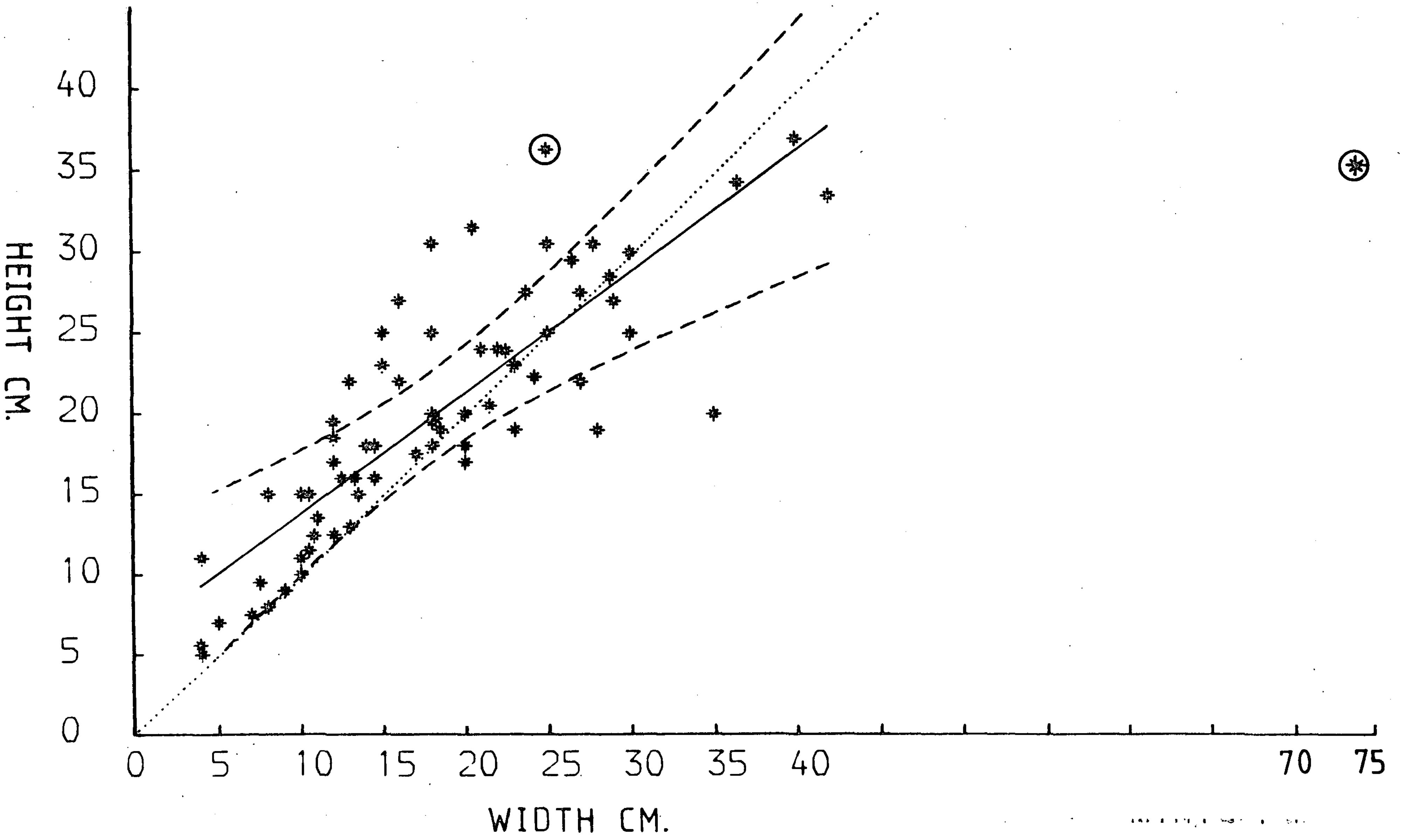
1.9 Comb shape : height versus width

The dimensions of colony height and width, and possible changes in their ratio as growth took place, were of interest in order to determine the most appropriate shape and size for frames to hold combs of *florea* - either for installation in hives and/or for ease of honey extraction. As might be expected there was a significant correlation between colony height and width ($r = 0.837$, $p < .001$) and a linear relationship between them ($t_{67} = 12.53$, $p < .001$). The regression line (Figure 6.6), with the positioning of all initial points above the 45° (equal height and width) line, shows that in

Figure 6.6 Comb shape and comb growth for *Apis florea* colonies in northern Oman as indicated by a plot of total comb height against total width. With most established colonies the measurements included the bees around the perimeter of the comb, giving a very close approximation to actual comb height and width, while with new colonies (where the bee cluster was usually much larger than the comb) the dimensions of the comb were used where possible. Records of the same colony in different months were only used in a few cases when the colonies had grown. Measurements of two exceptional colonies (points circled) were excluded from the regression calculations (see text). The dotted line at 45° represents even comb growth, height = width. The dashed lines indicate 50% confidence limits of estimated values of y for given values of x (after Sokall & Rohlf 1969).

Regression equation: $\text{Height} = 0.747 \times \text{Width} + 6.38\text{cm}$

$r = 0.837$, sig. $p < .001$


HEIGHT CM.
40
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
35
40
70
75
WIDTH CM.

the very early stage of colony establishment, height is greater than width. (The calculated intercept was 6.4cm, but any comb of course starts off with comb height and width both zero, and this figure just indicates initial comb construction was primarily of vertical, downward growth.) Once past this initial phase, the growth in colony width is slightly greater than that in height (note the gradient 0.747 is less than 1). Therefore, if shown accurately colony growth should initially be represented by a curve that quickly straightens. However, for frame purposes, it is the ratio of height : width as colonies grow larger that should be considered and for this the straight regression line is the best guide.

Measurements from two colonies were excluded because, when incorporated in the regression calculations their residuals (distance from the line) were so great to indicate abnormal circumstances. In one case this proved to be a colony which, rather than building along a supporting twig, had built its comb transversely so any extension widthways would have been without support; therefore the comb had been elongated downwards (tall and narrow, 44cm by 27cm). The other colony was the largest one found (designated IC) and attached to a piece of wood immediately above a solid surface, so extension of the comb downwards was strictly limited, while extra horizontal growth along the wood had been possible (35.5cm by 74cm).

Several of the other points at a greater distance from the regression line were from combs which could also have been excluded from the analysis for similar reasons eg in a cave or on a shrub branch close enough to the ground to limit downward growth; on the end (stump) of a cut palm-frond so that horizontal growth was limited; on a support branch at a steep angle so that colony height was exaggerated. These less extreme examples were included to reflect the range of shapes which did occur as a result of restrictions at nest sites.

It was such colonies that were mainly responsible for the apparent increase in variation of height and width as colonies became larger (Figure 6.6); the shape of such combs would not have been affected by these barriers when the colonies were small. Though a log transformation of the data might have reduced this variance increase, it was not considered applicable as the increase was primarily a result of restricted nest sites, not natural variation.

The main reason that extension of the brood comb vertically, after initial growth, is slower than horizontal extension I believe is the risk of the brood comb tearing away under its own weight from the honeycomb. This happened with colony FD at Khabura, 2 weeks after it was measured as 33.5cm high by 42cm wide and when it was still growing and full of brood. This was at the end of May (1980), a hot month with mean maximum shade temperatures of about 40°C. Wax loses tensile strength as it becomes warmer and softer and for tall colonies full of brood this must be a danger in hot weather. The tall colony (44cm by 27cm) mentioned earlier, though full of brood, did not collapse as it had smaller twigs passing through the brood comb lower down providing extra support.

1.10 Consequences of comb shape and size for frame dimensions

Including the few colonies in restricted sites and the two for which length but not height were measured, the mean colony height was 20.4cm (S.E. = 0.98, n = 71) and mean colony width 19.0cm (S.E. = 1.25, n = 73), but they were not significantly different,

t_{142} = 0.876. Considering just the 71 records where both height and width were measured, the ratio of width : height was 0.9287:1.

In a hive or otherwise suspended, a single frame to hold one colony's honey and brood comb, or two combined frames to hold them separately, should probably mimic such a ratio, but should cater for colonies at their likely maximum size, not their mean size. From Figure 6.6 a suitable maximum internal width would be 30cm (not so wide that the comb would remain unattached to a frame's side bars). According to the above ratio, inner frame height for brood and honeycomb would then be 32.3cm, but according to the regression equation would be 28.8cm; the latter would be a more suitable measurement, accounting for the greater increase in width as colonies get larger.

Therefore, if <u>one</u> frame was wanted for holding a comb of *florea*, then a "natural" internal size would be 30cm wide by 29cm high. If <u>two</u> frames were to be used one, with the honeycomb, above a second with the brood comb, suitable internal sizes might be 30cm x 7cm and 30cm x 22cm respectively, or even 30cm x 6cm and 30 x 23cm to ensure that some honey could be left with the brood comb, on removal of the upper frame.

Table 6.2 compares the width and height measurements made on *florea* colonies under the management of Nāsr Ahmad al- Ghaythi on 3 different occasions (Chapter IV), with those of wild colonies. If the ratio of mean width/mean height is expressed as $\bar{z} = \bar{x}/\bar{y}$, the standard error of the ratio can be calculated as $\sqrt{(\bar{x} \,.\, SE_x)^2 + (\bar{y} \,.\, SE_y)^2} / \bar{x}.\bar{y}$ (derived from Paradine & Rivett 1960). Thus the wild colony mean width/mean height ratio $\bar{z}_1 = 0.929$ ($SE_1 = 0.081$, n = 71) can be compared with the kept colony ratio closest to it (Visit VI, 11.iv.80)

$\bar{z}_2 = 1.612$ ($SE_2 = 0.068$, $n = 28$). Their variances were significantly different at the 5% level ($F_{27,70} = 0.2785$), so the Fisher-Behrens test, used instead of a t-test (Campbell 1974), gave $d = 6.433$ ($\theta = 40^{\circ}$, d.f. : $v_1 = 22$, $v_2 = 70$), significant at $p \ll .01$.

Table 6.2 Summary of dimensions (cm) of *Apis florea* colonies in Oman to compare the ratio "colony width (W) : colony height (H)" for wild colonies with the ratio for colonies under the management of Nāsr Ahmad al-Ghaythi at Zāhib (data from Chapter IV)

		Mean		S.E.		n		Ratio
		W	H	W	H	W	H	W:H
Wild Colonies		18.95	20.40	1.28	0.98	71	71	0.93:1
Kept Colonies Zāhib	Visit VI (11.iv.80)	26.75	16.59	1.07	0.60	28	28	1.61:1
	Visit IV (30.vi.79)	25.63	13.91	1.14	0.56	23	23	1.84:1
	Visit VII (6.vii.80)	23.93	14.50	0.96	0.55	23	23	1.65:1

Therefore the ratio of colony width/height is significantly greater for colonies under Nāsr's management than for wild colonies.

This will partly be a consequence of Nāsr's regular removal of the honeycomb from the top of colonies, reducing their height, but the difference is also a result of the mean width of Nāsr's colonies being greater than that of wild ones (see Table 6.2, first column). Therefore his various techniques, including removal of drone comb, presumably encourage lateral comb growth and possibly check downward construction.

Since his management operations are the most successful on record, frames for *florea* with dimensions similar to his colonies would be worth testing in case they have advantages, such as inhibiting the production of drone cells and swarming. For a frame area of $30 \times 29 = 870\text{cm}^2$, and with 1.6 : 1 as the ratio of width (x) : height (y),

$x \times y = 870\text{cm}^2$ and $x = 1.6y$. Solving simultaneously, $1.6y^2 = 870$ and therefore $y = \sqrt{\frac{870}{1.6}} = 23.3\text{cm}$ and $x = 1.6 \times 23.3 \simeq 37.3\text{cm}$. Rounding off the figures, a single frame with internal dimensions 36cm wide by 24cm high, or a shallow upper frame with internal dimensions 36cm wide by 6cm high plus a deep, lower brood frame 36cm by 18cm, would have overall areas of 864cm^2 and should be tried. The actual use of hives and frames is considered in Chapter VIII.

1.11 Seasonal cycle as manifested in two individual colonies

Having considered the seasonal cycle of *florea* in Oman as indicated by investigation of over 70 colonies, details of regular inspections of just two, one "small" and one "large", are presented here to give an understanding of how the general pattern can be manifested in the development of individual colonies and to show the variation which can exist. Table 6.3 outlines the critical features of development and growth of the two colonies. They were both found on the cultivated strip of the Batina coast and were only c. 0.5km apart, so mainly similar floral resources were available to them. The larger colony, FD, was on the DUKDP farm with a nest of waist height making frequent inspections relatively easy, but the smaller one, KAb, was high in a thorny *Acacia nilotica* tree in a private garden and consequently it was not visited so often and not at all in April or May. Nevertheless, the months in which it was inspected fell

Table 6.3 Outline developmental history of two *Apis florea* colonies, FD and KAb, at Khabura, Oman. FD had absconded from an experimental hive (b) to a *Bougainvillea* bush in a small enclosed garden on the DUKDP farm. KAb was in an *Acacia nilotica* tree in a date garden. (?) denotes that these events and/or their exact timing were deduced, not recorded.

	FD		KAb
(?)21.vi.79	Colony absconded to *Bougainvillea* taking some honey, pollen and wax to the new site. Initial colony numbers c.11,000 workers plus a few drones (calculated from weight of bees at old site on 12.vi.79).		
12.vii.79	Colony already a fair size (21cm wide, 24cm high) with new adults emerging and eggs, larvae and pupae throughout brood comb. Some stores of sealed honey.		
(?)15.viii.79	Colony re-queened and possibly sent off a swarm, but no drones reared. Little or no brood rearing and adult population much depleted (c.35% cover). Honey stores negligible.		
9.ix.79	Little change		
9.x.79	Brood rearing in central area of comb, more adult bees (75% cover). A little pollen stored near brood, virtually no nectar/honey.	(?)26.x.79	Colony arrived as a swarm with adult drones.
		11.xi.79	Whole comb 12.5cm wide by 16cm high. Brood comb full of eggs, larvae and pupae. A few drones still present. Honeycomb well expanded for a small colony and nearly full of "sidr" honey but only c. 10% of cells sealed. Some pollen stored
17.xi.79	Comb extended a little widthways, more adult bees (90% cover). Eggs, larvae and pupae in most of brood comb. Medium quantities of pollen and honey (much sealed) stored.		
1.xii.79	No further comb growth but 100% cover of bees. Some larvae and pupae, but oviposition much reduced. Still medium quantity of stored honey.		

cont. overleaf

Table 6.3 continued

	FD		KAb
		6.xii.79	Comb has not grown. No brood rearing, only a few cells (sealed and unsealed) with pupae. Thick, inactive cluster of bees round the comb (17.00h); when bees brushed aside for photo clump of c.200 fell, 5.5m to ground without bees taking flight. No drones. c.50% of honey remains, very little pollen.
8.xii.79	Brood rearing ceased completely: only a few scattered cells with sealed brood. Rather less honey. No foraging (16.00h).		
1.i.80	Colony still inactive (16.15h, no foraging). No brood, all sealed honey gone. <95% cover of bees but densely packed.		
(?)5.i.80	Regular foraging and oviposition (brood rearing) starting, facilitated by use of sugar syrup put c.40m away for other bees!		
		27.i.80	Comb has not grown. No brood earing. Fairly thick, inactive cluster of bees exposing sides of comb. Cluster temperature 26.5°C, ambient 23.2°C (16.45h). Little honey left, virtually no pollen.
28.i.80	Eggs, larvae and pupae fill brood comb. More bees (95% cover). A little nectar/sugar syrup being stored, but no pollen.		
		(?)10.ii.80	Brood rearing re-starting. Complete covering of bees, little comb expansion. No surplus honey being stored.
11.ii.80	Drone comb and eggs first recorded.		
16.ii.80	More drone comb and now larvae. Honeycomb not completely covered by bees. Sugar syrup stored, but little honey or pollen.		
20.ii.80	Sealed drone cells (pupae) seen.		
25.ii.80	Partly built queen cells first recorded.		
7.iii.80	Adult drones first seen.		
9.iii.80	Many drones flying. Sealed drone cells, but no eggs or larvae. Sealed and unsealed queen cells. Worker brood at all stages. Comb 27.8cm wide by 30.5cm high. 98% cover of bees. Little surplus honey or pollen.		

cont. overleaf

Table 6.3 continued

	FD		KAb
10.iii.80	Prime swarm left with old queen.		
12.iii.80	First new queen emerged.		
15.iii.80	Second new queen emerged. Later found dead beneath colony.		
16.iii.80	Second swarm left. Third queen emerged.		
20.iii.80	Just a little sealed worker brood present. Colony depleted, c.65% cover. Many adult drones, and nearly all pupae have emerged. Insignificant stores of honey and pollen.		
25.iii.80	Last workers from original queen emerging. Eggs from new queen first recorded.		
27.iii.80	Small worker larvae present.		
30.iii.80	New sealed brood first recorded.	30.iii.80	Whole comb 14cm wide by 18cm high, so only a little growth since Jan, but brood comb full of eggs, larvae and pupae. Complete covering of bees. Virtually no surplus nectar or pollen stored.
9.iv.80	New adult workers have emerged but cover of bees is thin (c.60% of comb). Adult drones still present. Some honey being stored.		
21.iv.80	Worker brood comb being extended to side of colony.		
28.iv.80	Much worker brood. Much pollen and some honey now being stored.		
5.v.80	New drone comb being constructed and drone eggs laid (old drone comb not used a second time). Previous adult drones still present.		

cont. overleaf

Table 6.3 continued

	FD	KAb
16.v.80	Comb even larger (42cm wide, 33.5cm high). Previous drones still present. New, open queen cells first recorded. Large quantities of pollen and honey stored.	
27.v.80	Brood comb tore away from honeycomb and fell into cardboard box beneath. Some bees clustered round brood comb, some round honeycomb.	No further inspections. Small quantity of honey (c.0.25kg) taken around the end of May by the owner.
29.v.80	Bees absconded.	

entirely within the period during which colony FD was under examination, so their growth and development are directly comparable. The table is self-explanatory, but the principal features will be pointed out and contrasted.

Even though the major spring/early summer period of blooming was over, colony FD was able to get well established and rear brood in June and July after absconding from its previous site; the flowers of lucerne and the exudate of ripe dates must have contributed significantly to this growth, and the large initial population of workers (c. 11,000). However, the end-of-summer dearth (August and early September) was apparent with no brood rearing taking place and the colony's weakness was exacerbated by a reduced population of workers following re-queening and possibly also swarming. In October and November the colony developed well with the flowering of *Ziziphus spina-christi*, but it appeared to be a relatively poor year (or locality) as drone production and swarming were not initiated, nor was a large quantity of honey stored. However, by the middle of November the colony was larger and had more stores than the colony in the *Acacia nilotica* tree, which had started life as a swarm 2 or 3 weeks previously (from a colony that must have been sufficiently large at the beginning of the "sidr" season for it to have reached swarming strength).

Brood rearing was reduced in both colonies towards the end of November when ambient temperatures became very low (at Khabura, mean minimum for the month was 14° C with temperatures going below 10°C, Whitcombe 1982d) and it ceased altogether in December. Their stores diminished during the month, but brood rearing started again in the larger colony (FD) in the first part of January (facilitated by their discovery of some sugar syrup, but not wholly dependent on it as pollen was essential too). However, brood rearing did not start again for at least another 3 weeks in the smaller colony and probably not till February, even though <u>some</u> forage must have been available (see Chapter VII). Presumably the low temperatures had a greater inhibitory effect on brood rearing in the small colony than the large one, and only in February when adequate forage was available <u>and</u> higher ambient temperatures were prevailing was it re-initiated in the former.

The early start to brood rearing had a pronounced effect on the development of the larger colony as it was initiating drone rearing on c. 11 February, the time the small colony was deduced to have just begun the rearing of worker brood for the first time in spring. Colony FD then proceeded to produce queen cells, send off at least 2 swarms and have a new queen mate and start ovipositing before the end of March, when the small colony had not even started to build drone comb.

No further inspections were made of the smaller colony, but it may well have reached a drone rearing and swarming state towards the end of May, the approximate time when its owner took a <u>small</u> quantity of honey. In comparison, colony FD, had it not grown so large that it collapsed, at the end of May, would have been sending off a <u>second</u> batch of swarms.

Therefore, though the colonies responded to changes in forage availability and temperature in <u>broadly</u> the same way, there was in spring 1980 a marked difference in their reproductive output (in terms of number of swarms produced and the timing of this reproduction). This was primarily a result of the one colony being smaller than the other at the beginning of December and this because it started its life as a swarm at the end of October, while the larger one started as an absconding colony 4 months earlier. Had both colonies remained intact, the smaller might have produced 2 swarms by June 1980, but the larger 4 swarms amd the 2 of these that arose first in March might themselves have produced swarms in June.

This information does not offer proof, but thermoregulation again appeared to be a crucial factor in the biology of *florea*, with the inability of smaller colonies to maintain a high temperature for brood rearing, or the energy costs of it being too great, having an effect on their development and fecundity. Furthermore, as a result of interrelated factors such as the need to abscond from unsuitable nest sites, predation, variation in initial colony size, difficulties in thermoregulation, *florea* colonies are far from synchronised in their growth and reproductive behaviour. This explains the large variation in colony size within any one month, compared to the small variation in mean colony size between months (Figures 6.5a,b and c). Without more data the reproductive success of colonies starting at different times of year, in terms of total number of colonies they give rise to in, for instance, the subsequent two years, cannot be ascertained. However, the evidence does suggest that there may be great selective advantage to colonies originating at particular times of year and, of course, to colonies which can enter a comparatively harsh period, eg of low temperature, in a strong state.

2. Absconding

2.1 Seasonal pattern

Figures 6.7 to 6.10 are based on essentially the same data, but analysed and presented in different ways to facilitate fuller interpretation. Overall, from 50-60% of colonies absconded within 15 days of "hiving" (Figure 6.7) and this indicates the high sensitivity

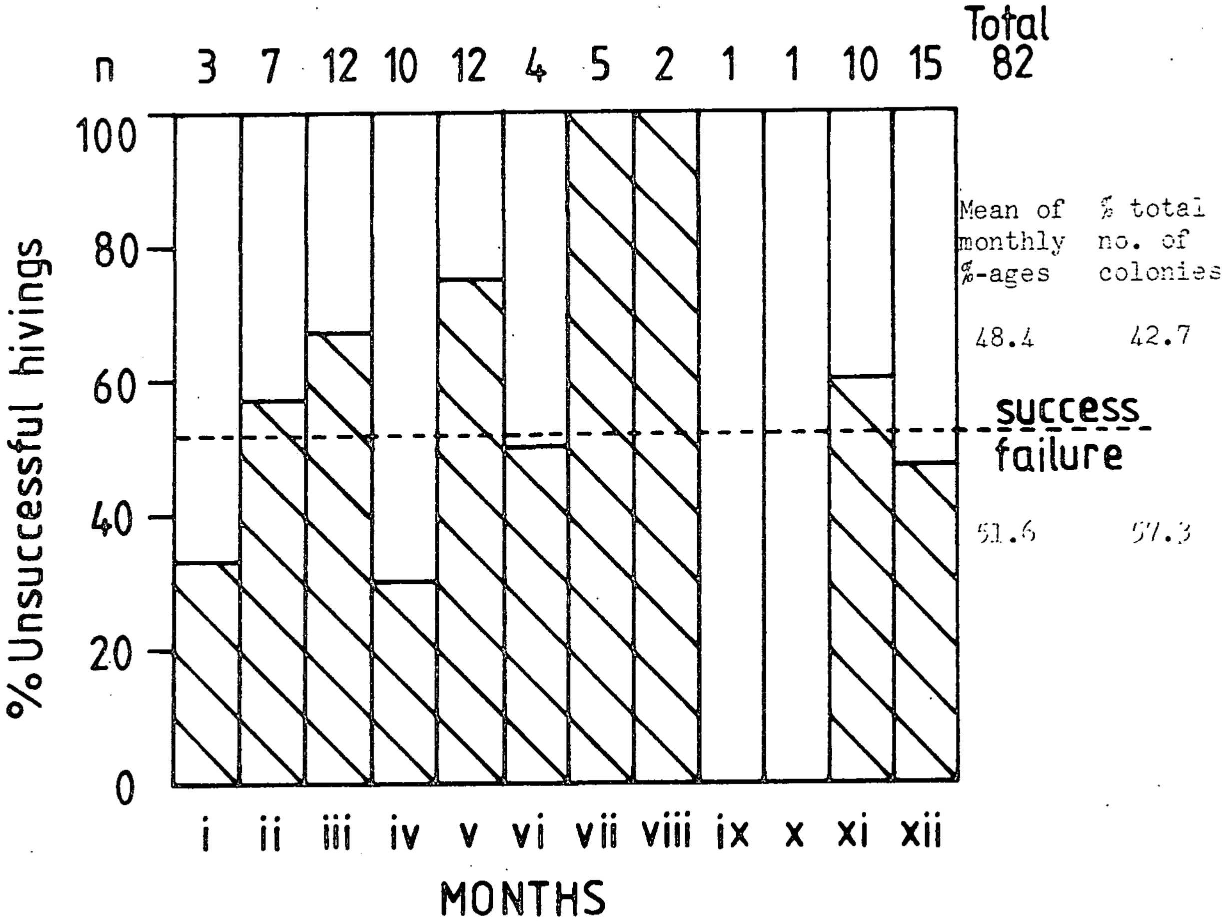
Figure 6.7 Percentage of *Apis florea* colonies absconding within 15 days of being installed in experimental hives or being re-established by an Omani method after honey removal ie % unsuccessful hivings, according to the month in which each colony was hived. Monthly records from different years (December 1977 to August 1980) combined. Dashed line indicates overall success/failure rate (mean of monthly percentages staying > and ≤ 15 days).

Figure 6.8 Total number of *Apis florea* colonies absconding from experimental hives and from traditional Omani management, according to the month in which each colony absconded.

Hatched areas	:	established colonies, absconding after 15 days
Stippled areas	:	numbers of colonies absconding that were "final swarms", at the end of a swarming phase, leaving no bees to perpetuate the colony on the parent comb
Unhatched areas	:	newly hived colonies, absconding in ≤ 15 days

Monthly records from different years (December 1977 to August 1980) combined.

6.7


Total
n 3 7 12 10 12 4 5 2 1 1 10 15 82
% Unsuccessful hivings
100
80
60
40
20
0
Mean of monthly %-ages
% total no. of colonies
48.4
42.7
success
failure
51.6
57.3
i ii iii iv v vi vii viii ix x xi xii
MONTHS

6.8

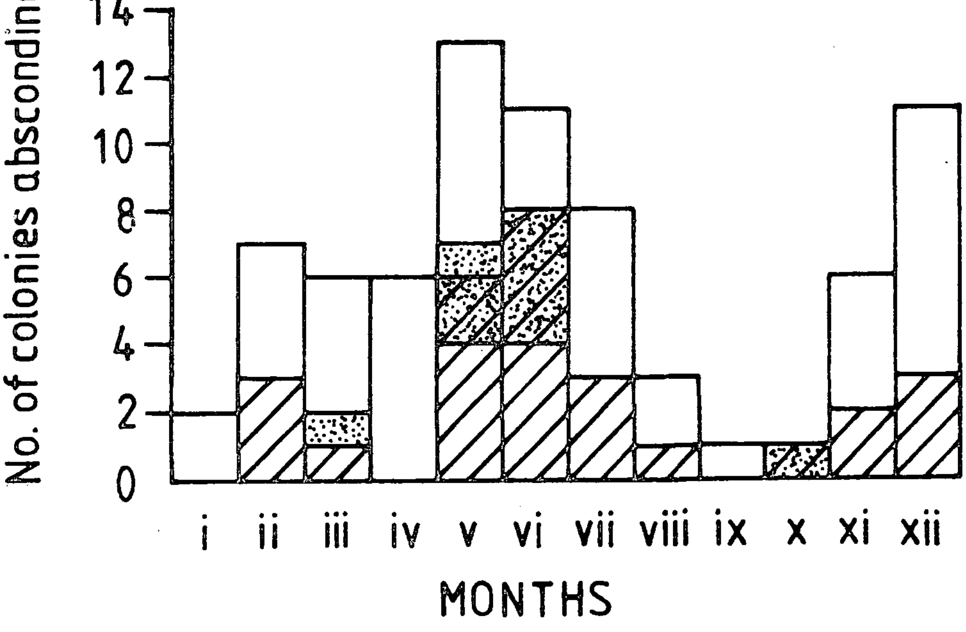

No. of colonies absconding
14
12
10
8
6
4
2
0
i ii iii iv v vi vii viii ix x xi xii
MONTHS

Figure 6.9 Total number of colonies present in each months (both those in experimental hives and a few kept by Omanis), eg a colony successfully hived in March and absconding in June is recorded as present in months iii, iv, v and vi and a colony hived in July and absconding in the same month is recorded as present in month vii. Monthly records from different years (December 1977 to August 1980) combined.

Figure 6.10 Percentage of colonies absconding out of the total number of colonies present each month (as per Figure 6.9).

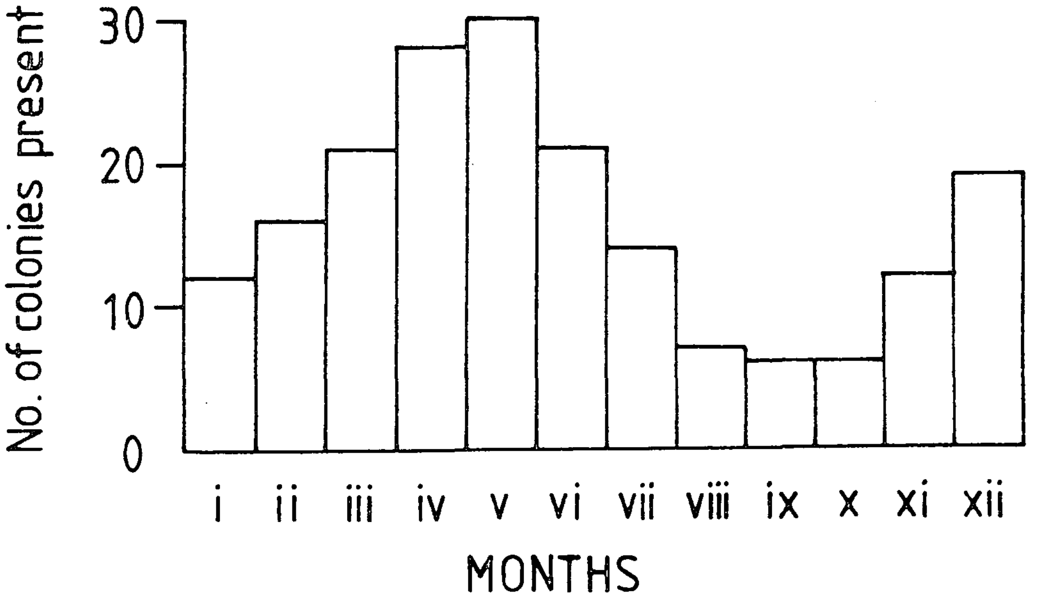
Hatched areas : established colonies (hived for > 15 days)

Stippled areas : "final swarms" leaving the parental nest deserted at the end of a queen rearing/swarming phase

Unhatched areas : newly hived colonies (hived for ⩽ 15 days)

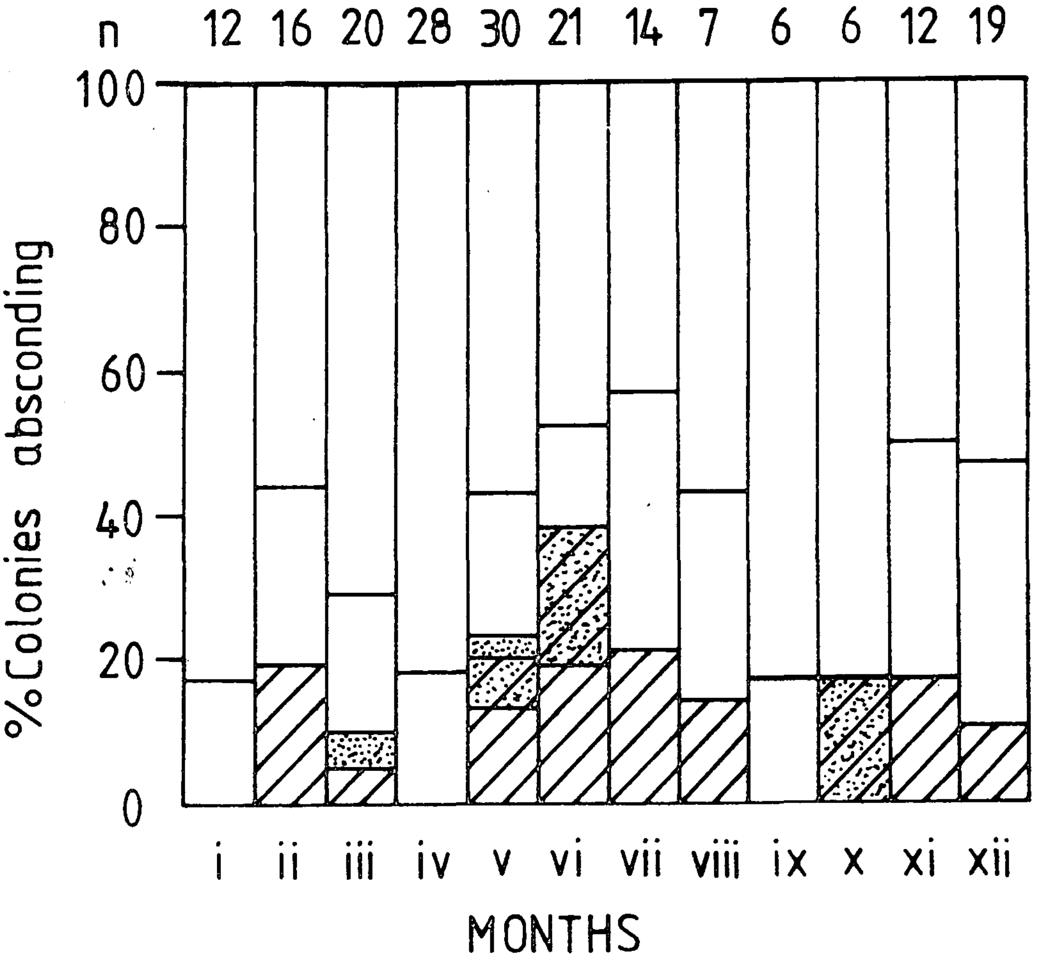
Monthly records from different years (December 1977 to August 1980) combined.

6.9



No. of colonies present
0
10
20
30
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

6.10



n
12
16
20
28
30
21
14
7
6
6
12
19
% Colonies absconding
0
20
40
60
80
100
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
MONTHS

of this species to disturbance. The propensity to abscond must partly depend on the extent of disturbance, with colonies that have their honeycomb removed and brood comb damaged being more likely to abscond than those moved to another site on their own supporting branch, without loss of honey or brood. However, on the reasonable assumption that there was not in any month a deliberate bias in the physical disturbance to which colonies were subjected, the propensity of colonies to abscond after "hiving" also appeared to depend on the season at which it was performed. Thus in April and the winter months of December and January, over half of the "hived" colonies became established, but in some other months, especially May and July, the absconding rate was high.

The sample sizes are small in September and October but they, and the other observations, are consistent with the hypothesis that absconding is less likely at the beginning of a honey flow (in April from *Acacia tortilis* and *Prosopis cineraria* and at the end of September/ October from *Ziziphus spina-christi*). Presumably the abundant supply of forage, and of stores if they are not removed, ameliorates the disturbance of hiving by facilitating comb repairs and permitting brood rearing to continue. Colonies hived in May, when the honey flow was ending, would already have been suffering from the pressure of rearing brood on diminishing resources, so would be more likely to abandon brood altogether when disturbed and to move to a new site. The site might be better shaded and thus more suitable for the hot summer months.

The proportion of colonies absconding soon after hiving, at the end of the *Ziziphus* honey flow (December) when it is cooler, appeared to be less than at the end of the *Acacia* flow in summer (Figure 6.7). It may be that as brood rearing stops altogether in many colonies in winter (Chapter VI, C. 1.2), moving a colony in a hive to another site is of lesser consequence than summer disturbance when brood rearing is usually maintained at a low rate (Figure 6.1a). Continuing this argument, the absconding rate increases again in early spring (February, March) when brood rearing recommences; interruptions to this and poorly chosen "hive" sites may be more critical than in April because forage, though available, is not super-abundant.

With an average greater than 50% of hivings being unsuccessful, the total number of colonies absconding in each month (Figure 6.8) in part reflects the number of attempts made to "hive" colonies in that and the previous month. Thus May - June and November - December were months when new colonies for hiving were more abundant following swarming (Figure 6.3a) and so the number of colonies absconding was high. However, distinguishing between the absconding of established colonies and that of newly hived colonies shows that in summer especially a substantial proportion (hatched areas Figure 6.8) were not absconding because of disturbance associated with the hiving process.

The relative absconding rates of established and newly-hived colonies can be understood better with reference to the total number of colonies present in any month (Figure 6.9) and the percentages of them absconding (Figure 6.10). The presentation of Figure 6.8 is nevertheless useful to a *florea* keeper in that it indicates the months when he should be most prepared for large numbers of colonies to abscond and most active in applying any preventative measures that may be effective.

The number of colonies present in any month (Figure 6.9) is a result of the balance between the gathering of new colonies and absconding. The former was not entirely consistent throughout the calendar year due to reduced search intensity in one or two months (Table 6.1) in some years, thus the numbers in May, August, September and October would probably have been a little greater if colony searching and hiving had been even throughout the study period. Nevertheless, the changes from month to month in overall numbers of colonies present are remarkably steady and show a distinct pattern, with a spring build-up to peak numbers in May, followed by a decline and a secondary, smaller peak in late autumn. It is very similar to the annual pattern in the numbers of colonies kept by Nāsr Ahmad al Ghaythi (Figure 4.3). The number of colonies kept by Nāsr did not drop as much in autumn (September) as in Figure 6.9; this is attributable in part to fewer hivings by myself at this season, but also to his greater skills as a *florea* keeper.

The important feature of this annual pattern of colony numbers is the clear cut absconding season, evident in the decline from May to September. As this absconding season was also apparent in the *florea* managed by Nasr (Chapter IV) it is evidently a general characteristic of the species in Oman. Other Omanis were aware of it too eg one July, a Khabura man commented that this was the "absconding season", after 3 colonies from which he had taken honey absconded and a 4th did so of its own accord.

Though there is little data on wild *florea*, this seasonal absconding behaviour is most unlikely to be restricted to managed colonies since Figure 6.10 shows that colonies hived successfully, some for several months, and thus established like wild ones, form a substantial proportion of those colonies absconding in summer. Therefore this summer absconding season is apparent both from the increase in unsuccessful hivings and from the higher absconding rate of established colonies.

Some of the established colonies (areas stippled and hatched Figure 6.10) that absconded did so at the end of a swarming sequence, with the last new queen to emerge successfully going to a new site with the remaining portion of the workers from the parent colony. Stores of honey and pollen were often depleted in such colonies, but why a large wax comb with considerable energetic value should be abandoned was not entirely clear. Maybe, despite cleaning, too many layers of larval and pupal exuvia accumulate in the cells, reducing their size, or maybe such combs have become so large that they are more conspicuous and likely to suffer predation. Yet if they have been able to grow so large that they have swarmed successfully without succumbing to predation, their existing sites must already be relatively inconspicuous to predators. The most likely explanation is that the absconding bees move to new nest sites with better microclimate for the time of year. Yet similarly the microclimate at a site deserted in June (hot) cannot have been totally inappropriate otherwise such colonies would not have been able to reach swarming strength in the preceding month of May, which is also hot. Perhaps a populous colony during a honey flow can cope adequately with a poor nest site microclimate, but not a smaller, final swarm on a large comb after a honey flow. Absconding to a new site might be a better option. Unsuitable microclimate is also the likely reason for the absconding in summer of smaller colonies that have not reached the swarming stage.

One or two of these seasonal absconding records did refer to established colonies kept by Omanis from which the honey had been removed; being re-installed in the same site they were not counted as a separate "hiving", but such colonies which did subsequently abscond presumably did so precipitately because of disturbance, poor microclimate and/or the inability to maintain brood rearing with depleted stores of honey and pollen.

Only one established colony (5%) absconded in March (and that was a colony doing well until the brood comb partly fell from its frame when I removed some supporting bars) and none in April. So, as also indicated by the high success rate of hiving in April, it appears that a good supply of forage and possibly optimal temperature conditions suppress absconding tendencies. At least two colonies I had in hives were subjected to quite severe inspections in April eg brushing and shaking virtually all the bees from the comb for photographs and measurements, but did not abscond.

A few established colonies also absconded at the end of the "sidr" season; some of them were small colonies which had been moved under the hive shelter at Khabura and were probably too shaded there so, encouraged by disturbance, may have been seeking warmer sites for the winter. In the cold month of January there was no movement of established colonies but in February, when brood rearing was again on the increase, a few colonies did abscond, presumably to sites with more appropriate microclimate.

Observations on absconding by wild *florea* were restricted to 6 colonies, but they were consistent with the pattern indicated by the managed colonies in that 4 absconded in the months of May, June and July (the hot summer months following the *Acacia* honey flow) and 2 in December (the cool month after the end of the *Ziziphus* honey flow). However, by no means did all colonies abscond in the summer as 3 which I saw in July and August 1980 had, according to garden owners, been there for several months. In one garden at Brayk Qotayt near Khabura I observed one of these wild colonies in both July and August and it had apparently been there since the winter. However, I was also told that 3 other colonies which were present in the same line of trees had absconded before the middle of July.

2.2 Residence times of managed bees

The mean length of time successfully "hived" colonies stayed after installation and/or honey removal was 101.6 days, S.E. = 19.5 days, n = 25 (23 in hives of my design, 2 supported according to Omani methods), range 17 - 493 days. These figures will be underestimates of the natural residence times as the ages of the colonies at hiving were excluded from the figures, being unknown in most cases. With colonies that abscond as "final swarms", the hive residence time will have depended on the age/size at which a colony was hived because a large colony will reach swarming size in a shorter time than a small one. Seasonal variation has been ignored too, but with the absconding tendency being greater in certain months it is obvious that colonies "hived" at or just before such a time will on average stay for shorter periods than colonies hived at other times. Seeley *et al* (1982) found for wild *florea* in Thailand that with colony mobility (probability of absconding) being greater at the start of the dry season than at the end, the mean residence time for colonies over the two periods were 2 months and 5 months respectively.

Though an underestimate, the mean residence time of just over 100 days in Oman is not very encouraging from the domestication viewpoint; but in a management rather than experimental situation colonies would not be constantly investigated and disrupted and this figure should be easily increased. The maximum of 493 days does show that colonies can be kept in one site all the year round and I am sure Nāsr Ahmad al-Ghaythi (Chapter IV) kept many of his colonies for over a year.

Mean residence times for colonies that were unsuccessfully "hived" are given in Table 6.4. It appeared that colonies with virgin queens, 3 originating from divisions of large colonies and one an introduction to a colony that had lost its fertile queen, absconded more quickly, but the difference was not statistically significant probably because of the small sample size. Ruttner *et al* (1972) found that with mating nuclei of *cerana* reared in Germany the bees frequently absconded with the queen on her mating flight. African (Fletcher & Tribe 1977) and Africanized (Winston 1979b) *mellifera* show similar behaviour with "queen-loss swarming", whereby c. two-thirds of colonies that have become de-queened issue swarms 1 - 4 days after new queens have emerged, but the process appears to be rare for European races. If substantiated for *florea*, the early departure of such colonies could be attributed to lack of brood and/or the habit of virgin queens to abscond quickly (with a swarm) to get fertilised and then to settle away from the parent colony.

Table 6.4 Mean residence time (days) for colonies of *Apis florea* in Oman that absconded within 15 days of "hiving". No significant difference between time stayed by colonies with fertile or virgin queens, $t_{44} = 1.743$.

	Mean	Standard Error	n
With fertile queen	5.8	0.7	42
With virgin queen	1.75	0.6	4

Of the colonies with fertile queens, some stayed for 15 days before absconding, while others absconded on the day of hiving. However, the mean residence period of nearly 6 days after disturbance (hiving), often with loss of honeycomb, suggests that absconding by *florea* in Oman has not evolved just as a response to escape predators quickly. In fact it indicates absconding "planned" in advance so that brood has time to emerge and is not wastefully left behind. This supports the hypothesis that absconding is primarily for microclimatic and possibly concealment reasons, as changes in these take place gradually as the seasons change, while predation is more rapid and drastic. There is little advantage in waiting several days at a nest site at which the brood comb has been destroyed or dropped to the ground where scavengers such as ants prey on the brood before it emerges.

Similarly, the habit of collecting wax and honey from a previous nest site, for up to several days after deserting it (Tirgari 1971; Akratanakul 1977; Dutton & Free 1979; Seeley *et al* 1982 and recorded many times by myself), implies that absconding is a deliberate migration, probably in response to microclimatic changes. Such retrieval behaviour would be of little value in response to sudden attacks by predators, such as man, that left no honey and wax behind. Therefore I believe that Seeley *et al*'s (1982) contention that in *Apis florea* "wax salvaging apparently co-evolved with making frequent but short nest moves <u>after predation</u> or loss of nest cover" is incorrect, at any rate in Oman, as far as predation is concerned. Loss of nest cover and consequent exposure to predators is a more valid explanation, but their assumption that "colony movement rates ... can indicate the rate of severe predator attacks and a species' reliance upon absconding as a defence mechanism" is not valid in Oman where a significant proportion of absconding appeared to be of a seasonal nature and unrelated to predation.

With colonies in my experimental hives, concealment during the period of residence, though not measured, was usually constant and high in those hives with front and back boards and only small mesh entrances. I therefore conclude that the seasonal element of absconding by *florea* in Oman was primarily for microclimatic reasons.

2.3 Distance moved by colonies of *Apis florea*

(i) Absconding colonies and final swarms

Only a small number of colonies that absconded or swarmed were found again and most of these were in or close to the DUKDP farm where many of the *florea* were kept. Little time was spent searching for these colonies at distances of greater than 2 - 300m from their previous site as the area to be covered increased rapidly with distance and the chances of finding them decreased correspondingly. As a result the data in Table 6.5 is likely to be a sample of absconding and swarming colonies that is biased towards those which moved a short distance. Reports of new colonies from neighbouring farmers were investigated but did not often reveal marked colonies. None of the various types of quick-drying paint used to mark queens stuck to them consistently (maybe *florea* workers had a greater tendency or ability to nibble the paint away than *mellifera* workers) so perhaps more colonies than realized were re-located but not identified.

Whether the sample is biased or not, it is clear that a number of absconding colonies moved to a new nest site only a short distance away (between 4 and 65m). This includes absconding by both new colonies that were badly disturbed during the hiving process (cf predation) and established colonies. This indicates that at least in some cases absconding is not because of a local shortage of forage, since moving such a short distance would not lead to any substantial change in the forage available to a colony. In the case of established colonies it suggests that the change in nest site would have been for micro-climatic reasons, since concealment from predators had presumably proved satisfactory already for a considerable period.

Table 6.5 Distance between original and new nest sites for absconding colonies and swarms of *Apis florea* in Oman. The 7 colonies grouped in the top part of the table absconded from their hive/nest site and the 6 colonies lowest in the table were swarms. The colony in the middle (c) absconded but as explained below was equivalent to a swarm. The colonies within the 2 groups are listed in order of distance moved.

Notes on individual colonies as per identifier:-

2b : this colony then absconded from its new (2nd) site, after being "robbed", to an unknown intermediate (3rd) site. It then appeared 180m from the 2nd site either as a primary swarm or after absconding again.

c : the parent colony, going through a swarming phase, was divided and the virgin queen left with this portion. She mated and started ovipositing within a few days, but 8 days after the division the bees absconded. The bees had presumably waited for sealed brood, remaining from the previous queen, to emerge and had then "swarmed" with their new queen.

d : origin of this swarm not 100% certain as queen had lost paint mark, but its appearance coincided with the loss of a prime swarm from a nearby colony.

5 : workers returned to collect honey and wax from abandoned comb.

HA 3b : this last swarm abandoned a comb with honey at a site exposed to the sun; workers were returning to collect it.

3 : represents distance travelled by the same colony after swarming twice with unknown intermediate site (that it absconded from the intermediate site was unlikely).

N.B. Mean distances, standard errors etc are not given for the groups as they probably represented biased samples of colonies that moved a relatively short distance. Other colonies probably went greater distances and were not located.

Table 6.5

	Colony/Hive Identifier	Date Absconded or Swarmed	Established (>15 days)+ Not Est. (≤15 days)-	Probable Cause	Distance Moved (m)
ABSCONDING COLONIES	32	7.vii.80	-	Hiving/loss of honey/ season	4 (vertically, to near original site)
	5	3. iv.79	-	Hiving	20
	2a	4. ii.80	-	Hiving	25
	9	14.xii.79	+	To warmer site	35
	b	21. vi.79	+	Season(?disturbance)	40
	2b	9. ii.80	-	Hiving	50
	FD	29. v.80	±	Long established but comb collapsed	65
	c	19. v.79	-	cf 2nd swarm, queen newly mated	185
REPRODUCTIVE SWARMS	d	27.iii.79	+	?Prime swarm	?25
	5	2. x.79	+	Final swarm	25
	HA 3b	11. vi.79	+	Final swarm	150
	3	c.20. x.79	+	?Prime swarm	425
	FD	16.iii.80	+	2nd swarm, virgin queen	>425
	6	7. v.80	+	2nd swarm, virgin queen	>800

Though the two "final swarms" (HA 3b and 5, Table 6.5), in having virgin queens, differed from those established colonies which were thought to have absconded because of microclimate, their reasons for deserting established combs appeared to be similar. Unless the comb being large and/or the cell sizes being reduced with accumulating exuvia (discussed in 2.1) are problems, I cannot see a reason other than microclimate why a colony should move such a short distance to abandon a wax comb in which there is a considerable energy investment.

One of the final swarms (HA 3b) absconded in June from a site well exposed to the sun in an *Acacia tortilis* tree where its comb, in a frame, had been hung. It moved to another *Acacia tortilis* tree so was still rather exposed, but less than before, being in the western end of the tree (pointing at 252°) and having some shade from above. The other colony (5) absconded in October from what I judged to be a cool site, in a hive beneath two vegetation layers (date palms, then bananas) to what must have been a "warmer" site at the top of a date palm. These examples supported the idea that final swarms (some) desert their combs for microclimatic reasons and that they do not move any great distance, so that they may remain near enough to their old nest to salvage wax and honey from it; both colonies did this.

That large combs are not abandoned as a matter of course after swarming is indicated by the size (74cm wide by 35.5cm high) reached by colony IC and colony FD (42cm by 33.5cm); the former must have gone through several swarming phases and FD went through two (Figure 6.3). IC was in a site unlikely to be disturbed and was nearly 100% shaded; having reached a large size it could presumably thermoregulate satisfactorily during the winter and the repeated use of its worker cells was not a problem.

(ii) Prime and secondary swarms

Except for colony d which travelled only 25m, but whose origin was not absolutely certain, prime and secondary swarms travelled further than absconding colonies and final swarms (Table 6.5). It is easy to explain the advantages of such behaviour in that a new colony established beyond the usual foraging range of its parent would not compete with it. The hypothesis would apply in an environment with evenly distributed food resources, but in a patchy environment it could be argued that there might be a selective advantage in staying near the parent colony, as that colony would only have reached swarming strength if the local forage supply was good. In this situation a new colony, unless it was able to identify another good patch of habitat within flight range, would do well to move just a short distance from its parent, in order to benefit from the same resources. More data and experiments are needed to substantiate these few observations and ideas.

(iii) Interim sites

Swarms of *mellifera* usually establish a temporary cluster at an interim site near to the hive, from which scout bees locate suitable nest sites; criteria used in this selection are size of entrance, volume and orientation (Seeley & Morse 1976 and 1978; Avitabile *et al* 1978; Seeley 1982a). Whether the forage available in the region surrounding the nest is another criterion is not known for certain, but Koeniger & Koeniger (1980) thought it likely that migrating swarms of *dorsata*, which have interim cluster sites, moved in the direction of a good nectar flow and Fletcher (1978) suggests that certain migrations of *A.m. adansonii* are best explained by the long-distance perception of floral odours, possibly involving anemotaxis. Though their dance language shows that bees are able to recognize areas of good forage, many forage sources are likely to be available for only a short time every year (Chapter VII) in which case it might be disadvantageous for a swarm's choice of nest location to be influenced by the position of forage at the swarming season only.

In Thailand Akratanakul (1977) claimed that "In all the cases of swarming and absconding of colonies of *florea* ... bees usually established a cluster at an interim site about 3 to 20m away from the parental nest site", remaining there for 2 - 7 days. However, there are no other published records of interim sites or whether forage availability is taken into account when new nest sites are chosen. Of the 2 swarming colonies I followed (FD and 6), neither established an interim site near the parental colony. Similarly on other occasions when I knew colonies had swarmed, but was not present to witness the event, I never found a temporary swarm cluster nearby - even though on at least one occasion I knew the colony had swarmed less than an hour previously. The same applied to all instances of absconding except the one described below from hive c.

In this case, I had checked the presence of a recently divided and hived colony one evening (18.v.79, 17.30hrs) but on checking again the next morning (10.30hrs) the bees had departed. Approximately 150 workers were salvaging wax and honey which indicated they had already started to build a comb at a new site. By searching the gardens in the direction in which these bees were flying, I located the new site, c. 185m away and at a bearing of 320°, about an hour later. I also heard from boys working in the intervening garden that they had seen a large swarm settle "temporarily" on a date frond mid-rib c. 2.0m from the ground at approximately 08.45h. This was almost certainly the same absconding swarm, as this interim site reported to me was at a bearing of 300^{o} from the original one and approximately 135m away ie on virtually the same line as and only 50m from the site finally chosen.

This then was the only exception to the more general pattern observed that absconding and swarming *florea* in Oman did not have interim sites and certainly not for several days like *mellifera.* Therefore, either scout bees must determine a new nest site before absconding or swarming, or the whole colony flies in a particular direction till meeting a suitable nest site in its path. The latter behaviour would not suit *mellifera* with its very specialized nest sites, but might be appropriate for *florea.* Though *florea* in Oman did favour nest sites with particular characteristics (Chapter II), the trees and bushes offering these would be more frequent than trees with hollow trunks suitable for *mellifera.*

(iv) Local opinions

Humayd Sulayman al-Shimili (of al-Ghubby) had rather different ideas on the distances moved by swarms and absconding colonies of *florea*, though maybe more allegorical than factual. He said that swarms, whether in the mountains or in gardens, did not go far from the parent colony because they were of the same family. An absconding colony, he said, went further away till it found a suitable place.

The concept of *florea* migrating considerable distances to areas of more suitable forage was widespread among farmers and bee-keepers in Oman. For instance, when new colonies "appeared" in the Bātina gardens in early summer, it was often said they had come from the "jabal" (mountains) which were visible from the coast, but in the order of 25km distant. Similarly when bees absconded from mountain caves in summer, bee-keepers would say they had gone to the gardens of the Bātina.

There was no direct evidence to support either of these claims. To me, local movement was a far more plausible explanation than a longer distance migration to new pastures. Though the appearance of swarms in the Bātina gardens did coincide with the advent of the hottest period of the year, it also coincided with the main swarming period and honey-harvesting time (with consequent absconding). That the bulk of "new" colonies came from these sources was far more likely than that they came from the mountains.

However, seasonal short-distance colony movements from sites inside oases and coastal date gardens to sites in the "sayḥ" (adjacent plains) and vice versa, in addition to movements within each habitat, were plausible. Indeed the swarm from Hive 6 (Table 6.5) was, in May, flying from a hive in an area of open silty/sandy plain with scattered *Acacia tortilis* trees towards the coastal date gardens near Khabura. Though I lost track of it after c. 800m the swarm had only to travel another 2 - 300m to reach the gardens; these would have offered many more shady nest sites for the summer (and more forage after the flowering of *Acacia tortilis*) than the habitat the colony was leaving. It would be this sort of local movement that Nāsr Ahmad al-Ghaythi of Zāhib was emulating by using two apiaries: a summer one in the oasis and a winter one in the gravel plains.

Finally, some cases of apparent migration of *florea* colonies can best be explained in terms of populations fluctuating with dry and wet periods. On a visit to Wuqbah, a mountain village with gardens flanking a wadi in the Dhahira region of Oman, on 12.xi.78 I was told by villagers that there were many colonies in the mountains but not in the gardens. Yet about 8km away, where a small garden had been started between low hills by mountain pastoralists, I was told that there were not many colonies in the mountains. I in fact saw *florea* workers gathering water from the wadi at Wuqbah and a wild colony in the small garden in the hills, so bees were present at both localities. Therefore it seemed that there had not been a wholesale migration of colonies from one locality to the other as the inhabitants thought (though some local movement was probable), but a decline in the total population of *florea* in the whole area, during a dry period that was extended by the summer that had just passed.

D. CONCLUSION

1. Seasonal cycle

Though determined from small monthly samples, the seasonal cycle of wild *florea* in Oman appeared to follow a pattern similar to that shown by other tropical species and races of *Apis*, as discussed in the Introduction, in that brood rearing continued nearly throughout the year but at a reduced rate in winter. The *florea* colonies under the traditional management of Nāsr Ahmad al-Ghaythi also showed this pattern (Table 4.14), their annual cycle matching that of wild colonies very closely. However, the winter reduction in brood rearing by *florea*, ceasing altogether in up to 50% of colonies (particularly the smaller ones) and continuing at a lower rate in others, appeared to be more marked than has been reported for *cerana* and Africanized *mellifera*. Thus at Bangalore, India, though the mean brood area of *cerana* colonies was more than halved in winter, brood rearing continued all year (Reddy 1980). Similarly it continued all year in French Guiana for Africanized *mellifera*, but at a rather lower level during the winter (wet season) (Winston 1980a).

In these two latter regions, the reduced winter brood rearing appeared by and large to be a result of relative floral dearth, but for *florea* in Oman whether it is a reflection of scarcer forage or of the lesser ability of *florea* to thermoregulate is difficult to ascertain. Chapter VII indicates that some forage was available in winter and it appeared that brood rearing in colony FD was being reduced before its stores were exhausted (Table 6.3), so I think it likely that low temperatures were a particularly critical factor. It was also in winter that *florea* stopped brood rearing altogether in northern India (Sandhu & Singh 1960). Studies on the brood rearing cycle of *mellifera* in Oman should give an independent indication of forage availability in winter and at other times of year and thus shed further light on the matter.

Whether the seasonal rearing of worker brood is a direct response to conditions of forage availability and temperature or whether there is a genetic component through an endogenous rhythm or a response to particular photoperiods or a changing photoperiod, as for temperate *mellifera* (Avitabile 1978; Kefuss 1978; Cornuet & Louveaux 1981) is difficult to prove without experiments. However, the variability in timing of the initiation of brood rearing as indicated in Table 6.3 and the occurrence of drones throughout much of the year (albeit with clear cut peaks, Figures 6.2a and b) suggests that any genetic component is not overriding and that environmental factors and colony size and demography exert a strong influence. This flexibility would be important in a region whose rainfall can be variable from year to year and is often localized.

As appeared to be the case in India (Sandhu & Singh 1960) and Iran (Tirgari 1971) queen rearing and swarming (Figure 6.3a) in Oman occurred over more restricted periods than did drones. This may partially have been a result of higher predation levels on large colonies, but the restriction of swarming to within periods of adult drone availability, so that queens can mate, is clearly essential. Peak swarming in April - May, towards the end of the main *Acacia tortilis* honey flow, may not be optimal for the establishment of new colonies that would have to survive a subsequent period of low forage availability. Early swarming and establishment, however, may not be so critical as for *mellifera* in temperate climates; most colonies swarm at the beginning of summer (Burgett & Morse 1974) and have to reach a strong state rapidly, to gather enough stores to survive a long winter (Seeley 1983; Seeley & Visscher unpublished). Compared to the demands of such overwintering, only small amounts of energy (honey) would be needed for *florea* to thermoregulate (mostly keeping cool) in the summer. Nevertheless there did appear to be clear advantages in early development as indicated by colony FD (C.11.1 and Table 6.3) and there must usually be sufficient available forage, for strong colonies to exploit, such that two periods of swarming are possible in the one season. Therefore, some natural selection for rapid development in spring and early queen rearing may have occurred (hence the more restricted periods of swarming). However, with some swarming in autumn and the need to respond to irregular rainfall and supplies of forage, it is unlikely that selection for such characteristics has been excessive.

Though no absolute measurements are presented, the large numbers of queen cells found on various colonies, the swarming potential (incompletely fulfilled) of colony FD (C.11.1) and the observations of Omanis indicated that the swarming or reproductive rate of *florea* was high. Dutton & Free (1979) also reported Omani observations that large colonies produced up to 8 swarms a year and elsewhere up to 15 (Tirgari 1971) and 20 (Ghatge 1949; Thakar & Tonapi 1962) queen cells have been recorded. These figures indicate that *florea* colonies in

Oman and elsewhere have a high reproductive rate, comparable with that of the other warm climate honeybees. Colony reproductive rates in the latter are illustrated by the following records:- *cerana* in Pakistan (Ruttner *et al* 1972) produced up to 10 swarms per season (average 6); Africanized *mellifera* may swarm 3 - 4 times during an 8-month swarming season, producing a prime swarm and an average 1.9 afterswarms at each episode (Winston 1979b; Winston *et al* 1980; Otis 1982; Winston *et al* 1983) while indigenous *mellifera* in Africa (Chandler 1976; Fletcher 1978; Fletcher & Tribe 1977) appear to be equally productive. These rates are generally higher than those recorded for European races of *mellifera* whether in the tropics (Winston 1980a) or in temperate climates (Seeley 1978; Winston 1980b) where the duration of suitable conditions may be limiting (Winston *et al* 1981) and winter mortality is high (Seeley 1983; Seeley & Visscher unpublished).

However, even without actual values, my impression was that the average colony reproductive rate of *florea* in Oman was not as high as that reported for Africanized bees in French Guiana which Otis, according to Winston *et al* (1983), observed were increasing approximately 16-fold annually, despite high losses. The increase in Guiana, though, may have been exceptionally high because of limited intraspecific competition and the perceived rate in Oman rather low because of the dry years in which my fieldwork was undertaken. The main losses in Oman were probably due to predation, especially by man (see Appendix I), and secondarily starvation, but the balance between natality and mortality of colonies must have been fairly unstable with both seasonal and annual fluctuations in population occurring as a result of irregular rainfall.

2. Absconding

Though the data on absconding came almost entirely from managed colonies and small numbers of them, I was satisfied that the behaviour of wild colonies followed a similar pattern, but probably at rather lower rates of absconding because of less interference and more appropriate nest sites, chosen by the bees themselves. In fact, most studies on *mellifera*, on this and other topics, have been carried out on hived colonies too, so my research is not exceptional in this respect.

From the findings presented here and the research discussed in the introduction, it is apparent that many causes of absconding can be listed, eg Fletcher (1978). However, it is instructive to assemble these into categories and I conclude that the following grouping into two major causes and one minor one, with the rider of an underlying seasonal trend, best explains the observations and does so in a practical way pertinent to management operations.

(i) Predation/Disturbance - by natural enemies, pests, beekeepers, fire, flooding. In general, these are drastic factors requiring fairly prompt action.

(ii) Inappropriate Nest Site - primarily because of microclimatic factors such as excess or insufficient insolation (*florea*) and insulation (*mellifera*, Fletcher 1976), but also including inadequate concealment from predators (Seeley *et al* 1982), obscurement of the sun/sky for communication dances and the abandoning of old combs.

(iii) Dearth - of forage or water.

The seasonal trend, with absconding rate greatest in the summer for *florea* in Oman and in the wet season for *mellifera* in South America (Winston *et al* 1979) applies to all 3 categories. Predation pressure may be approximately constant throughout the year, but the response to it appeared to vary from month to month in Oman (Figure 6.7) and seasonally in South America. (After severe manipulations absconding attempts "were more common during the wet season", according to Winston *et al* 1979).) The other causes in themselves are likely to be seasonal in nature, but are not necessarily so eg a water supply could dry up or shade diminish, by the falling of a branch, and result in absconding at any time of year.

I feel that the two basic types of absconding recognized by Winston *et al* (1979) give a less satisfactory understanding of the situation - (1) Disturbance-induced, in which they incorporated inferior nest sites and (2) Seasonal, including high temperatures and dearth of resources.

For instance, Winston *et al* thought that overheating was the cause of the absconding of 3 weak *mellifera* colonies in the low-absconding rate dry season in South America and with their categorization this would constitute disturbance-induced absconding. Yet applying their categories to Oman, such absconding in the dry (hot) season would have been grouped with seasonal abscondings even though it was"disturbance" induced. According to my categories the direct cause of absconding in such a case would be the same in South America and Oman, poor microclimate ie (ii) inappropriate nest site, but with the underlying tendency to abscond at the "dry" season in each country being different.

Thus the season does not automatically induce all colonies to abscond. Instead their propensity for absconding, whether from predation, inferior nest site or dearth, changes with the seasons in a manner adapted to each region.

Most cases of environmental deterioration indicated by (ii) and (iii) are likely to be seasonal and gradual and absconding preparations (cessation of brood rearing, engorgement by workers) may be started over 10 days in advance. This distinguishes them from most cases of severe predation which necessitate absconding "at short notice". Actual "starvation" absconding, (iii), may not be as frequent as is supposed (eg Free 1981), it being necessary to draw a distinction between cause and effect (Fletcher 1975; 1976) with honey absent from a colony when it absconds, not because no nectar is available, but because the bees have been engorging themselves in preparation.

Bearing such information in mind it can be appreciated that the seasonal element of absconding in *florea* and tropical *mellifera* must have a genetic basis. From studies on *dorsata*, Koeniger & Koeniger (1980) came to a similar conclusion, in that the species had an annual cycle of migration in Sri Lanka that seemed genetically fixed. Similarly, the low level of absconding in temperate *mellifera* is also seasonal (Martin 1963) and must have a genetic basis. This seasonal element of absconding must have evolved in each species and region primarily as a means of anticipating months with adverse conditions of climate and flora. That a colony adopts this habit in a given season need not be absolutely fixed. Thus the response may also depend directly on microclimatic conditions at the nest site and forage availability; hints that these are not quite right will be reacted to readily in the absconding season (as "experience" has shown that at this season conditions will then continue to deteriorate) but will not be reacted to immediately at other times of year when "experience" has indicated the problems are likely to be temporary. Furthermore, the age or developmental stage of a colony may determine the response in conjunction with the season, as Winston *et al* (1979) have shown that

Africanized *mellifera* that had swarmed just prior to the absconding season and which had low numbers of young workers, had a higher probability of absconding during the wet season.

On the question of distances moved by absconding and reproductive swarms of *florea* it is evident that more research is needed to find out for certain the range of distances involved and the proportions of colonies which move seasonally within one habitat and which move between habitats (date gardens and plains or mountains). Clarification of the pattern should help further the understanding of the causes of absconding, but I am fairly certain that the long distance migrations which *florea* have been said to perform in Oman and elsewhere can be explained in terms of local movements and/or fluctuations in the numbers of the local populations.

3. General

As Winston *et al* (1981) have pointed out for European and Africanized *mellifera* when studied in near "natural" conditions in temperate and tropical climates respectively, it is difficult to separate the genetic from environmental factors that control their life history. They also considered that, in addition to climate and resource availability, aspects of intra-colony demography, especially worker mortality rates, were important in determining colony growth and reproductive patterns. Whatever the genetic and phenotypic components of *florea*'s habits, it is clear that its annual cycle, while remaining flexible, is fairly well synchronized with the usual floral phenology (Chapter VII) and temperature regimes (Appendix II) of Oman, and its reproductive rate and absconding enables the population to cope with predation pressure, periods of drought and seasonal extremes of temperature. Therefore, though less able to cope with "winter" and migrating shorter distances than *dorsata* and *mellifera*, in many respects the seasonal biology of *florea* bears many similarities to that of the other tropical *Apis* species, but not to that of temperate *mellifera*.

The main consequences of these findings for the management of *florea* are as follows:-

(i) Feeding of sugar syrup in early spring should belp accelerate brood-rearing and colony development.

(ii) Inspections/interference should be kept to a minimum, particularly in the summer absconding season.

(iii) All the honey should not be removed from a colony at or just before the end of a honeyflow (especially in summer).

(iv) Colony divisions, as they necessitate the mating of virgin queens, should only be carried out at times of peak drone abundance (March - May and October - November).

(v) Divided colonies should always have brood at all stages present, to inhibit absconding of the new colonies with virgin queens on their mating flight. Transferal of a fertile queen from a small undisturbed colony to the queenless half of a division might help, as long as a virgin queen was introduced immediately to the undisturbed colony.

(vi) If brood rearing drops or stops, or a colony is weakened after swarming, so that absconding is likely, appropriate measures should be taken, such as moving the colony to a new site, feeding, providing brood from another colony or the uniting of colonies. If brood rearing stops in winter the colony should be left alone or, if small, could be united with another colony, or moved to a "warmer" site.

CHAPTER VII

SOURCES OF FORAGE : COMPOSITION, PHENOLOGY AND ECOLOGY OF THE HONEYBEE FLORA AND PATTERNS OF EXPLOITATION BY *APIS FLOREA* AND *APIS MELLIFERA*

A. INTRODUCTION

1. Vegetation of northern Oman

Though Muscat and its surroundings have been visited sporadically in the 19th and 20th centuries by plant collectors, prior to the 1970s the only detailed investigation of the flora of the Jabal al-Akhdār had been that of Aucher-Éloy in March 1838 (Mandaville 1977); most of his plant collections were published by Boissier (1867-1888) and subsequently by Blatter (1919-1936) and Schwartz (1939). Joseph Fernandez, botanist on a geological survey in 1925-6, was said to have collected about 3,000 specimens in Bahrein and northern Oman and particularly from the mountains inland of Khabura where much of my work was undertaken (Blatter 1919-1936), but their present whereabouts proved to be something of a mystery (Mandaville 1977). Investigations revealed that some of his plants reached the Royal Botanic Gardens, Kew, but that others were never sent or were thrown away because of their poor condition (Whitcombe 1981), so those few specimens found at Kew proved of less value than I had hoped.

Before undertaking my research, just two botanists had made recent investigations on the flora of northern Oman, J. Mandaville (Aramco) and A. Radcliffe-Smith (Kew), but only Mandaville (1977) published a description of the vegetation and a floristic list, with identifications by D. Hillcoat (BMNH). One or two other biologists (Edmondson 1980; Munton, in press) made plant collections at the same time as I did. Such work since 1972 has revealed numerous species new to Oman and Arabia and a few new to science; papers with details have been recently published or are in preparation (Hedge & Lamond 1978; Léonard 1980; Hillcoat *et al* 1980; Miller *et al* 1982b; Hedge 1982; Miller & Whitcombe 1983; Gamal-Eldin 1984; Miller 1984). Similarly there have been relevant re-classifications, nomenclatural changes and papers on adjacent regions as new material has become available and interest in the Arabian flora increased (Davies 1978; Friis 1978; Cope 1980; Stork & Wüest 1980; Hedge & King 1983; Wagenitz 1984). Miller *et al* (1982a) have published a botanical bibliography of the Arabian peninsula and Wickens (1982) a biographical index of plant collectors; they are comprehensive, cover Oman and provide the best guide to the relevant literature and botanical exploration of Oman.

Thus investigations of the Omani flora and vegetation are at an early stage and most publications have been taxonomic. Mandaville (1977) and Mandaville & Bovey (1978) do give some details of vegetation types and of the ecology of individual species, but are concerned primarily with the plants of the central Jabal al-Akhdār. Mandaville (1977) considered there were five vegetation zones:-

(1) *Acacia* Desert Parkland 0 - 600m
(2) Mountain Wadi Associations 350 - 1050m
(3) *Euphorbia larica* Shrub Slopes 450 - 1350m
(4) *Reptonia* (now *Monotheca)-Olea* Woodland, 1350 - 2300m
(5) Juniper Summit Zone, 2300 - 3050m

My observations in general concurred with this broad classification so no further description is given here and his paper should be consulted for details, especially of zones 1 to 3 since relatively few colonies of *Apis* had access to the higher altitude flora. However, Table 3.8

lists the flora characteristic of limestone mountain wadis and Table 4.5 that of an alluvial plain in the Sharqiya. In addition, Gallagher & Woodcock (1980) give a useful guide to the physiographic regions of the Sultanate, mentioning characteristic plants. None of these authors described the vegetation of cultivated land, which proved to be important to honeybees, though Mandaville evidently collected some plants from such areas. A thorough description is not given here but Tables 7.1 and 7.2 give the honeybee flora for such oases and gardens, other species found are included in Appendix III and salient features are pointed out in the Results and Discussion section. Tables 2.2 and 2.4 (Chapter II) enumerate the tree (fruit, shade, ornamental etc) composition of Bātina and Interior gardens and agricultural surveys of Dutton & Letts (1982) indicate the crops grown overall and modes of irrigation and cultivation. Table 4.4 lists the flora of a date garden in the Sharqiya.

2. Previous information on the honeybee flora

At the outset of this study, the only "known" sources of forage were a few species reported by the Omanis to be important honey plants (Dutton & Simpson 1977), namely "sidr" (*Ziziphus spina-christi*), "sarḥ" (*Maerua crassifolia*), "samur" (*Acacia tortilis*), lucerne (*Medicago sativa*) and apparently the exudate of ripe dates, "rutab", (*Phoenix dactylifera*). To date there is no published list, of which I am aware, of nectar and pollen sources for honeybees for any locality in the Arabian peninsula, though Ingrams (1936) gives details of the physical analysis of a honey sample from the Wadi Hadhramaut (South Yemen). It was dextro-rotatory (normal honey is laevo-rotatory) and thought to be of a honeydew type, but I suspect it may have been derived from the exudate of ripe dates. Furthermore, I know of no published investigations of Arabian pollens for taxonomic, melissopalynological or other purposes.

As my knowledge of the Omani flora grew, I was able to guess potential sources of forage before I saw honeybees using the plants or even before they flowered, from reference to the literature on the honeybee plants of adjacent regions, especially north and east Africa and the Indian sub-continent. Most of the literature concerned *Apis mellifera* and *Apis cerana*, with relatively little on *Apis florea*, and not all was available while doing fieldwork in Oman, but the following publications were among the most useful:- Rahman 1945; Smith 1956, 1957; Latif *et al* 1958; Thakar *et al* 1962; Batra 1967; Atwal *et al* 1970; Saraf 1972; Crane 1973, 1975b; Indian Standards Institution 1973; Papadopoulo 1973; Ibrahim 1976; Oustuani 1976; Shahid & Qayyum 1977; Koeniger & Vorwohl 1979; Chaubal & Kotmire 1980; Gadbin 1980; Ricciardelli D'Albore 1980; Ricciardelli D'Albore & Vorwohl 1980; Eisikowitch & Masad 1982. Crane (1978, Parts 15, 19 and 21) was the source from which many of these references was obtained and she gives others of interest pertaining to particular plant species and families found in Oman. Free (1970), McGregor (1976) and Free & Williams (1977) were especially valuable for information on the exploitation of crop plants by honeybees. Thus from field observations, pollen analysis and the literature a catalogue of the majority of honeybee plants in Oman, their distribution and flowering periods, was to be drawn up and the importance of each assessed.

3. Plant phenology and honeybee-flower inter-relationships

In addition to determining the availability of the various honeybee plants and their importance, it was hoped these investigations would shed light on the overall seasonal pattern of flowering in this arid region, and on related topics. To what extent had honeybees (and other pollinators) influenced this pattern or was it environmental factors such as rainfall and temperature that controlled flowering and thus the activity of the honeybees? Did the annual cycle of *florea* in particular correspond to changes in forage availability or were seasonal temperature changes more important? Also, were there any obvious differences between *florea* and *mellifera* in the species they exploited or in their overall foraging strategies?

As Janzen (1967) and Opler *et al* (1980) have pointed out, in considering the factors determining flowering time and other plant and insect phenological events (eg leaf production and fall, diapause) it is important to distinguish between proximate and ultimate causes. Thus increasing photoperiod or rainfall might be proximate physiological stimuli inducing flowering at a particular season, but pollinator activity may have been the ultimate selective force that brought about the use of these stimuli to induce plant reproductive activity. Treatises on plant physiology (Wareing & Philips 1970; Schwabe 1971) discuss the various proximate factors and physiological processes involved in the control of flowering, such as day length, moisture, temperature (vernalization), dormancy and nutrition. Some factors are external to the plant (eg day length) but others may arise within the plant itself as in day-neutral species. Furthermore, the various environmental factors can interact with each other and with the genetic constitution of the plants in different ways (Wareing & Philips 1970; Pemadasa & Lovell 1974).

In arid regions such as Oman one might expect rainfall to be the primary factor stimulating plant germination, growth and flowering, especially in annuals/ephemerals, but in fact dormancy and temperature requirements can prevent seeds from responding (Mott 1972). Mechanisms such as this could result in plants flowering at more appropriate times as far as pollinators or temperature conditions are concerned and not at extreme seasons, for instance in response to light showers during the heat of summer. To my knowledge, little or no work on these "proximate" factors has been published with respect to the Omani or Arabian flora, though such studies have been conducted in other arid regions (eg Tevis 1958a and b; Koller 1969; Mott 1972, 1973 and 1974) and tropical ones (Opler *et al* 1976).

Similarly, I do not know of any flowering phenology studies on the Arabian flora and even 10 years ago there had been few phenological studies anywhere at tropical latitudes (Frankie *et al* 1974a). Over recent years, however, and particularly in the wet and dry forests of tropical America, such investigations have revealed some of the varied flowering patterns occurring and the biotic and abiotic factors determining them, such as the activity of pollinators and seed predators and climate (Janzen 1967; Frankie *et al* 1974a and b; Huxley & Van Eck 1974; Monasterio & Sarmiento 1976; Heithaus 1979a; Opler *et al* 1980; Augsperger 1981; Bawa 1983; Frankie & Haber 1983; Opler 1983). Other studies have been carried out in temperate (Heinrich 1975b and 1976b; Ranta *et al* 1981; Gross & Werner 1983) and arctic (Hocking 1968; Williams & Batzli 1982) environments.

In temperate and arctic regions prevailing temperatures may largely determine the optimal conditions for pollinator activity and thus of flowering by zoophilous plants. In the arctic, Hocking (1968) concluded there was competition between flowers for pollinators rather than vice versa, while in temperate Alberta, Mosquin (1971) found that pollinating insects were abundant and competed for relatively scarce pollen and nectar resources in spring, but subsequently flowers competed for pollinating insects. In tropical latitudes temperatures may be equable for insect activity throughout the year and instead wet and dry seasons may be more important (directly and indirectly) in determining insect and flowering activity. Bawa (1983) discusses some of the flowering patterns that can result (extended and mass blooming, synchronous and asynchronous, supra-annual blooming, multiple or episodic flowering), but points out the comparative lack of information on the phenology of pollinators. The diversity of species and flowering patterns suggests to me that there has been intense competition for pollinators, but then there is also diversity and specialization among the pollinators (bees, wasps, butterflies, beetles, flies, hummingbirds, bats) and they overlap in their resource use and may compete (Heithaus 1974, 1979b and c).

What is the situation in an arid region like Oman where both high and low temperatures may restrict insect activity, including that of honeybees (Chapter V), and where wet and dry periods must also have a strong influence on both plant and insect phenology? How do polytropic honeybees influence and exploit the flowering patterns? Their colonial habit facilitates brood-rearing and foraging activity throughout the year and they use a wide variety of flowers (yet are flower-constant on the majority of individual foraging trips). Thus honeybees are different from many mono- and oligotropic (and mono- and oligolectic) pollinators eg many solitary bees that may have short activity periods associated with the flowering of one or two species only (Linsley *et al* 1955; Linsley 1958; Percival 1965; Hurd *et al* 1971; Moldenke 1976; Faegri & Van der Pijl 1979; Roubik 1982; Batra 1984). Do these various pollinators compete for scarce resources for much of the year, between periods of mass-blooming and competition for pollinators among the plants?

"Floral calendars" indicating the plants used by honeybees for nectar and/or pollen during the course of a year, or part of a year, have been produced for various localities in Europe (Hodges 1978; Bauer 1982), the U.S.A. (Adams & Smith 1981; Severson & Parry 1981), Palestine/

Israel (Bodenheimer & Ben-Nerya 1937; Eisikowitch & Masad 1980) and India (Thakar *et al* 1962; Atwal *et al* 1970; Chaubal & Kotmire 1980), while Ibrahim (1976) has listed plants available at different seasons in Egypt. These can be valuable to bee-keepers in the regions concerned and the last 6 publications mentioned, having species in common with Oman, had some relevance to this study. However, apart from Bauer (1982) and to a minor extent Gross & Werner (1983), the ecological significance of the phenological sequences has not been considered for honeybee-flower associations in the way that it has been for other insect-plant communities (Heinrich 1975b and 1976b; Heithaus 1979a; Ranta *et al* 1981). In many of these areas the presence of crop plants and other introductions, weeds and *mellifera* itself in many areas including northern Oman, will have distorted natural patterns of forage availability and of competition between plants for pollinators and between pollinators for nectar and pollen(eg Moldenke 1976; Percival 1974; Roubik 1982; Gross & Werner 1983). Nevertheless, by examining the phenology of the flowers and honeybees, this study might indicate some of the critical biotic and abiotic factors that govern these patterns and interrelationships in an arid country. Also, periods should be highlighted when certain management techniques might best be employed (feeding, honey extraction) and crucial gaps in forage availability identified, which might be filled by judicious planting.

B. MATERIALS AND METHODS

1. Plant identification

During the whole study of *florea* and *mellifera* in Oman, efforts were made to collect and identify, or record, as many plant species as possible. No group of plants was deliberately omitted as, at the outset, it was not known which of the species would prove to be of use to the honeybees; even grasses and sedges, which produce no nectar but can be sources of pollen, were covered. At the beginning of the study, Dorothy Hillcoat's list of James Mandaville's plant collections, primarily from the Jabal al-Akhdar (Mandaville 1977), was the only available "guide" to the northern Oman flora but it could not help with plant identification. Nevertheless, while in the field with Omanis who could provide reliable local names of certain plants, I was able to deduce the likely scientific name from the list of Arabic names that Mandaville (1977) had recorded. Further tentative identifications were made in Oman with the aid of the "Student's Flora of Egypt" (Täckholm 1974) and the published volumes of the Flora of Iraq (ed. Guest *et al*); however, determinations using their descriptions and keys were potentially misleading as numerous Omani species were not dealt with, while many species absent from Oman were covered.

To confirm preliminary identifications nearly 900 gatherings of plants were made, where possible each gathering providing enough material to make 2 or 3 herbarium sheets. The specimens were pressed in the field in the standard manner (eg Davis 1961). Specimens were numbered and relevant details recorded (date, provenance, habitat, flower colour and smell, local name and so on). Colour photographs were frequently taken to record habit , flower colour and shape. A reference set of specimens was maintained in Oman (now at the Oman Natural History Museum) and another set deposited at the herbarium of the Royal Botanic Garden, Edinburgh, where nearly all were positively identified by reference to other herbarium specimens and the botanical literature. (Special thanks are due to Tony Miller, Ian Hedge, Jennifer Woods, Rose King and colleagues for their help.)

Later in my study, "Wild Flowers of Northern Oman" (Mandaville & Bovey 1978) proved valuable, illustrating approximately 85 species though I had already identified the majority of these by the time it appeared. Most crop plants were identified using Purseglove (1968 and 1972) and various trees with El-Hadidi & Boulos (1968).

2. Flowering and honeybee foraging records

As my familiarity with the flora grew, I was able to make field records on many of the plant species without resort to collecting them, although this was still necessary with closely related taxa. In this way, during c. 2½ years' fieldwork, a large mass of data was gathered on the distribution and flowering times of a substantial proportion of the northern Omani flora. Notes were made of the plants in flower around colonies of bees in a wide range of localities and habitats, and also of those plants growing in areas where bees were not found or were not known to occur, as the composition and abundance of the flora would be a key factor explaining the distribution, density and condition of the honeybee colonies.

No regular transects were established but hundreds of spot observations were made on the insects, especially honeybees, foraging on plants throughout northern Oman according to locality, date, time of day and whether they were gathering nectar or pollen. However, apart from Tables 3.8, 4.4 and 4.5 (in Chapters III and IV) of the plants and sources of forage of limestone hills and of Zāhib and its environs, lists of the records from each locality are not presented here. Instead, once the plants were identified, the core of the relevant data from the collections, lists and spot observations were transferred to record cards for each species back in the U.K. This proved time-consuming, there being cards for c. 470 species and with anything from 1 to 50 records for each. Therefore, once a sizeable portion of the data had been transferred onto the cards and knowing from field observations, initial pollen analyses and the literature those plants most frequently used by honeybees, only those records which filled gaps in the flowering calendars of the bee plants, were subsequently added. Having been selective in this way, it is probable that certain useful records on the flowering times of certain plants have been accidentally excluded, but in general the data presented in this chapter should give a fair indication of the overall composition and phenology of the Omani honeybee flora.

Due to periods of absence from fieldwork, records from the months of May, August, September and October (see Chapter VI, C 1.1 and Table 6.1) are somewhat under-represented. Also, because of the apparent scarcity of *florea* in habitats away from cultivation and the generally poor state of the vegetation (the consequence of low rainfall during the study period), foraging records on plants in the "wild" category probably did not include a number of plants that can provide nectar and/or pollen in wet periods, particularly among those found in the central Jabal al-Akhdār where natural plant diversity and abundance appeared greatest.

Finally, some additional records on flowering were obtained from examination of herbarium specimens of Omani plants at Edinburgh, and a few at Kew, collected by other botanists (J.R. Edmondson in particular). A few other records of flowering and foraging came from reliable informants in Omān.

3. Pollen analysis

3.1 Collection of samples

To supplement the data obtained on sources of forage from visual records of honeybees visiting plants, samples of pollen were taken from combs of *florea* and *mellifera* and from foragers returning to their colonies. Samples from combs were usually cut out with a knife from one or two cells, put in small cellophane packets or triangles of folded paper and stored. If present, separate samples of different coloured stored pollen were sometimes taken and their relative proportions estimated. Unless the colony or comb was new and its construction had started on a known date, such samples did not reliably indicate the month in which the pollens were gathered, but could demonstrate the exploitation of sources of forage not immediately apparent in the area, because they occurred at some distance from the colony or because they had been in flower in previous months.

Samples of pollen from returning foragers were gathered either (a) at random while inspecting nests or (b) at regular intervals during the course of experiments on temperature regulation and foraging activity of the 2 *Apis* species (Chapter V). In the latter case samples of c.10 returning workers were caught with an insect net at the hive entrance at hourly or 2-hourly intervals and the size of any pollen loads recorded on a 5 point visual scale. They were dissected immediately and the quantity of any nectar/water in their crops estimated, also on a 5 point scale, and its concentration measured with Bellingham & Stanley pocket refractors (0% to 50% and 40% to 85%). The whole insects were retained for analysis in the U.K. of pollen loads or the pollen on their bodies. This provided data on the forage available to the 2 honeybee species at a particular locality on a given day and indicated the quantity and quality of nectar and/or pollen from different species and variations in their production/presentation during the course of a day. With (a), the returning foragers collected at random, sometimes the bees were released after the removal of a pollen load, but on other occasions the crop contents were investigated and the bodies kept for pollen analysis as described under (b).

Pollen traps were not used; they were not available in Oman for *mellifera*, and for *florea* it would have been necessary to design and develop one. In any case, with forage often scarce because of drought conditions, it was not desirable to place extra stress on the few colonies of each species that were available for study.

3.2 Preparation of pollen reference slides

Several techniques were tried, from simple degreasing with a solvent (alcohol, ether) and staining with basic fuchsin in ways similar to that described by Sawyer (1981) to Erdtman's full acetolysis method as described by Louveaux *et al* (1978). However, a method of watch-glass acetolysis based on that described by Hou (1969) was eventually adopted as it was suited to small samples of pollen, was relatively quick (20 - 30 samples could be processed in a day) and produced well-cleared pollen grains. The method is outlined here:-

(i) Individual flowers were taken from herbarium specimens at Edinburgh, put in watch-glasses (preferably solid block ones for stability) with 70% alcohol and the anthers were separated under a dissecting microscope. The debris (petals, sepals etc) was removed and the anthers crushed with forceps to release the pollen grains before being left to dry.

(ii) The watch-glasses were transferred to an electric hot plate (slide warming tray) which was heated to a temperature of c. 100°C in a fume cupboard. A few drops of freshly prepared acetolysis mixture (1 part concentrated sulphuric acid added very slowly to 9 parts acetic anhydride) were pipetted onto the pollen in the watch-glasses.

(iii) The watch-glasses were agitated intermittently and after c. 3 mins removed from the hot plate to cool.

(iv) The reaction was stopped by the addition of several drops of 70% alcohol and partial washing was achieved by pipetting this mixture into a small tube (3.8cm x 1cm, or a little larger), centrifuging and removing the supernatant with a pipette (<u>not</u> decanting as pollen grains were liable to be lost this way). Centrifuging and pipetting was repeated with tertiary butyl alcohol and then a few drops of silicone fluid were added to the pollen, stirred and the tubes left to stand overnight (plugged loosely with cotton wool) for the remaining butyl alcohol to evaporate.

Silicone fluid was a better mounting and storage medium than the widely used glycerine jelly in which pollen grains swell with time. The grains could also be stained but the brown colouring left after acetolysis usually made this unnecessary. If pollen was abundant in the sample more thorough washing could be achieved with glacial acetic acid (x1), distilled water (x2), tertiary butyl alcohol (x1), centrifuging and pipetting away the supernatant each time. Hou's (1969) method of removing surplus acetolysis mixture by soaking it up with tissue paper was found to be unsatisfactory as the pollen grains were drawn onto the tissue as well.

(v) The pollen grains in the silicone fluid were mounted on glass slides, with cover slips, and sealed with DPX (a mixture of Distrene, Plasticiser and Xylene from BDH). Each preparation was usually sufficient to make several slides.

If the grains were required for examination under the scanning electron microscope, the thorough washing was needed to remove excess acid and the grains were stored in 70% alcohol not silicone fluid.

3.3 Preparation of pollen samples

Stored pollen and pollen loads from foragers were treated by watch-glass acetolysis as above, though if from their colour, locality etc the pollen was thought to be of a common, distinctive type and therefore easily identifiable (eg *Citrus, Prosopis cineraria, Ocimum basilicum, Asphodelus fistulosus*) a quick check was made first by examination of a few grains stained with basic fuchsin. If identity was thus established no further analysis was necessary, but if such samples were not identifiable after this treatment another portion of the pollen would be acetolysed.

The predominant pollen type on the body of a honeybee *(mellifera)* has been shown to be that of the plant species being foraged on, whether the bee was collecting pollen, nectar alone or even acting as a nectar thief (Free & Williams 1972). Therefore the bodies of returning foragers without pollen loads were examined under a dissecting microscope and pollen in the combs of the basitarsus or on the body was either scraped or washed off (cf Williams 1977) for identification, using acetolysis if necessary. Pollen counts gave the predominant pollen type and the most likely nectar source.

3.4 Pollen identification

In identifying pollen grains, my own reference slide collection (170 species) was supplemented by access to slides in the collections of the Departments of Botany and Geography in Durham. The following publications were also useful: Erdtman 1952; Kapp 1969; Moore & Webb 1978; Bonnefille & Riollet 1980; Sawyer 1981. Numerous other publications, particularly those given in Crane (1978, Part 21) were also consulted to aid in the identification of the many unfamiliar pollen grains.

A scanning electron microscope (Cambridge Stereoscan 600) was also tried for pollen identification, but the samples still needed treating to remove the pollenkitt (Klungness & Peng 1983) and the method in general proved to be slow and somewhat erratic at the high magnifications required. However it was useful for comprehending the 3-dimensional structure of some pollen grains and for investigating others that were difficult to distinguish.

This pollen work was more difficult and time-consuming than anticipated, which was not surprising considering the Omani flora as a whole, let alone the honeybee flora, was poorly known and no palynological work had previously been undertaken. Though the pollen reference collection was thought to contain many of the Omani "bee plants", there proved to be numerous omissions making it difficult to identify a small but significant proportion of the samples. To do this successfully, a complete reference set of the Omani pollen flora was necessary, but time for its preparation was not available. For the same reasons samples of *florea* and *mellifera* honey from Oman were not analysed. Smith (1956) undertook a similar study as the sole topic of a D.Sc. thesis, "Bee Botany in Tanganyika" and also underestimated the work required. "By 1955 I had realized that the task I had set myself would require a lifetime to complete". Thus the bulk of his thesis was pollen descriptions and only a small proportion on the analysis of pollen and honey from bees.

4. Presentation of results

Because only a representative selection of all the pollen samples obtained was finally analysed, the details of (i) the pollens identified from the regular collections made during the foraging activity recordings, (ii) the counts of pollen grains on the bees' bodies and

(iii) the proportions of different pollens from comb samples, are not presented here. However, such data were transferred to the plant record cards where they filled gaps in the half-monthly data already compiled from visual records of flowering and foraging. Some species (eg *Abutilon muticum*) not seen to have been visited by honeybees in the field were identified as sources of forage only by this pollen analysis. The frequency of occurrence of pollen loads recorded from each plant species, the size of these loads and the quantity and concentration of any nectar present were taken into account when assessing a plant's importance as a source of forage.

From all the flowering, foraging and pollen analysis data, Tables 7.1 - 3 were drawn up in the following way to indicate the honeybee flora in each of 3 broad habitat categories.

The record cards for each plant species had been grouped, irrespective of origin, distribution and so on according to plant family. The families were arranged alphabetically and also the cards within each family, according to genus and species. The plants were initially listed in this order on draft tables for each habitat category. Plant species could occur in more than one table, the Batina and Interior gardens having many in common.

For each species the year was divided into ½-monthly intervals and an entry was made on each preliminary table, from the data on the cards, of its flowering (or fruiting) status in each period and whether or not it had been used then by *florea*. The assessment of whether a species was in a "peak" flowering phase or not was based on the proportion of the flowering records occurring in that period and notes on the relative numbers of plants involved and their intensity of flowering.

The 3 preliminary tables of family groups in alphabetical order were then re-arranged to produce 3 floral calendars (Tables 7.1, 7.2 & 7.3).

The species in each table were put into one of 5 groups according to their flowering pattern:-

(I) Restricted flowering period; not more than 4 months, except for a few cases, and often much less (1 - 2 months).

(II) Apparently unrestricted flowering period; ie recorded as flowering or evidently capable of flowering during most months of the year.

(III) Extended flowering period between spring and autumn (the hotter, summer months).

(IV) Extended flowering period between autumn and spring (the cooler, winter months).

(V) Flowering pattern not determined.

Within group (I) of each table, and to a lesser extent with the other groups, the species were listed in order of the months in which they started flowering. Thus the sequence of flowering could be seen for the species with a restricted flowering period, while the plants in flower for most of the year, for the summer and for the winter were distinguishable. With species for which there was only minimal flowering data, both the allocation to a group and the position within a group was speculative. As extra records become available, more accurate flowering patterns will become apparent and the tables improved.

The timing and extent of flowering in any one year in part depends on weather, especially the timing and quantity of rainfall, in that year and previous years. For these tables, records from more than one year have been combined, and therefore they indicate the overall range of time within which flowering is likely to occur in a single year. Because the study years were unusually dry it is probable that the flowering of certain plants in wet years may extend beyond the ranges given in the tables.

For each plant it was also indicated whether it was a source of nectar and/or pollen for *florea* and separately for *mellifera* (but not distinguishing between the indigenous *jemenitica* and the imported races). Details of the ½-monthly periods in which *mellifera* were recorded as having exploited the various sources of forage are not presented.

Where plants did occur in more than one habitat category there was not, for most species, sufficient data to indicate whether there were differences in phenology or patterns of exploitation by bees between habitats. Therefore, on the tables for each habitat all flowering and foraging records are given for a plant species irrespective of habitat type. Thus the flowering and foraging records for such species, as presented, are the same in all 3 tables.

The information gained in Oman on the sources of nectar and pollen for the 2 species of honeybee was supplemented, where necessary, with literature records from other countries. When information was still lacking on the use of certain plants by *mellifera, Apis cerana* records were added because of the similarity between the 2 species in tongue-length, 5.44mm (*jemenitica*, Dutton *et al* 1981) and 5.30 - 5.38mm (Mattu & Verma 1983) respectively. However, differences in the floral preferences of the 2 species have been noted (eg Atwal & Goyal 1974), so these sources of forage important to *cerana* are not necessarily well suited to *mellifera*.

When, in the literature, the use of some plants by honeybees was evident only from the occurrence of their pollen grains in honey, this has been indicated; the plants could have been exploited by the bees for their nectar and/or their pollen.

On the basis of their recorded exploitation by *florea* in Oman, their rewards in terms of nectar and pollen, their known value as sources of forage/yielders of surplus honey in other countries and on their length of flowering, distribution and abundance within Oman, the importance of each species to *florea* as a source of forage/honey was assessed according to a 4-point scale:-

S : Substantial
I : Intermediate
M : Minor
N : Negligible

though subjective, this assessment was based on a considerable body of data and field experience of the vegetation in most regions of northern Oman, and I believe for the majority of plants gives a reasonable estimation of their value. Examples of the different values are discussed in the Results and Discussion, Section 3.1 (v).

Ranta & Lundberg (1981a) compared 3 data collection methods for examining the food niches (sources of forage) of bumblebees, (a) direct observations of flower visits, (b) analysis of pollen loads and (c) analysis of pollen in nectar loads. The number of flower species found to be utilized was the same by all 3 methods so, if only the spectrum of flower species used by the bees was required, they concluded that method (a), the least time-consuming, was justifiable. Therefore it is hoped the use of both methods (a) and (b) in this study, plus reference to the literature, means that, whatever the importance of its individual components, the bulk of the forage spectrum for both *Apis* species in Oman has been covered.

C. RESULTS AND DISCUSSION

1. Vegetation

1.1 Overall flora

A species list of the plants I collected, photographed or recorded in northern Oman is presented in Appendix III. Additional species found by others, especially Mandaville (1977), have been incorporated and it is believed this list encompasses about 95% of the total indigenous and naturalised flora; recently introduced ornamental and crop plants were less well recorded. A simple code indicates briefly the origin, distribution and "nature" (wild plant, segetal weed, crop etc) of each species. From this information an indication of the status and habitat of each is provided, for example:-

(i) In Appendix III the code for mango, *Mangifera indica*, gives it as a plant that is naturalized, a crop and as occurring in the mountains below 1600m, on the Bātina and in the plains. This indicates a widespread plant cultivated in oases/gardens in most regions of Oman, except at high altitudes where frosts might occur.

(ii) *Periploca aphylla* (Asclepiadaceae) is an indigenous, wild plant growing in the mountains above and below 1600m.

(iii) *Leptadenia pyrotechnica* (Asclepiadaceae) is an indigenous wild plant of the plains of interior Oman and the Bātina.

Further subdivisions of the habitats of plants (eg into alluvial plains, rocky desert, sandy desert, wadis, limestone hills, serpentine hills and so on) have not been attempted though the lists in Tables 3.8, 4.4 and 4.5 do indicate the plants occurring in 4 defined areas; in any case the differences between habitats were not always immediately apparent. Such detailed knowledge is potentially useful to bee-keepers but is the work of a Flora and phytosociological studies beyond the scope of this thesis. Appendix III nevertheless does provide relevant information on those plants already identified as sources of honeybee forage and will do so for others which are recognized, in the future, to be "bee plants".

1.2 Cultivated areas : Interior and Bātina Coast gardens

Although the total compositions of the floras of interior oases and Bātina Coast gardens are not portrayed in Tables 7.1 and 7.2, the rather higher number of honeybee plants occurring in the former (106 spp as opposed to 88 spp, Table 7.5a), does reflect a fundamental difference between them, of importance to honeybees. Part of this difference in species richness can be attributed to the inclusion in the interior gardens category of plants such as *Silene apetala, Veronica polita* and *Clematis orientalis* that grew as segetal or ruderal weeds in the few villages, such as Sayq, above the frost line, but apparently not at lower altitudes. However, there were plants eg *Malvastrum coromandelianum, Verbascum omanense, Oxalis corniculata, Eclipta alba* and *Ranunculus muricatus,* occurring in the lowland gardens of interior Oman, but not recorded from the Bātina Coast gardens. In contrast there were very few plants that occurred in the Bātina gardens but which were not recorded from the interior gardens. Some of these qualitative differences in the flora may have been the consequence of inadequate vegetation surveys. Other floristic variations are likely to be the result of major differences in the irrigation systems operating in the 2 types of garden. However, it was the effect of these systems on the quantity of vegetation that was considered to be of greater significance to the honeybees.

Most of the interior gardens were irrigated with water channeled from near permanent springs or other groundwater aquifers, often many kilometres distant, by means of under and overground aqueducts called "falaj" (pl. "aflaj"), (see Wilkinson 1977; Dutton & Letts 1982). These usually fed large irrigation basins "galba", each containing several date palms and/or other trees and crops. In contrast, all irrigation water on the Bātina gardens had to be lifted (previously by animals, now by pumps) from wells, so was less freely available and was directed into "gayl", much smaller, circular irrigation basins (usually less than 3m in diameter) around individual trees. Dutton & Letts (1982) discuss these irrigation practices further, but the main consequence for the vegetation, including that exploited by honeybees, was that the herbaceous ground flora (of crops and weeds) was considerably more abundant under the date palms of the interior gardens, their large "galba" being flooded regularly.

No quantitative measurements were made of the density of the weed flora in the 2 sets of gardens, but the fundamental differences between them were also reflected in the greater density of trees in the interior gardens (see p. 71-2) and in the crops grown beneath and interplanted (Dutton & Letts 1982). For instance *Vicia faba* and *Sesamum indicum* were grown at Rustāq and are sources of forage to honeybees, but were not recorded on the Bātina. *Citrus* spp. formed 13.1% of the trees in "falaj" gardens, but only 6.1% in the Bātina gardens where other fruit trees also appeared to be less frequent (see Tables 2.2 and 2.4). Furthermore, on the Bātina, many date-gardens and their irrigation, and consequently weed flora, were being neglected, while there was a trend towards the cultivation of more fodder crops, especially lucerne (*Medicago sativa*), vegetables, melons (*Cucumis* sp.) and watermelons (*Citrullus* sp.).

Dutton & Letts (1982) detail some of these differences and changes, but as far as the honeybees were concerned it was evident that the "falaj" gardens of the interior generally provided a superior foraging area, to a small extent qualitatively (ie more forage species, Table 7.5a) but especially quantitatively with more abundant crops, particularly *Citrus* spp., and weeds. In addition, nectar secretion and pollen production in the thoroughly irrigated "galba" crops was probably higher than in the rather neglected "gayl" crops of the Bātina.

On the other hand, the greater areas of lucerne and cucurbits on the Bātina were potentially profitable to honeybees as sources of forage in the summer; however, the potential was not fully realized as much of the lucerne was cut before flowering and the cucurbits were often sprayed with pesticides (these were almost certainly the cause of considerable worker mortality in colonies of imported *mellifera* at Qusabiyat, near Khabura, in 1979; *florea* colonies probably suffered too.)

1.3 Wild Habitats

The number of bee species in wild habitats was lower than in interior oases and Bātina gardens (Figure 7.5a) and in particular in the more important S, I and M forage categories. This was consistent with the apparent scarcity of *florea* away from cultivation. Nevertheless, the 3 "S" species, *Acacia tortilis, Prosopis cineraria* and *Ziziphus spina-christi* were more abundant in the wild habitats than they were in the oases and gardens. It can be seen that the species in the list of wild honeybee plants (Table 7.3) were mostly different from those in the gardens. A few wild plants that thrived on disturbed ground, such as *Calotropis procera* and *Zygophyllum simplex,* did occur in the gardens, particularly on fallow and neglected areas, and two of the trees mentioned above, *Prosopis* and *Ziziphus*, were even deliberately encouraged for their shade, timber and other uses. However, only such wild plants that were of some importance to honeybees were listed in all 3 habitat categories.

According to my observations, some plants were fairly restricted in their distribution. For instance, *Moringa peregrina* and *Periploca aphylla* to mountainous areas and especially the rocky sides of wadis; *Dipterygium glaucum*, *Zygophyllum coccineum* and *Leptadenia pyrotechnica* to sandy and silty plains and *Berberis* sp. and *Cotoneaster* sp. to the very summit of the Jabal al-Akhdār (the latter 2 species were both potential honeybee plants but probably out of range to *mellifera* and *florea* which were not seen at this altitude (c. 3000m)). Other species such as *Euphorbia larica* were particularly abundant on mountain slopes above wadis, but also occurred in the plains and on coastal hills. Some such as *Acacia tortilis* were widespread, occurring in mountain, plain and wadi associations. This diversity cannot be detailed nor fully taken into account, but it was evident that trees, shrubs and herbs were most abundant in and near to wadis. This could be seen in the field and on aerial photographs, whether the wadis were steep, boulder-strewn ravines near their source in the mountains, or broader, stony channels winding through the foothills or large, temporary "rivers" flowing through and creating the sandy/silty outwash fans in the plains away from the mountains. The relatively high water flow over these features, the presence of running or standing water at certain sites for much of the year and the proximity of the water-table to the surface, as well as producing a greater density of vegetation, also appeared to stimulate more prodigious and regular flowering. It was in or close to wadis, in the mountains and plains, that most colonies of *florea* were found in "wild" habitats and it was at the edge of such a wadi that Nāsr Ahmad al-Ghaythi kept his colonies in the cooler months (Chapter IV). Away from these areas the supply of water and forage would be too low and irregular to support permanent populations of *florea*.

However, from nest sites in and near to oases, the Bātina gardens and wadis, honeybees are in a position to exploit not only the flora in their immediate habitat but also that in "wild" areas, which may be poorly vegetated, up to several kilometres distant. For much of the time such areas will have little to offer but in years when rainfall has been high, the shrubs and ephemerals of desert and mountain communities flower more profusely. Unfortunately heavy rainfall was infrequent during the study years and data on the exploitation of these sources of forage were relatively scarce. Thus a few species that were not seen to flower in profusion but were suspected to be potential sources of forage, such as *Argyrolobium roseum* and *Medicago orbicularis* (both Papilionaceae) have been included in Table 7.3. Many more wild species not listed probably provide valuable supplementary forage from time to time, especially in parts of the central Jabal al-Akhdār where average rainfall is higher (Gallagher & Woodcock 1980) and the vegetation correspondingly richer.

Notwithstanding this, visual records and pollen analyses showed that ephemerals such as *Zygophyllum simplex* and *Tribulus* spp. and particularly *Asphodelus fistulosus* were widespread in barren regions and seasonally useful sources of forage. Various shrubs and small trees such as *Ochradenus arabica* sp. nov. and *Maerua crassifolia* though more abundant in or close to wadi beds grew at a distance from them too, and their flowering, like that of ephemerals, appeared to be affected to some degree by rainfall, so in wet years their value as sources of forage is probably enhanced.

Tables 7.1, 7.2 and 7.3

Floral calendars of honeybee forage plants in northern Oman, with records per half month.

7.1 Gardens in the interior of the country away from the Bātina coast, mostly oases irrigated by "falaj".

7.2 Gardens of the narrow, cultivated strip along the Bātina coast, irrigated from wells.

7.3 Wild habitats, including mountains, wadis and plains.

Details of how the data were obtained and the 3 tables prepared are given in Materials and Methods (p. 316). The key below to the symbols and suffixes applies to all 3 tables.

Symbols within main chart

X : At flowering peak, with *Apis florea* recorded foraging.

O : At flowering peak, without *Apis florea* recorded foraging.

x : In flower, but not at peak; with *Apis florea* recorded foraging.

o : In flower, but not at peak; without *Apis florea* recorded foraging.

- : Recorded not flowering (only inserted for some species).

f : Fruit but no flowers recorded, indicating flowering at an earlier date.

( ) : Aberrant plant recorded flowering outside usual period. Excluded from totals in Table 7.4.

Other symbols and suffixes

FAM. NO. : Indicates plant family to which species belongs according to Appendix III.

IMP. : Importance of species as a source of forage for *A. florea*. S: Substantial, I: Intermediate, M: Minor, N: Negligible.

N & P : Indicates whether the species is a source of Nectar or Pollen.

The symbols below indicate the origin of the information in the N & P columns

+ : Oman record; observation and/or pollen analysis.

? + ? : Source of forage, but whether for nectar and/or pollen not clear.

R : Records in the literature.

G : Closely related species, usually in same genus, recorded as a source of forage in Oman.

* : Closely related species, usually in same genus, recorded as a source of forage in the literature.

A : Recorded in the literature as a source for "honeybees" but not clear which *Apis* species. *A. cerana* and/or *A. mellifera* most likely.

cont. overleaf

Tables 7.1, 7.2 and 7.3 continued

C : Recorded in the literature as a source for *Apis cerana.*

H : Recorded in the literature as occurring in honey samples. Could be a source of nectar and/or pollen.

O : Omani informant (pers. comm.); could be source of nectar and/or pollen.

- : Pollen or nectar not available.

Where symbols (such as R) denote that records have come from the literature, it was the following sources that provided most information, especially on *Apis mellifera*:- Crane (1975a, esp. Ch. I), Free (1970), Free & Williams (1977), Hodges (1978), McGregor (1976), Purseglove (1968 & 1972), Robinson & Oertel (1975), Sawyer (1981).

Each of the references below gave a smaller number of additional records:-

Atwal *et al* (1970)
Batra (1967)
Bhatnagar (1975)
Bisht (1975)
Chaubal & Kotmire (1980)
Dubois & Collart (1950)
Eisikowitch & Masad (1980, 1982)
Gadbin (1980)
Ibrahim (1976)
Indian Standards Institution (1973)
Jain & Kapil (1980)
Keeler & Kaul (1979)
Kleinschmidt & Kondos (1977)
Koeniger & Vorwohl (1979)
Latif *et al* (1958)
Nair & Singh (1974)
Oustuani (1976)

Papadopoulo (1973)
Percival (1955)
Percival (1974)
Phadke (1967)
Rahman (1945)
Mohana Rao *et al* (1981)
Ricciardelli D'Albore (1980)
Ricciardelli D'Albore & Vorwohl (1980)
Saraf (1972)
Shahid & Quayyum (1977)
Sharma (1972)
Sidhu & Singh (1961, 1962)
Smith (1956)
Thakar *et al* (1962)
Verhagen (1971)
Vorwohl (1981)
Williams (1977)

°Additional notes, according to suffixes a, b, c, ... u, v.

a : Recorded above 1600m only.

b : Flowering record from Ja'alān region only, possibly under some influence from summer, SW monsoon.

c : May include records of similar *Schanginia aegyptiaca*, which might be used by honeybees too.

d : Pollen determined from description of Davies (1978), not reference slide, therefore identification not 100% certain.

e : Pollen determination was not 100% certain as several other Compositae were also present in the vicinity.

cont. overleaf

Tables 7.1, 7.2 and 7.3 continued

f : Inclusion of this species in the Bãtina category not 100% reliable (some doubt over provenance of specimen brought to me).

g : Pollen close to that of *Euphorbia peplus* too, but only *Euphorbia helioscopia* recorded in vicinity of sample.

h : Some records could be of *Ocimum hadiense* and/or *Ocimum basilicum.*

j : Some pollen was collected, but honeybees may not be able to trip the *Sesbania sesban* flowers themselves, nor those of *Tephrosia* spp.

k : Only a little pollen found on those returning foragers which were examined.

m : Record from Myrtaceae pollen on *Apis mellifera : Eucalyptus* sp. most likely, but *Psidium guajava* also possible.

n : *Prunus persica* (peach) was probably the most abundant source, but the other *Prunus* species would be used too. Their pollen could not be distinguished.

p : Pollen on *Apis mellifera* could have been *Lantana petitiana* or *Verbena officinalis.* Both are likely to be used in Oman.

q : The April record refers to hundreds of *A. florea* feeding on the sugary exudate of dried dates, from the previous year, packed in sacks. The June-August records refer to fresh dates, "rutab", still on the trees or recently harvested.

r : Nectar from the flowers and also, according to R.W. Dutton (pers. comm.), from extra-floral nectaries below the flower.

s : As well as foraging in the flowers of *Ipomoea pes-caprae,* honeybees were often seen to take nectar from extra-floral nectaries at the base of the sepals and at the end of the petioles, close to the leaf base. See Keeler & Kaul (1979).

t : *A. florea* seen foraging on extra-floral nectaries around the buds.

u : *A. florea* gathered pollen and presumably nectar from the flowers, but were also seen foraging on extra-floral nectaries.

v : Extra-floral nectaries appeared to be the primary source of forage, but *A. florea* were also seen to take nectar from the flowers without tripping them. See McGregor (1976).

N.B. Records for plants in the S (Substantial) and I (Intermediate) categories are in heavy type.

FAM. NO.	PLANT	IMP	Apis florea N	Apis florea P	Apis mellifera N	Apis mellifera P	1	2	3	4	5	6	7	8	9	10	11	12
	I 67 species Restricted Flowering																	
46	Eucalyptus sp.	M	R	R	+	+	o^m											
24	Ipomoea batatas	M	G	G	+	+	X	– –				– –	–	–				
69	Veronica polita[a]	N			R*	R*	o^a f^a	o^a										
29	Euphorbia helioscopia	M	$+^g$	$+^g$	C*	C*	o^a o	o x^a										
25	Sisymbrium erysimoides	M			+	+	o^a o	o o	o o									
44	Morus sp.	N			C	C	o o	o	o o	f								
57	Anagallis arvensis	N	? + ?				o o	o o	o	o o^a								
75	Coriandrum sativum	M	+	+	R	+	o		x									
64	Haplophyllum tuberculatum	N	O				o	O	o	o o		o						
37	Trigonella foenum-graecum	M	+	+	C	R	o X											
64	**Citrus spp.**	S	+	+	+	+	x X	X X	X o	f f	f	f		f f			f	f
4	**Mangifera indica**	I	+	+	R	R	o O	X X	x o			f						
23	Sonchus oleraceus	M	+	+	R	R	o^a	o o^a	X	o	o		o^a					
62	Prunus persica[n]	M	+	+	+	+	X^a	X^a X^a		$-^a$	f^a		f^a					
41	Althaea rosea	N	R		R	R	o^a		o	o								
52	Plantago spp.	N			–	R	o	o o^a	o	o^a		o^a						
20	Chenopodium spp.	N				C*	o	o^a	o	o o			o^a					
89	Phoenix dactylifera ♂	M	–	+	–	+	o	X X										
37	Vicia faba	M	$+^u$	+	+	+		X										
25	Raphanus raphanistrum	N			R	R		o										
29	Euphorbia peplus	N	G	G	C*	C*		o		o								
37	Melilotus indicus	M	+	+	R*	R*		o x	X X	o o^a								
75	Apium graveolens	M			R	R		o o	O O	o								
85	Allium cepa	M	+	+	R	R		x o	x X	X								
36	Ocimum hadiense	M	$+^h$	$+^h$	$+^h$	$+^h$		x^h o	o		o x^h	o		o				
12	Cordia myxa	M	+		C	C		X				f	f					
09	Verbascum omanense	N			R*	R*		o										
19	Silene apetala	N			+	$+^k$		x^a										
25	Erucastrum arabicum[a]	N			R*	R*		o^a										
37	Vicia sativa	N			R*	R*		o^a										
62	Prunus amygdalus	M	(+	+	+	+		X^a		$-^a$ f^a								
62	Prunus armeniaca	M	n (+	+	+	+		X^a		$-^a$ f^a								
62	Prunus domestica	M	(+	+	+	+		X^a		$-^a$ f^a								
23	Carthamus tinctorius	M	+	+	R	R		O	O X									
22	Terminalia catappa	M	$+^r$	+	R*	C*			X	X		f				x	o	
85	Agave sp.	N			R	R			o									
70	Datura sp.	N	+	+	R	A			x									
75	Ammi majus	M	+	+		R			X	X	o							
75	Anethum graveolens	M	+	+	R	R			o	o o	o o	o f						
23	Helianthus annuus	M	+	+	+	+			o	o X	o o		o					
37	**Prosopis cineraria**	S	+	+	+	+	– –	– –	– x	X X	x o	– –	– –	– –	f –	– –	(o) –	– (o)
75	Pimpinella ?sp. nov.	M	+	+	H					X								
25	Brassica oleracea var. capitata	N	+	+	R	R				x								
59	Ranunculus muricatus	N			R*	R*				–	–							
58	Punica granatum	M	? + ?		C H	C				x o^a		o	f^a	f	f		f	
37	**Acacia tortilis**	S	+	+	+	+	– –	– –	– –	X X	X o	– –	– –	– –	– –	– –	– –	
25	Eruca sp?	N	R	R	R*	R*				O		f						
37	**Medicago sativa**	I	+	+	+	+	– –	– –	– –	x o	O O	X X	X o^a	o		o –	– –	– –
26	**Cucumis melo (cultiv.)**	I	+	+	+	+					x o	X o	x					
39	Lawsonia inermis	M		+		C					o		x o	o				
37	Vigna unguiculata	M	$+^v$	–	R^v	–					x	o x	o					
83	Pennisetum sp.	M	–	+	–	R*						X						
26	**Citrullus lanatus**	I	+		R	R						x o	x o	o				
89	**Phoenix dactylifera ♀ (fruit)[a]**	I	+	–	O	–				(x)		o o	X o	o				
19	Stellaria media	N			R	R							o^a					
46	Myrtus communis	M			R	H	$-^a$			$-^a$			X^a					
36	Mentha longifolia	M	+	+	R	C							X^a	o				
59	Clematis orientalis[a]	M	–	+	–	H							X^a	O^a		f^a		
61	**Ziziphus spina-christi**	S	+	+	+	+	(o) (o)	– f	f –	– f^a	(x) –	– (x)	(x) (x)	– –	– x	X X	X x	x f
37	**Acacia nilotica**	I	+	+	G	R	(o)		f		(o)	(o) (o)	(x) (o)	(o)		o x	X X	o x
11	Tecoma stans	M	+	+	R	R										o	x O	X X
37	Sesbania sesban	M	+	$+^j$	+	$+^j$									o	o	o o	X X
51	Sesamum indicum	M	+	+	R	R						–				o		
29	Euphorbia heterophylla	M	+	+	C	C	x						–				o	x
37	Pithecellobium dulce	M	+	+	+	+	O o	o	o	o							o	X X
23	Bidens biternata	N	R	R	R*	R*												o
25	**Raphanus sativus**	I	+	+	+	+	X X	X X	X x	f								x X
	II 19 species Unrestricted Flowering																	
36	Ocimum basilicum	M	+	+	+	+	X	o		o x	o	o o	x	o x	x	o		o
24	Ipomoea pes-caprae	M	$+^s$	+	$+^s$	+	x x	x	x	x o	x x	o	o	o		o x	x x	x x
23	Flaveria trinerva	M	$+^e$	$+^e$			o	x^e		o		o	o	o	o	o		
24	Convolvulus arvensis	M			R	R	o	o o	o	o	o	o	o o^a		o			–
77	**Phyla nodiflora**	I	+	+	R	R	o	o	x X	X x	o	o x	x	o o	o o	o o	o	x x
86	**Musa spp.**	I	+	–	+	–	o	x	x X	X o		o	x				–	x
41	Malvastrum coromandelianum	M			R*	R*	o^a o		o	o		o	o^a					
24	Ipomoea obscura	N	G	G	G	G	o					o						
23	Vernonia cinerea	M	+	+	R*	C	o	x o	o	x^e	o	o	o o		o		o	x
24	Ipomoea sp. indet.	N	+		G	G	x	x	x	o		o	o			o		
50	Oxalis corniculata	N			H	H	$-^a$						– –	$-^a$				–
82	Cyperus rotunda	M	–	+	–	+			o	o		o x	x				X x	o
85	Aloe vera	N			R*	R*			o								o	
24	Ipomoea cairica	N	$+^t$		G	C			o	o	o	o	o	o o		o	o	o
23	Eclipta alba	N	R							o		o		o				o
23	Launaea sp. of nudicaulis	M	G	G		G				o			o			o		o
37	Cassia sophera	N		+	H					o							x	
26	Cucumis melo (Weed)	N	G	G	G	G						o				o	o	
37	Tamarindus indica	M			R	A			–			o				o	o	
	III 8 species Extended Summer Flowering																	
62	Rosa sp.	N	–	+	–	R		o o		o o^a		o o		o x				
8	Calotropis procera	M	+	–	+	–		O	O X	X o		o	x x	o		o o		
56	Portulaca oleracea	M	+	+	+	+			O	o	o o	o	X x	x o	o		O	
8	~~Carica papaya~~	N			R	R			o				o	o			f	
83	Sorghum sp.	M	–	O	–	R			o			o o		o		o o	o	
83	Echinochloa colonum	N	–	+	–	G*			o		o	x	x o	o				
83	Cynodon dactylon	M	–	+	–	R				x o		x x	o				x x	o
83	Pennisetum sp. 2 (Millet)	N	–	O	–	O						o o						
	IV 6 species Extended Winter Flowering																	
3	Aerva javanica	N	+				o	o	o o						(o^b)		x	o
41	Sida spp.	N			C*	+		o	o						o	o	o	o
56	Portulaca quadrifida	M	G	G	G	G		o								o	o	o
41	Gossypium spp.	M	R	R	R	R			o							o	o	o
37	Cajanus cajan	N	R	R	R	R		o	o							o^a		
36	Salvia aegyptiaca	N			R*	R*			o	o^a								
	V 6 species Flowering Season Unknown																	
23	Lactuca sativa	N				R												
29	Ricinus communis	N		R	R	R						–			f			
46	Psidium guajava	M			R	R			f									
62	Malus domestica	N			R	R												
70	Nicotiana sp.	N			R	R								–				
79	Vitis vinifera	M			R	R												
		IMP	N	P	N	P	1	2	3	4	5	6	7	8	9	10	11	12
			Apis florea		Apis mellifera													

TOTAL: 106 species

TABLE 7.2 FLORAL CALENDAR OF 88 HONEYBEE PLANTS IN BATINA COAST GARDENS OF NORTHERN OMAN

FAM. NO.	PLANT	IMP	Apis florea		Apis mellifera		MONTHS OF THE YEAR											
			N	P	N	P	1	2	3	4	5	6	7	8	9	10	11	12
	I 50 species Restricted Flowering																	
46	Eucalyptus sp.	M	R	R	+	+	σ[m]											
24	Ipomoea batatas	M	G	G	+	+	X	- -				- -	-	-				
25	Sisymbrium erysimoides[l]	M			+	+	o o	o o	o o									
44	Morus sp.	N			C	C	o o	o	o o	f								
57	Anagallis arvensis	N	? + ?				o o	o o	o	o σ[a]								
75	Coriandrum sativum	M	+	+	R	+	o		x									
64	Haplophyllum tuberculatum	N	0				o	0	o	o o		o						
37	Trigonella foenum-graecum	M	+	+	C	R	o X											
64	**Citrus spp.**	S	+	+			x X	X X	X o	f f	f	f		f f			f	f
4	**Mangifera indica**	I	+	+	R	R	o 0	X X	x o			f						
23	Sonchus oleraceus	M	+	+	R	R	σ[a]	o σ[a]	X	o	o		σ[a]					
41	Althaea rosea	N	R		R	R	o[a]		o	o								
20	Chenopodium spp.	N				C*	o	o[a]	o	o o			σ[a]					
89	Phoenix dactylifera ♂	M	-	+	-	+	o	X X										
37	Melilotus indicus	M	+	+	R*	R*		o x	X X	o o[a]								
75	Apium graveolens	M			R	R		o o	0 0	o								
85	Allium cepa	M	+	+	R	R		x o	x	X	X							
12	Cordia myxa	M	+		C	C		X				f	f					
23	Carthamus tinctorius	M	+	+	R	R		0	o X									
75	Daucus carota	N	+	+	R	R			x									
22	Terminalia catappa	M	+[r]	+	R*	C*			X	X		-				x	o	
29	Euphorbia sp. indet.	N			C*	C*			o									
37	Parkinsonia aculeata	N	R		R	R			0									
70	Datura sp.	N	+	+	R	A			x									
75	Ammi majus	M	+	+	R				X	X	o							
25	Sinapis arvensis	N			R	R			o	o								
75	Anethum graveolens	M	+	+	R	R			o	o o	o o	o f						
23	Helianthus annuus	M	+	+	+	+			o	0 X	o o		o					
20	Salsola baryosma[c]	M	+	+					x	x x		x x	x				o x	
37	**Prosopis cineraria**	S	+	+	+	+	- -	- -	- x	X X	x o	- -	- -	- -	f -	- -	(o) -	- (o)
25	Brassica oleracea var. capitata	N	+	+	R	R				x								
58	Punica granatum	M	? + ?		C H	C				x σ[a]		o	f[a]	f	f		f	
37	**Acacia tortilis**	S	+	+	+	+	- -	- -	- -	X X	X o	- -	- -	- -	- -	- -	- -	- -
25	Eruca sp?	N	R	R	R*	R				0		f						
42	Azadirachta indica	M			A H	C			-	0	o o	f	f					
37	**Medicago sativa**	I	+	+	+	+	- -	- -	- -	x o	0 0	X X	X σ[a]	o		o -	- -	- -
26	**Cucumis melo (cultiv.)**	I	+	+	+	+					x o	X o	x					
39	Lawsonia inermis	M		+		C					o		x o	o				
37	Trifolium alexandrinum	N	R	R	+	+					x	o						
37	Vigna unguiculata	M	+[v]	-	R[v]	-					x	o x	o					
23	Cichorium intybus	N			R	R						o						
83	Pennisetum sp.1	M	-	+	-	R						X						
26	**Citrullus lanatus**[g]	I	+		R	R						x o	x o	o				
89	**Phoenix dactylifera♀ (fruit)**	I	+	-	0	-				x		o o	X o	o				
61	**Ziziphus spina-christi**	S	+	+	+	+	(o)(o)	- f	f -	- f[a]	(x) -	- (x)	(x)(x)	- -	- x	X X	X x	x f
37	**Acacia nilotica**	I	+	+	G	R	(o)		f		(o)	(o)(o)	(o)(o)	(o)		o x	X X	o x
11	Tecoma stans	M	+	+	R	R										o	x 0	X X
37	Sesbania sesban	M	+	+[j]	+	+[j]	0 o	o				-			o	o	o o	X X
37	Pithecellobium dulce	M	+	+	+	+	0 o	o		o	o						o	X X
25	**Raphanus sativus**	I	+	+	+	+	X X	X X	X x	f								x X
	II 16 species Unrestricted Flowering																	
36	Ocimum basilicum	M	+	+	+	+	X	o		o x	o	o o	x	o x	x	o		o
24	Ipomoea pes-caprae	M	+[a]	+	+[a]	+	x x	x	x	x o	x x	o	o	o		o x	x x	x x
23	Flaveria trinerva	M	+[e]	+[e]			o	x[e]		o		o	o	o	o	o		
23	Launaea procumbens	M	+	+	+	+	o		x o	o			x	x o				x
24	Convolvulus arvensis	M			R	R	o	o o	o	o	o	o	o o		σ[a]			-
77	**Phyla nodiflora**	I	+	+	R	R	o	o	x X	X x	o	o x	x	o o	o o	o o	o	x x
86	**Musa spp.**	I	+	-	+	-	o	x	x X	X o		o	x				f	x
37	Caesalpinia bonduc	M	? + ?				o		f			o 0						x
23	Vernonia cinerea	M	+	+	R*	0	o	x[e] o	o	x	o	o	o o		o		o	x
24	Ipomoea sp. indet.	N	+	G	G	G	x	x	x	o		o	o			o		
82	Cyperus rotunda	M	-	+	-	+			o	o		o x	x				X x	o
41	Abutilon muticum	M				+			o			o		o	o o	o		
85	Aloe vera	N			R*	R*			o								o	
24	Ipomoea cairica	N	+[t]			C			o	o	o	o	o	o o		o	o	o
26	Cucumis melo (weed)	N	G	G	G	G						o				o	o	
37	Tamarindus indica	M			R	A			-			o				o	o	
	III 10 species Extended Summer Flowering																	
62	Rosa sp.	N	-	+	-	R		o o		o 0[a]		o o		o x				
8	Calotropis procera	M	+	-	+	-		0	0 X	X o		o	x x	o		o o		
83	Sporobolus spicatus	M	-	+	-	+			x x	X X	x x	x x	X X	X x	o		X X	X X
56	Portulaca oleracea	M	+	+	+	+			0	o	o o	o	X x	x o	o		0	
18	Carica papaya	N			R	R			o				o	o			f	
83	Sorghum sp.	M	-	0	-	R			o			o o		o		o o	o	
83	Echinochloa colonum	N	-	+	-	G			o		o	x	x o	o				
83	Cynodon dactylon	M	-	+	-	R				x o		x x	o				x x	o
83	Chloris barbata	N	-	+	-	G				o		o	x					
83	Brachiaria eruciformis	N	-	+	-	G				o				x				
	IV 6 species Extended Winter Flowering																	
3	Aerva javanica	N	+				o	o	o o						(o)[b]		x	o
41	Sida spp.	N				+		o	o						o	o	o	o
56	Portulaca quadrifida	M	G	G	G	G		o								o	o	o
41	Gossypium spp.	M	R	R	R	R			o					-		o	o	
23	Conyza dioscorides	M	+	+					o x							o		x x
37	Cajanus cajan	N	R	R	R	R		o	o									o
	V 6 species Flowering Season Unknown																	
23	Lactuca sativa	N			R	R												
29	Ricinus communis	N		R	R	R												
36	Mentha sp.	N	G	G	R	R												
45	Moringa pterygosperma	N			R	R												
46	Psidium guajava	M			R	R						-			f			
79	Vitis vinifera	M			R	R								-				
		IMP	N	P	N	P	1	2	3	4	5	6	7	8	9	10	11	12
			Apis florea		Apis mellifera													

TOTAL 88 species

TABLE 7.3 FLORAL CALENDAR OF 75 HONEYBEE PLANTS IN WILD HABITATS OF NORTHERN OMAN

FAM. NO.	PLANT		Apis florea		Apis mellifera		MONTHS OF THE YEAR											
		IMP	N	P	N	P	1	2	3	4	5	6	7	8	9	10	11	12
	I 41 species Restricted Flowering																	
26	Cucumis prophetarum	N	G	G	G	G	o		o						f			
16	**Maerua crassifolia**	I	+	+	H*		o o	X X	o o	f								
45	Moringa peregrina	M			R*	R*	o	O	o o	o		f		–				– –
80	Zygophyllum simplex	M	+	+	+	+	x o	o	X	X o	o				σ^b			
37	Medicago orbicularis	N	G	G	G	G	o	o o^a										
23	Reichardia tingitana	N					o		o									
60	Reseda aucheri	N			R*	R*	o	o	o									
23	Launaea mucronata	N	G	G	G	G	o	f	o									
41	Malva parviflora	M			R*	R*	o	o σ^a		f o^a								
26	Citrullus colocynthis	M	G		R*	+	o		f	o								
63	Jaubertia aucheri	M	O				o	o	o O	o	o					– –	–	– –
52	Plantago spp.	N			–	R	o	o o^a	o	o^a		o						
29	Euphorbia larica	M		+	C	C		X	X o						σ^b)			o
11	Tecomella undulata	N	G	G	R*	R*			o	o O	O o							
23	Grantia aucheri	N	+	+					X									
55	Pteropyrum scoparium	M	+	+	+	+			X X	o		–				–	–	o
37	Acacia ehrenbergiana	M	? +	?	G	G			x o	O				–			–	o –
23	Vernonia arabica	N	G	G	R*	$+^d$			o O						σ^b)			
72	Tamarix arabica	N	? +	?	R	R			X									
23	Centaurea siniaca	N			R*	R*			o	o								
23	Echinops spinosissimus	N			R*	H*			o	o								
60	Oligomeris linifolia	N							O	O								
37	**Prosopis cineraria**	S	+	+	+	+	– –	– –	– x	X X	x o				f –	– –	(o) –	– (d)
72	Tamarix aphylla	N			R	R		–		O								
37	Dalbergia sissoo	N			R	R				o o								
77	Lantana petitiana	N			$+^p$	$+^p$				o^a σ^a								
37	**Acacia tortilis**	S	+	+	+	+	– –	– –	– –	X X	X o	– –	– –	– –	– –	– –	– –	– –
23	Crepis sp.	N								o^a								
37	Alhagi maurorum	N	+	+	A ?	A					x		o					
37	Acacia gerardii	M	G	G	G	G	f –			–			O^a			–		
59	Clematis orientalis[a]	M	–	+	–	H							X^a	O^a		f^a		
61	**Ziziphus spina-christi**	S	+	+	+	+	(o)(d)	– f	f –	– f^a	(x) –	– (x)	(x)(x)	– –	– x	X X	X x	x f
36	Plectranthus rugosus	N			+	+										o^a		
8	Leptadenia pyrotechnica	M	+	–		–		o									O O	X O
37	Crotalaria aegyptiaca	N	R*O	R*	R*	R*	o	o	o	o								o
85	**Asphodelus fistulosus**	I	+	+	+	+	O X	X X	o o	o o						f		X o
25	Physorrhynchus chamaerapistum	M	+	+	+	+	X O	X X	o		f	–		(b)	(d)			O
37	Argyrolobium roseum	M					o		o o									o
25	Diplotaxis harra	M			R	R	O		o									o
80	Tribulus spp.	M		+	R*	H	o	x x	o o	o			o^a					o
37	Astragalus spp.	N			R	H	ó	o	o	o o^a								o
	II 10 species Unrestricted Flowering																	
12	Heliotropium spp.	M	+	+			o x	X	O O	O	o o	o		o	o	o		
37	Tephrosia spp.	M	+	$+^j$	+	$+^j$	o o	x O	O O	x	x		o –	o	σ^b)o	o o	o	o o
24	Convolvulus spp.	N			O		o o	o	o			o			o			o
23	Euryops arabicus[a]	N					o^a σ^a	σ^a		o^a σ^a			σ^a	o^a		o^a σ^a		σ^a
77	Verbena officinalis[a]	N			$+^p$	$+^p$	o^a			o^a σ^a			σ^a					
37	Indigofera spp.	N	G	G			o o		o o	σ^a			o	o	o	o		
23	Pulcaria spp.	N					o	o	O O	o				o	(σ^b)			
50	Oxalis corniculata	N			A	A	σ^a						o o	o^a				o
23	Conyza stricta[a]	N	G	G			σ^a			σ^a						σ^a		
16	Dipterygium glaucum	M	+	+				x	o o				o		o			o
	III 4 species Extended Summer Flowering																	
8	Calotropis procera	M	+	–	+	–		O	O X	X o		o	x	o		o o		
21	Helianthemum lippii[a]	N				R*				σ^a σ^a				o^a		o^a		
61	Ziziphus sp. nov.	M	G	G	G	G				o^a o^a				o^a		f		
36	Teucrium mascatense	N			H					o^a			σ^a			σ^a		
	IV 15 species Extended Winter Flowering Winter																	
60	**Ochradenus sp. nov.**	I	+	+	? +	?	X x	o	x x	o		– –	f		–		o x	o x
3	Aerva javanica	N	+				o	o	o o						(σ^b)		x	o
36	Lavandula aff. subnuda	M			R*H*		o o	o	O					–		o	o	o
60	Ochradenus aucheri	M	G	G	G		o	o	x o	o					–		o	
37	Lotus spp.	N			R*	R*	o	o	o o						(σ^b)	o		
23	Launaea spinosa	N	G	G		G	o											o
80	Zygophyllum coccineum	M	G O	G	G	G	f	o		f								o
8	Periploca aphylla	M	+	–	+	–		O	X	o								x
34	Cometes surattensis	N	? +	?					o o							o		
36	Leucas inflata	M	+	+	R*H				O o	o o^a								x
36	Salvia aegyptiaca	N			R*	R*			o o	σ^a						σ^a		
36	Salvia macilenta	N			R*	R*			o o								o	
37	Taverniera glabra	M	+	+					X o						(σ^b)		o	
83	Chrysopogon aucheri	N	–	O	–				o									o
37	Indigofera oblongifolia	M	+	+					o	X o							o o	
	V 5 species Flowering Season Unknown																	
10	Berberis sp.	N			R*	R*												
53	Limonium spp.	N			R*	R*												
62	Cotoneaster sp.	N			R*	R*												
65	Salix spp.	N			R*	R*												
9	Avicennia marina	N			R*	R*												
		IMP	N	P	N	P	1	2	3	4	5	6	7	8	9	10	11	12
			Apis florea		Apis mellifera													

Total: 80 species

b. Gardens of the narrow, cultivated strip along the Bātina coast, irrigated from wells
c. Wild habitats, including mountains, wadis and plains

The total numbers of plant species used by honeybees (as determined from studies in Oman and the literature) that were recorded in flower, in each month, are given.

Separate figures are presented for (i) species at a flowering peak (FP) and those not at a flowering peak (NFP), ie species starting to flower, finishing flowering or flowering at a steady level over an extended period, (ii) species which were assessed to be S : Substantial, I : Intermediate, M : Minor and N : Negligible sources of forage. The different groupings of (i) and (ii) are apparent in the tables.

Cautionary comments on the interpretation of this table are given in Results and Discussion 3.1,p.345-347.

(a)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
	S I M N	S I M N	S I M N	S I M N	S I M N	S I M N	S I M N	S I M N	S I M N	S I M N	S I M N	S I M N
FP	1 2 5 0	1 2 9 2	1 3 9 1	2 2 6 2	1 1 0 0	0 2 1 0	0 2 4 0	0 0 1 0	0 0 0 0	1 0 0 0	1 1 3 0	0 1 3 0
NFP	0 2 13 11	0 2 14 15	1 1 13 17	0 1 16 14	1 2 12 3	0 4 15 10	0 4 14 7	0 4 9 6	1 1 5 1	0 2 13 5	0 1 9 6	1 3 8 7
FP+NFP	1 4 18 11	1 4 23 17	2 4 22 18	2 3 22 16	2 3 12 3	0 6 16 10	0 6 18 7	0 4 10 6	1 1 5 1	1 2 13 5	1 2 12 6	1 4 11 7
	5 + 29	5 + 40	6 + 40	5 + 38	5 + 15	6 + 26	6 + 25	4 + 16	2 + 6	3 + 18	3 + 18	5 + 18
TOTAL	34	45	46	43	20	32	31	20	8	21	21	23
FP	8	14	14	12	2	3	6	1	0	1	5	4
NFP	26	31	32	31	18	29	25	19	8	20	16	19

(b)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
FP	1 2 4 0	1 2 4 2	1 3 9 1	2 2 7 2	1 1 0 0	0 2 2 0	0 2 2 0	0 0 1 0	0 0 0 0	1 0 1 0	1 1 4 0	0 1 3 0
NFP	0 2 12 7	0 2 12 7	1 1 16 17	0 1 16 10	1 2 13 3	0 4 16 9	0 4 14 6	0 4 9 5	1 1 7 1	0 2 13 4	0 1 9 5	1 3 9 4
FP+NFP	1 4 16 7	1 4 16 9	2 4 25 18	2 3 23 12	2 3 13 3	0 6 18 9	0 6 16 6	0 4 10 5	1 1 7 1	1 2 14 4	1 2 13 5	1 4 12 4
	5 + 23	5 + 25	6 + 43	5 + 35	5 + 16	6 + 27	6 + 22	4 + 15	2 + 8	3 + 18	3 + 18	5 + 16
TOTAL	28	30	49	40	21	33	28	19	10	21	21	21
FP	7	9	14	13	2	4	4	1	0	2	6	4
NFP	21	21	35	27	19	29	24	18	10	19	15	17

(c)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
FP	0 2 2 0	0 2 7 0	0 0 11 6	2 0 5 3	1 0 0 0	0 0 0 0	0 0 2 0	0 0 1 0	0 0 0 0	1 0 0 0	1 0 1 0	0 1 2 0
NFP	0 1 11 18	0 1 9 12	1 3 9 17	0 2 11 15	1 0 4 1	0 0 2 2	0 0 4 6	0 0 4 5	1 0 3 2	0 0 4 9	0 1 5 2	1 1 12 8
FP+NFP	0 3 13 18	0 3 16 12	1 3 20 23	2 2 16 18	2 0 4 1	0 0 2 2	0 0 6 6	0 0 5 5	1 0 3 2	1 0 4 9	1 1 6 2	1 2 14 8
	3 + 31	3 + 28	4 + 43	4 + 34	2 + 5	0 + 4	0 + 12	0 + 10	1 + 5	1 + 13	2 + 8	3 + 22
TOTAL	34	31	47	38	7	4	12	10	6	14	10	25
FP	4	9	17	10	1	0	2	1	0	1	2	3
NFP	30	22	30	28	6	4	10	9	6	13	8	22

Table 7.5a Numbers of Substantial (S), Intermediate (I), Minor (M) and Negligible (N) sources of honeybee forage in each of 3 broad habitat types and overall, in northern Oman. Determined from the floral calendars presented in Tables 7.1-3. Some species occur in more than one habitat so the sums of individual totals do not equal the totals for "All Habitats"

HABITAT	NUMBER OF SPECIES				
	Importance as source of forage (category)				
	S	I	M	N	TOTALS
Interior Gardens	4	9	53	40	106
Bātina Gardens	4	9	45	30	88
Wild Habitats	3	3	27	42	75
All Habitats	4	12	85	88	189

Table 7.5b Numbers of Substantial (S), Intermediate (I), Minor (M) and Negligible (N) sources of honeybee forage in Oman, broken down according to their flowering pattern as classified in the floral calendars, Tables 7.1-3

FLOWERING PATTERN	NUMBER OF SPECIES				
	Importance as source of forage (category)				
	S	I	M	N	TOTALS
RESTRICTED	4	9	52	46	111
UNRESTRICTED	0	2	15	14	31
EXTENDED SUMMER	0	0	6	8	14
EXTENDED WINTER	0	1	10	9	20
UNKNOWN	0	0	2	11	13
TOTALS	4	12	85	88	189

2. Flowering phenology; its relationship with and importance to honeybees

2.1 Cultivated Areas

The flowering times of some cultivated annuals (possibly day-neutral species) used by honeybees appeared to depend on the sowing date, presumably chosen to best suit the growing requirements of the species. Thus white radish, *Raphanus sativus*, was grown as a winter crop and was seen in flower from December through till March, following various sowings in the autumn. Melons and water-melons were grown as summer crops and flowered in May, June and July. Perennial crops, both herbaceous ones such as lucerne flowering in the summer (April - July/ August) and trees such as mangoes (January - March) and limes, *Citrus aurantifolia* (January - March) flowering in spring, had their own regular rhythms. Some weeds flowered throughout the year as long as water was available (eg *Phyla nodiflora*, Verbenaceae), but some mainly in the warm and hot months (eg *Portulaca oleracea).* Other annuals must have had certain dormancy requirements and though their satisfactory growth must have depended on adequate rainfall, they germinated, grew and flowered only at particular times of year (eg *Melilotus indicus*, February - April). Temperature must also have had some effect; for instance, the last-mentioned species flowered a little later at high altitude (1900m) than at sea level (Table 7.1). Whether such intraspecific variations were genetic in nature, with different ecotypes existing, or due directly to environmental conditions was not known.

Florea, being quite abundant in the gardens, was probably amongst the major pollinators of some of these plants; but to what extent the flowering periods had co-evolved with the requirements of *florea* is not known, particularly with the knowledge of other pollinators in Oman being virtually zero. In a study of winter annuals in the USA, Parish & Bazzaz (1978) concluded that the separate flowering time of an introduced plant, and thus niche differentiation for the pollinators, was probably a pre-adaptation resulting from co-evolution with other species. Thus with introduced crops and weeds in Oman having evolved in other environments, the influence of both native pollinators, such as *florea*, and the blooming of indigenous plants on their flowering pattern, is probably small. With naturally wind-pollinated plants as the date palm is thought to be (Proctor & Yeo 1973), the short flowering period in February is probably timed so that the fruit can ripen in the hot summer and not for the benefit of honeybees, which nevertheless gathered copious pollen from the relatively few male trees.

There was no obvious difference between the flowering phenology of plants within the range of *jemenitica* in the Jabal al-Akhdār and those in other areas, so this introduced species too has probably had negligible influence on flowering patterns since its arrival c. 280 years previously (p. 11-13).

Studies of honeybee foraging strategy in a temperate, deciduous woodland in the USA (Visscher & Seeley 1982) suggested that foraging at a given time was focused on a few patches offering the best rewards. If applicable to *mellifera* and *florea* in Oman, there being a variety of flowering patterns exhibited and a floral succession, it is probable that both *Apis* species use whatever happen to be the most suitable floral resources available at the time. These will change from day to day and the honeybees should therefore be able to exploit to the full their colonial capability of rearing brood and storing food at almost any time of the year, providing other environmental conditions are not too extreme. This is in contrast to the strategy of many mono- or oligolectic solitary bees whose life cycle and short active period may be geared to the flowering of only one or a few plant species (eg Linsley *et al* 1955; Linsley 1958; Percival 1965; Hurd *et al* 1971 Heinrich 1975c; Moldenke 1976; Faegri & Van der Pijl 1979; Batra 1984).

2.2 Wild Habitats

i) Introduction and trees

The flowering times of wild plants are more likely to have co-evolved with the activities of indigenous pollinators than are the flowering times of plants in cultivated areas. However, with no systematic investigation of flower visitors in Oman, any conclusions drawn here must be tentative. Water availability and extreme summer temperatures must be the main physical factors ultimately determining the phenology of both plants and pollinators, and the effects of flowers and insects on each other are not obvious. Are pollinators limiting in this extreme environment and are plants therefore competing and adjusting their flowering patterns to attract the insects? Or do the plants call the tune and flower at a time best suited to climatic conditions because there is a surplus of insects which themselves are competing for limited nectar and pollen? Or does the real situation lie between the two?

A glance at Tables 7.3 and 7.4c shows that comparatively few plants are in flower during the summer (excluding those growing above 1600m), but in the cooler months some floral succession and not total overlap is evident. Consider the main tree species, whose flowering time can be relatively independent of rainfall (unlike ephemerals) as they have roots reaching towards the water table.

It can be seen that *Maerua crassifolia* flowers primarily in February, *Acacia ehrenbergiana* in March and the first part of April, *Prosopis cineraria* primarily during April and *Acacia tortilis* from about the first week of April till mid-May. Then the main flowering period of *Ziziphus spina-christi* is in October and into November. I have seen *Maerua crassifolia* and to a lesser extent *Acacia ehrenbergiana* attract large numbers of insects, including honeybees, when in full flower and it is probably a deliberate strategy (through natural selection) that their flowering only partly coincides with that of the much more abundant *Acacia tortilis*.

The flowering of *Acacia tortilis* in Oman does not coincide with its maximum leaf production (autumn), so the prominence of the blossoms and their pervasive fragrance must help to attract the pollinators which are probably in short supply when one considers the large populations of this tree that is dominant on the plains and mountainsides of much of northern Oman. The blooming episode is fairly short and intense, and at a time when temperatures may well be suited to insect activity, but does not extend long into the hot summer. It coincides with the maximum development of *florea* colonies (Chapter VI).

The temperature conditions in April - May are similar (see Appendix II) to those in October and the first part of November when the other tree that is so attractive to honeybees (and other insects) and provides the second major crop of honey, *Ziziphus spina-christi*, comes into flower. That the two major tree species flower at different times, thus avoiding competition for pollinators, and that they flower when temperature conditions are similar, is probably no coincidence.

The onset of flowering in these various tree species is probably triggered by photoperiod, though with some influence from water availability and temperature. The records on flowering of *Ziziphus spina-christi* indicated that in the dry years studied, the onset was more even and a little earlier in the Bātina gardens than in wild habitats. This was attributed to the effects of irrigation and the proximity of the water-table near the coast. Similarly, some of the data on *Acacia tortilis* suggested it started flowering a few days later in the mountains than on the Bātina plain, maybe because of differences in temperature, rainfall or the water-table. The flowering of *Acacia tortilis* was intensive and remarkably constant and it was not seen in flower outside April and May. That of the other tree species was a little more variable and extensive. Occasionally individual trees or groups of trees of the other species even flowered several months away from the usual time eg a *Ziziphus spina-christi* tree was seen in full flower in June and July at Khabura and *Acacia ehrenbergiana* in partial flower in the Sharqiya (eastern region) in December. Augspurger (1981) has shown that reduced pollination of asynchronously flowering specimens should lead to intense selection against such temporally isolated individuals. These selective pressures probably maintain the intraspecific blooming synchrony of these major trees in Oman and the exceptions are presumably the consequence of unusual local conditions.

Overall, the recorded flowering patterns of these tree species do suggest that interspecific competition to attract pollinators has been active in determining the observed floral succession and where there are many trees in bloom the insects, including honeybees, may not always be able to exploit all the nectar and pollen that is available. On the other hand, the paucity of pollinators cannot be so severe that flowering by some tree species has become necessary in the middle of the hot summer and in these months those insects, like the honeybees, that are still active may themselves be competing for scarce resources.

(ii) Shrubs

The flowering patterns of shrubs will have been determined by the same range of biotic and abiotic factors as trees, though where their roots do not penetrate so deeply or their water-retaining capacity is less, rainfall is likely to exert a greater influence on the exact timing, duration and intensity of flowering. Most shrubs flowered in the spring, a timing that must be well adapted to follow the period, winter, when rainfall is most frequent and heavy over much of northern Oman (Horn & Nielsen 1977a; Gallagher & Woodcock 1980) for instance, *Euphorbia larica, Jaubertia aucheri, Pteropyrum scoparium.* The flowering patterns of just a few shrubs such as *Tephrosia* spp. and *Calotropis procera* appeared to be less restricted, perhaps because water availability was greater in and near the cultivated areas where they were also recorded. The flowering patterns of a number of other shrubs, mostly in group (IV), the winter category, of Table 7.3 are worthy of further consideration as the data suggests "episodic" flowering as discussed by Bawa (1983) ie they display at least two discrete flowering and fruiting episodes per year. Thus plants, used or thought to be used by honeybees, such as *Ochradenus arabicus* sp. nov., *Lavandula subnuda* and *Leucas inflata* were seen flowering in autumn and again in spring with intervening periods when flowering was not recorded.

Unfortunately nearly all the records suggestive of episodic flowering were from different specimens and regions and continued observations on individual plants are required. The following records on one plant of *Ochradenus arabica* sp. nov. at Khabura suggest that the pattern might occur:-

18. xi.79 In full flower, many insect visitors including *florea* (09.15h)

26.xii.79 Still in flower, no honeybees (09.15h)

5. i.80 Flowers finishing, ants and Diptera but no *Apis* (10.00h)

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9.iii.80 Flowering again, many insect visitors including *florea* (c. 10.00h)

18.iii.80 Still flowering, many insect visitors including *florea* (c. 12.00h)

Therefore the shrub was flowering in November and December, stopped (presumably setting seed) and then flowered again in March. Whether this flowering pattern was just a response to 2 separate periods of rainfall (and/or irrigation water from nearby fields) or was the normal rhythm was not certain, but 2 flowering episodes in the previous year were indicated as the same plant was seen flowering in January 1979 and again had a few flowers and was starting to fruit in April. From November to the beginning of April various other *Ochradenus arabicus* sp. nov. specimens were seen in flower on the Bātina, but no individual was "followed" for all this period and it is possible that a proportion (not necessarily all) of the plants bloomed twice.

Does the same pattern occur in the other species such as *Lavandula subnuda*? Given that rainfall can be irregular, maybe the plants are capable of flowering at any time (and more than once) in the cooler months, but water is required to trigger this. Thus the plants would not flower in autumn unless there was rain then, and this perhaps was the case with those shrubs I recorded in flower in November and December.

Records on *Salsola baryosma* indicate rather irregular episodic flowering (see Table 7.2; it is a ruderal weed found in the deserted, saline areas of the Bātina gardens but best discussed here). It was seen in flower and being visited by *florea* between 24 March and 16 April 1979, but then no foraging on this particular patch was observed again until 13 June. The flowers on this succulent species were, however, very difficult to discern and it was just possible that the plants were still flowering in the latter half of April and May, but this was not noticed as the honeybees (which themselves had previously drawn my attention to the plants) were foraging on *Acacia tortilis* in preference. After the second bout of foraging in June and July there were no further records until *florea* were again seen visiting plants in the same patch in the latter part of November 1979. Were the specimens in flower on each occasion different individuals or the same plants, and was it water (rainfall or irrigation) that initiated the flowering or was it an internal mechanism?

An understanding of these processes is important if the forage available to honeybees is to be gauged from year to year. Closer field observations and experimental research are required, with careful attention to the behaviour of individual plants and periods of non-flowering as well as flowering by members of a population. This should help elucidate the natural blooming patterns and to distinguish between fixed flowering rhythms triggered by photoperiod, and thus plants available to honeybees every year, and those triggered by rainfall. Whatever the primary determining factors, the flowering of most shrubs in early spring before *Acacia tortilis* and secondarily in late autumn/winter after *Ziziphus spina-christi* must result in reduced competition between the plants for pollinators and a succession of forage for the polytropic honeybees.

(iii) Ephemerals

The growth and flowering of ephemerals (herbaceous perennials and especially annuals) was far more dependent on rainfall than was so for shrubs and trees. However, no data were available on the dormancy requirements of the various species, nor on the frequency and quantity of rainfall needed to stimulate their germination and development, nor on their response to rainfall at different times of year (but see comments on *Melilotus indicus* in Results 2.1). With rainfall usually highest in winter months in most areas of northern Oman, Table 7.3 shows that some ephemerals start flowering in December eg *Asphodelus fistulosus*, *Diplotaxis harra*, whereas others were not recorded till January eg *Zygophyllum simplex*, *Malva parviflora* or even March eg *Centaurea pseudosinaica* (incorrectly called *sinaica* on Table 7.3). Some species may take longer or need more rain to reach flowering than others, though tiny plants which were little more than seedlings were often seen flowering and setting seed after light rain. This was a clear adaptation to a desert environment with irregular rainfall, as other specimens of the same species grew into quite large plants if there was a good supply of water. Some of these ephemerals were seen in flower frequently over several months eg *Physorrhynchus chamaerapistum*, *Asphodelus fistulosus*, others only occasionally eg *Reichardia tingitana*, maybe because some respond to rainfall at any period during the winter, others at more restricted times determined by dormancy or photoperiod. Also, the rainfall may have been insufficient and/or distributed inadequately over certain months in the study years, for some of the species to have exhibited their full flowering range.

Thus honeybee forage from these ephemerals will show marked quantitative, spatial and temporal variation according to rainfall.

Asphodelus fistulosus appeared to be the most widespread, abundant and reliable source (it seemed to require relatively little rainfall), with *Physorrhynchus chamaerapistum* and *Zygophyllum simplex* also featuring well in the dry years concerned. It was interesting to note that much of the flowering of these ephemerals too did not overlap with that of *Acacia tortilis, Prosopis cineraria* and *Ziziphus spina-christi.* With pollinators perhaps limiting, the advantage of avoiding simultaneous flowering with ephemerals must have been an additional selective pressure determining the phenology of these tree species.

2.3 Overall flowering patterns of bee forage plants in Oman

Table 7.5b gives a summary. It can be seen that the majority of forage plants (111) flower for only a limited period each year and inspection of Tables 7.1 - 3 shows this is the case in all 3 habitat categories. The 31 species exhibiting unrestricted flowering and the few (14) showing extended summer flowering occurred mostly in gardens where irrigation must have made such patterns possible. Most (15) of the 20 extended winter flowering species occurred in wild habitats, reflecting equable temperatures and the prevalence of rainfall at this time of year in Oman. Of the 16 species in the "Substantial" or "Intermediate" forage importance categories, 13 exhibited restricted flowering. This highlights the seasonal character of the Omani bee flora and that bee-keepers should pay attention to the location and phenology of this flora in order to site their colonies and time their management operations appropriately. Details of this seasonality are considered in the next section.

3. Annual cycle of forage for *Apis florea*

3.1 Cultivated habitats

The Bātina gardens irrigated by well and the interior ones irrigated by "falaj" will be treated together because of their floristic similarities, but the differences between them in species composition and especially abundance of vegetation, as discussed in Results 1.2, should be borne in mind. Tables 7.4a and b summarize Tables 7.1 and 7.2 indicating the total numbers of species considered to be honeybee plants that were flowering in each month. Sub-totals are also given of the numbers of Substantial, Intermediate, Minor and Negligible sources and of numbers in peak flower. These results should be compared with those in Chapter VI on the annual cycle of brood rearing, honey storage and so on, especially Figures 6.1 - 6.5; these figures (Chapter VI) represented all colonies, irrespective of habitat, but the majority came from gardens. However, it must be stressed that the figures in Table 7.4 must only be taken as an incomplete guide to the availability of forage throughout the year, for the following reasons in particular:-

(i) Some of the plants included, I have not positively recorded as being used by *florea* in Oman, the information coming from the literature, Omani and other sources.

(ii) Some species actually used by honeybees in Oman will have been missed. In fact, it was decided to omit from the tables a number of species that occurred in Oman, even though they or closely related species were recorded in the literature as being used by honeybees; this was done because the plants appeared to be particularly scarce or because their flowering status or insect visitors were poorly known. For instance *Scirpus maritimus* (Rahman 1945), *Fumaria parviflora* and *Boerhavia diffusa* (Latif *et al* 1958), *Solanum melongena* (Batra 1967), *Abelmoschus esculentus* and *Lycopersicon esculentum* (Choudhury *et al* 1973), *Opuntia* sp. (Papadopoulo 1973), *Campanula* sp., *Ephedra* sp., *Olea* sp., *Polygala* sp., *Rhus* sp. (Oustuani 1976), *Corchorus olitorius* (Free & Williams 1977), *Capparis* sp. (Gadbin 1980). It was thought that other plants too were potentially sources of forage eg *Blumea* spp., *Cleome* spp., *Galium* spp., *Sonchus maritimus*, but no foraging or pollen records were obtained.

(iii) Though the main flowering periods have been well-covered for the more common species, some of the months in which the scarcer species and those not originally recognized as bee plants did flower, will have been missed. Some of the totals will therefore be underestimates.

(iv) The monthly totals do not reflect the finer changes in the numbers of flowers available. The numbers can change day by day, not just ½ month by ½ month as indicated in Tables 7.1 - 3, and will vary from year to year and according to region, weather, altitude, grazing pressure, cultivation practices and so on. Bee-keepers must judge these finer details for themselves when timing management operations.

(v) The overall assessment of the importance of each species as a source of forage in Oman may be applicable in one area or just one garden, but not in another. For instance, *Vicia faba* potentially can provide large crops (50 - 100kg/ha) of honey (Crane 1975b) but was not widely grown in Oman so overall was considered to be only a minor source of forage. It was completely unavailable in many areas, but where crops of it were grown it could constitute a significant proportion of the incoming forage for a period (eg at Rustaq for both *florea* and *mellifera* in February 1979; Chapter V and unpublished data).

The same was true for fenugreek, *Trigonella foenum-graecum*, which was used by *florea* for nectar and pollen but was only grown on a small scale in winter. Lucerne, *Medicago sativa*, on the other hand was grown in most areas of northern Oman; potentially it too was a substantial source of forage to both *Apis* spp. in the summer but probably reached this status only where the crop was grown for seed. It was usually cut before or as it came into flower, thus providing some forage but not its full potential; it was therefore assessed as an Intermediate source, though its value would differ from garden to garden depending on the cutting regime and the farmer's requirements for seed. Other plants may not have been particularly favoured sources of forage, possibly *Calotropis procera* which produces nectar but not normal pollen (only "sticky" pollinia which it appeared were not consumed) and grasses such as *Cynodon dactylon* that produce some pollen but no nectar. At places and times when other forage was abundant they were probably avoided, but were not put in the "Negligible" category because they were widespread and sometimes available when other forage was scarce ie in the summer. Thus overall they were considered to be valuable minor sources.

(vi) Recording effort was not exactly the same in each month (p.319).

Table 7.4a and b shows that the number of species, useful to honeybees, coming into flower starts to increase in January, rising to a maximum number in March (49 species, Bātina; 46, Interior). Citrus trees, mainly limes, probably constituted the single most valuable cultivated source in this spring period, supplemented by other crops (fenugreek, radish, mangoes, onions, male date-palms) and numerous herbs and weeds. Some of the latter flowered intermittently for much of the year, but possibly rather more at this time eg *Ocimum* *basilicum*, *Phyla nodiflora*, *Launaea* spp., *Vernonia cinerea*. Others flowered primarily at this time eg *Sonchus oleraceus*, *Melilotus indicus*, *Ammi majus*.

This maximum corresponds well with the spring increase in brood rearing by *Apis florea* (Figure 6.1a) but Figures 6.4a and b show that usually little honey or pollen is stored at this time. The supplies from these abundant flowers must therefore be devoted mainly to colony growth; the sources of forage may not often be sufficiently plentiful to allow both rapid development and the provision of a surplus honey crop.

Though some species were recorded as coming into flower for the first time in April, eg *Pimpinella* sp., *Acacia tortilis*, *Azadirachta indica*, *Medicago sativa*, and in May, eg *Cucumis melo*, *Lawsonia inermis* (henna) and *Vigna unguiculata* (cowpea), the total number of species in flower started dropping, particularly between April and May, with many of the crops (*Citrus* spp., mangoes, radish, date-palms) and weeds setting fruit. Nevertheless it is during this period that brood rearing (Figure 6.1a), adult drone production (Figure 6.2b), queen-rearing and swarming (Figure 6.3a), pollen storage (Figure 6.4a) and honey storage (Figure 6.4b) by *florea* colonies reach their peak.

This developmental peak and honey flow coincides with and is primarily attributable to the blooming of *Acacia tortilis* and *Prosopis cineraria*; the former is most abundant outside cultivated areas but it was apparent that adequate numbers of both species grew within foraging range of most oases and Bātina gardens, and inside them, to explain the peak. Other species to a lesser extent must have contributed to the honey flow; pollen analysis of the honey would be needed to confirm absolutely that *Acacia tortilis* and secondarily *Prosopis cineraria* were in fact the main sources, but investigations of the pollen in *florea* combs and on returning *florea* and *mellifera* foragers (and their crop contents) eg at Khabura in May (Chapter V, p. 216-7) strongly suggested this was so. However, the honey flow would certainly not have been so great without the earlier abundance of flowers that allowed colony populations to reach satisfactory strength in sufficient time to exploit the *Acacia tortilis* and *Prosopis cineraria* fully.

The numbers of honeybee plants (species) recorded in flower increased again somewhat in June, but not to the levels of March and April. This may partly have been due to a relative up-turn in flowering by some plants that could flower throughout the year plus the summer flowering of long-day plants; thus crops such as *Medicago sativa*, *Cucumis melo* (melon), *Citrullus lanatus* (water-melon), *Pennisetum* spp., *Musa* spp. and the sticky exudate of ripening dates were particularly important at this time. These species are probably the primary constituents of the "qaydh" honey that is sometimes harvested at this hottest period of the year (Dutton & Simpson 1977), but which was not much in evidence in 1978, 1979 or 1980.

However, the apparent increase, in species recorded flowering, from May to June may partly have stemmed from 2 other causes, (i) rather less fieldwork in May and (ii) attraction of *florea* workers to the flowers of *Acacia tortilis* away from minor sources (such as *Calotropis procera* and *Cynodon dactylon*) which therefore cropped up less frequently in pollen samples and caused me to ignore these species even though they may have been in flower. Therefore, the number of species in flower in May has probably been a little underestimated and any increase from May to June exaggerated.

As the summer continues from June into September, the number of honeybee plants in flower declines to its lowest level; furthermore, none of the species were considered to be at a flowering peak and the numbers of species that were considered to be "Substantial" and "Intermediate" sources were at a minimum. The colonies must have been subsisting on any stores of honey and pollen remaining and a few 'Minor" and "Negligible" sources such as *Ocimum basilicum* and *Portulaca oleracea.* Nevertheless, in these hot months, despite the scarcity of forage, the reduction in the proportion of colonies rearing brood was not as great as in the winter (Figure 6.1a).

However, at the end of September, mainly in October and also in November, depending on local conditions, *Ziziphus spina-christi* flowered. A small to medium-sized tree that was frequent in gardens, as well as abundant in wadis, it produced a mass of flowers in these months that provided pollen and particularly nectar in considerable quantities. The September trough in numbers of species flowering may have been a little exaggerated as a result of inadequate field observations, but as it became cooler in October and November the number of forage species flowering did seem to pick up a little and included *Ipomoea pes-caprae, Cyperus rotunda, Cynodon dactylon* and *Aerva javanica.* *Acacia nilotica* had a rather patchy distribution but flowered primarily in this period; in localities where it was abundant it probably made a significant contribution to the development of *florea* colonies and to any surplus honey crop. Apart from this tree, however, the other sources of forage were unimportant in comparison to *Ziziphus spina-christi.*

As the development of *florea* colonies in the autumn depended primarily on this one species, which was probably only in flower for about one month at any single locality, it was not surprising that queen cell production and swarming was achieved by a smaller proportion of colonies than in April/May (Figure 6.3b) when the *Acacia tortilis* flowering of similar or even shorter duration, was preceded by the blooming of many spring flowers. Nevertheless it was evident, without recourse to pollen analysis, that *Ziziphus spina-christi* was an excellent source of forage that enabled colonies of *florea* to gather in a short time a surplus of light coloured honey that was popular with the Omanis.

During and following the *Ziziphus spina-christi* honey flow, in November and December, 3 other species of small tree used by *florea* came into bloom, *Sesbania sesban, Tecoma stans* and *Pithecellobium dulce*. *Sesbania* was quite widespread in some of the gardens, the leaves being used as animal fodder, but *Tecoma* and *Pithecellobium* were recently introduced ornamental/shade plants and localized in distribution. None appeared to be particularly good sources of pollen (the papilionaceous flowers of *Sesbania* seemed to be too large for *florea* to trip). In addition various weeds were available eg *Euphorbia heterophylla, Phyla nodiflora, Vernonia cinerea, Launaea procumbens, Conyza dioscorides,* and radish *Raphanus sativus* was coming into flower. However, these sources cannot have been sufficient to prevent the reduction and cessation of brood rearing that was recorded (Chapter VI, C 1.2) in various colonies, especially the smaller ones, during this relatively cold period (December - beginning of January). However, with the increases in temperature and number of species flowering in the new year, brood rearing started to pick up again at the end of January/beginning of February.

3.2 Wild Habitats

The data in Table 7.4c on numbers of honeybee plants flowering in each month in wild habitats, for the same reasons as outlined at the beginning of the previous section (3.1) is only a guide to the annual cycle of forage availability. One further reason of particular significance to these areas away from cultivation and irrigation is the variability in the timing and amount of rainfall; as a result the bee forage from ephemerals especially, but also from perennials, will vary from one locality to another and from year to year. Having been gathered over 2 - 3 years the data probably represents the broad pattern of seasonal variation, but not the extremes which can occur in some years.

34 plant species used by honeybees, the 3rd highest monthly total, were recorded in flower in January, but only 4 of these (*Asphodelus fistulosus*, *Physorrhynchus chamaerapistum*, *Diplotaxis harra* and *Ochradenus arabicus* sp. nov.) were registered at a flowering peak. There was a slight drop in the total, probably of no significance, in February to 31 species, but 9 of these were at a flowering peak, notably *Maerua crassifolia* and *Euphorbia larica*. However, March was the month with both the total number of species in flower at a maximum (47) and with the greatest number of species at a flowering peak (17). The totals in all 3 months comprise both perennials and annuals/ephemerals; however, the perennials were more in evidence in March than they were in January and February (eg *Grantia aucheri*, *Pteropyrum scoparium*, *Vernonia arabica*, *Leucas inflata*), while many annuals figured in all 3 months (eg *Zygophyllum simplex*, *Reseda aucheri*, *Asphodelus fistulosus*, *Astragalus* spp., *Tribulus* spp.).

The total number of species in flower and the numbers of those at a flowering peak drop from March to April, but *Acacia tortilis* and *Prosopis cineraria* became the major sources of forage. A further drop to only 7 honeybee species in flower in May is particularly dramatic and though probably exaggerated by reduced fieldwork and the dry years concerned, was real enough and emphasizes the impact of high summer temperatures. Thus once the *Acacia tortilis* had finished flowering, the forage available through the summer till the end of September at lower altitude in wild habitats was almost non-existent; however, above 1500m a few species did flower in the summer eg *Acacia gerardii*, *Clematis orientalis*, *Tribulus* sp., *Euryops arabicus* that were known or thought to be used by *florea*. In October and November the numbers picked up a little with some shrubs coming into flower eg *Leptadenia pyrotechnica*, *Lavandula subnuda*, *Taverniera glabra*, *Ochradenus arabica* sp. nov., but several of the species potentially providing forage such as *Plectranthus rugosus*, *Helianthemum lippii*, *Teucrium mascatense*, *Salvia aegyptiaca* were found primarily at higher altitudes out of range of nearly all colonies of *florea*. As in the cultivated areas, the only source of major significance at this time was *Ziziphus spina-christi*.

In December, the influence of early winter rains was evident as the total number of species, useful to honeybees, in flower jumped from 10 to 25, including both annuals eg *Asphodelus fistulosus*, *Argyrolobium roseum*, *Diplotaxis harra* and shrubs/shrublets eg *Launaea spinosa*, *Zygophyllum coccineum*, *Periploca aphylla* and *Leucas inflata*. This flourish at the end of the year continued into spring with the numbers increasing in January and rising again to their March peak.

The information on the annual cycle of *florea* colonies in Chapter VI was based mainly on colonies found in cultivated/irrigated areas and relatively few colonies in wild habitats. The broad pattern of colony build-up in spring, surplus honey from *Acacia tortilis* in April/May, summer dearth and so on appeared to be similar for the honeybees in the 3 habitat categories, but some differences were evident. For instance, it was interesting to note that the only colony seen to have adult drones in February was one in hills above Birkat-al-Mawz. Similarly, a colony in hills to the side of the Wadi Hawasina was probably the strongest of any seen at the end of December, with the whole lower comb being used for rearing worker brood; had its honey not been removed, leading to its absconding, I considered that it too would have reared adult drones by February. In contrast, in gardens at Khabura, brood rearing at the end of December had totally ceased in some small colonies (eg KA b, Table 6.3) and even in large ones (eg FD, Table 6.3).

Thus the winter blooming period, in localities and years with sufficient rainfall, seemed to start earlier in these wild habitats than in the cultivated areas, before the New Year (approximately) as opposed to the end of January, which was the time when crops such as *Citrus* and mango became available. This earlier supply of forage, coupled with more exposed nest sites that provide a warmer microclimate (Chapter II), may therefore be responsible for increased brood rearing activity in wild habitats at this time of year. In wet years Omani keepers/hunters of *florea* claimed a crop of honey could be obtained from these wild flowers and they, including *Maerua crassifolia* (local name "sarḥ"), would be responsible for the winter "sarah" honey that Humayd Sulayman described to Dutton & Simpson (1977). These observations support Nāsr Ahmad al-Ghaythi's practice of keeping his bees at the wadi/plains apiary away from his garden at this time of year (Chapter IV).

Even more than for colonies in date gardens, *Acacia tortilis* and, where present, *Prosopis cineraria* must provide the main honey crop in April-May for colonies in wild habitats, though the minor constituents and sources responsible for prior colony growth would be different. Pollen analysis of honey would probably indicate species such as *Euphorbia larica, Pteropyrum scoparium, Jaubertia aucheri,* where abundant on mountain slopes and wadi beds, and plants such as *Tephrosia* spp., *Dipterygium glaucum, Ochradenus* spp., *Asphodelus fistulosus* and *Zygophyllum* spp. would be more prominent in samples from the outwash plains away from the mountains.

However, once the *Acacia tortilis* blossom is over, with the dearth of summer forage in wild habitats, there is no chance of a further honey crop, like the "qaydh" of cultivated areas (p. 349) until the *Ziziphus spina-christi* flowers in the autumn. This dearth of forage was probably an extra cause of the absconding, hot nest micro-climate being the major one, by colonies in caves in the Wadi Hawasina (Chapter II, 6.6) and which was also apparent in hived colonies during this period (Chapter VI, Results 2.1). However, absconding for this reason would be of little value unless to a site that provides rather more forage at this time of year, such as an oasis, and colonies that have sufficient stores of honey and pollen from the *Acacia tortilis* flow to last the rest of the summer presumably stay if in a suitable nest site.

Furthermore, with only 10 species in the "all year" flowering category (II) (as opposed to 19 and 16 respectively in the Interior and Bātina gardens) and 3 of these occurring only at high altitude, and just 4 in the "summer" flowering category (III) (8 and 10 species respectively in the Interior and Bātina gardens) with 3 of these restricted to higher altitudes, colonies in wild habitats will have little forage on which to build up strength prior to the *Ziziphus spina-christi* honey flow. Therefore, in general one would not expect the honey yields from this species to be quite as high in wild habitats as in the irrigated areas with their relative abundance of all year and summer flowering weeds and crops. Nevertheless large colonies, whose stores and brood rearing activities have not been completely reduced during the summer, and colonies in areas where the flowering of *Ziziphus spina-christi* trees is extended and other natural vegetation is particularly abundant, should be able to develop rapidly enough to store honey and even swarm before the flow has finished. Further investigations are needed to elucidate such details.

4. Sources of forage for *Apis mellifera* and differences from *Apis florea*

4.1 Mortality and honey yields in dry periods

Detailed investigations of the annual cycle of *mellifera* and its sources of forage were beyond the scope of this thesis. However, from my own experience in Oman with colonies of *mellifera* kept in Langstroth hives (both introduced *mellifera* from Australia and indigenous *jemenitica*) and from discussions with Omanis who kept colonies in "tubūl" (hollow date-logs), it was evident that peaks of development for this species too coincided with the flowering of *Acacia tortilis* in April and May and *Ziziphus spina-christi* in October and November and that these trees contributed very significantly to surplus stores of honey. However, it was also apparent, again from observations on the project's colonies, on those of Omanis and from their comments, that in dry years many colonies of *florea* would survive, even after the set-back associated with gathering them from the wild, and produce harvestable quantities of honey. In contrast, many colonies of *mellifera* died out and many of those surviving produced virtually no honey.

For instance, at Misfah near Al Hamra on the southern flank of the Jabal al-Akhdār, Ali Mas'ood had c. 70 "tubūl". In December 1977, 19 out of a block of 22 looked at were occupied, ie 86%. In July 1980, only 8 out of 42 looked at were occupied, ie 19%. (Out of the total c. 70 "tubūl" I had seen workers at the entrance of 13 and assumed the colonies were active, but Mas'ood said only 10 were "alive"; maybe some colonies were queenless or so weak that he did not include them.) Whatever the exact figures, the population of *jemenitica* had crashed here and from an inspection of one colony, those surviving had virtually no honey stores; a number of excursions to other apiaries indicated the situation was the same elsewhere in the Jabal al-Akhdār region.

It was difficult to assess overall population changes for *florea* because their natural nest sites were dispersed and they were rarely kept together in apiaries. The impression gained from keepers and hunters of *florea* was that their numbers had dropped a little in this period too, but not to the same extent as *jemenitica*, and that those colonies remaining could still yield a little surplus honey. For instance, Nāsr Ahmad al-Ghaythi, taking into account seasonal variation, had similar numbers of colonies and also worthwhile honey yields in 1978, 1979 and 1980 (Chapter IV). Then, in the above-mentioned village of Misfah there was another bee-keeper, Said Ali Āmr, who kept both *florea* and *jemenitica*. In July 1980 he had 10 colonies of Little Bees which, from the amount for which he told me it had been sold, I estimated had yielded 5-6kg of honey between them (a mean of just over 0.5kg each); a small but satisfactory harvest. I inspected 3 of the colonies and they were in a reasonable condition for the time of year. However, the state of Said's *jemenitica* was just as bad as those of Ali Mas'ood, with only approximately 20% of his "tubūl" occupied, and he had harvested no honey from them that year.

Both bee-keepers thought the use of insecticides had been responsible for initial mortality in their colonies, but we considered it was the drought over the previous 2 years which had become the main cause of their demise. In normal years one *mellifera* "tubūl" may yield 2-3kg of honey (Dutton & Free 1979). An isolated colony (*jemenitica* x Australian hybrid) in a Langstroth hive in a stretch of the Wadi Tifli (off the Wadi Hawasina) with abundant *Acacia tortilis* yielded c. 20kg overall in the early summer of 1980 and a colony (of Australian origin) at Khabura yielded 9.5kg at the beginning of August 1980 (most probably came from lucerne, bananas and "rutab", maybe with some *Acacia tortilis* gathered earlier, so could be called "qaydh" honey - see p. 349).

So at times and localities with abundant forage, colonies of *mellifera* in Oman can thrive, but when forage is poor their condition deteriorates. It seems they cannot exploit forage when it is scarce as successfully as *florea*. The problem of scarce forage for *mellifera* is undoubtedly exacerbated by gross overstocking in many areas of the Jabal al-Akhdār where apiaries may contain 300-400 colonies (Dutton *et al* 1981), but more fundamental differences in the foraging patterns of the two *Apis* spp. may provide a further explanation. These are considered below.

4.2 Patterns of forage utilization

Though a significant amount of work was undertaken in Rustaq and other regions of the Jabal al-Akhdār where *jemenitica* was found (Figure 1.1) and observations on the foraging of introduced *mellifera* were made on the Bātina coast and pollen samples from both regions analysed, a greater amount of time and effort was devoted to determining the forage of the more widely distributed *florea*. This is thought to be the primary reason why the number of plant species, according to records from Oman, determined to be sources of forage for *florea* was much greater than the number of sources determined for *Apis mellifera* (Table 7.6). The number of forage species recorded for *florea* is approximately double that recorded for *mellifera*, whatever the habitat category.

Table 7.6 Numbers of species of forage in Oman for *Apis florea* and *Apis mellifera*, in 3 habitat categories, as determined (a) by observations in and pollen samples from Oman and (b) by adding records, in the literature, from other countries

	(a) Oman Records		(b) All Records	
	florea	*mellifera*	*florea*	*mellifera*
Interior Gardens	61	28	78	101
Bātina Coast Gardens	56	26	70	81
Wild Habitats	27	16	43	57

However, when records from the literature are added, the number of species known to be used by *florea* rises relatively little (eg from 56 to 70 of the plants in the Bātina gardens habitat) but substantially for *mellifera* (eg from 26 to 81 in the Bātina gardens) and above the totals for *florea*. The literature on sources of forage for *florea* is very poor but that on *mellifera* quite rich (though less so for Asia, which is why some records on the similar-sized *cerana* have been incorporated). Bearing this in mind, the numbers given for *florea* are probably slight underestimates and in reality I guess that the totals in Oman for the 2 species of honeybee are approximately equal and by and large they are capable of exploiting the same species of plant.

Indeed all the species categorized as "Substantial" and "Intermediate" sources of forage could definitely be used by both.

Though not measured for Omani specimens (samples of workers and drones were sent to Professor F. Ruttner, Institut für Bienenkunde, Oberursel, GFR, for morphometric analysis*) the tongue-lengths of Indian *florea* workers, 3.27 - 3.44mm (Narayanan *et al* 1960) are shorter than those recorded for *mellifera:* only 5.44mm for *jemenitica*, the smallest described race (Dutton *et al* 1981), but the tongue-length can be as long as 7.2mm in *A.m. caucasica* (Ruttner 1975). The short tongue-length of *florea* workers must completely exclude them from a small proportion of the flowers, with long and narrow corollas, whose nectaries can be reached by the longer-tongued *mellifera*, in the way that short-tongued races of *mellifera* cannot work red clover while the long-tongued races can (Ruttner 1975).

In fact the subject of the relationship between tongue-length of insects, particularly Apoidea, and the corolla/nectary-depth of the flowers they visit has been the subject of considerable research (for instance, Taniguchi 1954; Brian 1957; Heinrich 1976a; Inouye 1977; Corbet 1978; Morse 1978; Ranta & Lundberg 1980 and 1981b; Pleasants 1983; Ranta 1983). The flower preferences of bumblebees have indicated that there is some foraging niche separation associated with tongue-length (Brian 1957; Heinrich 1976a), but studies have also demonstrated that the food niches of bumblebee species show a wide overlap and that species with a long proboscis could use flowers with short corolla tubes while the reverse was rare (Ranta & Lundberg 1980). Morse (1978) has shown that larger workers of *Bombus vagans* with longer tongues concentrated their foraging upon deeper florets of *Vicia cracca* while the smaller, shorter-tongued individuals concentrated on the smaller florets. Ranta & Lundberg's (1980) hypothesis, based on

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* Measurements communicated to me just prior to submission of thesis: Oman *florea* proboscis length 3.31 - 3.39mm.

an analysis of published data and Ranta's (1983) observations, that foraging efficiency is maximal when the proboscis length of a species corresponds to the corolla-tube depth of the flower visited, are convincing and should also be applicable to species of *Apis*. Thus *florea* and *mellifera* probably do have some preferences associated with their tongue-lengths for particular plant species in Oman. However, when the nectar rewards from the favoured plants are low or they are not flowering at all, these polytropic honeybees must revert to the exploitation of other plant species to which they are structurally less well-suited.

Thus the plant species which *florea* and *mellifera* are capable of exploiting in Oman, with certain exceptions, are probably much the same. However, the energetics of the situation may mean that, in a country where the density of many forage species is low, at a certain season or on a particular day, the patterns of exploitation by the two species may be rather different.

There have been numerous investigations and discussions concerning various pollinating animals such as hummingbirds, hawk-moths, honeybees and particularly bumblebees in a range of habitats and climatic regimes and of their foraging behaviour, energetics and patterns of utilization of plants with different rewards, structure, spacing, competitors and so on (eg Baker & Hurd 1968; Heinrich 1975a and c, 1976a, 1979a, 1981d; Morse, D. 1977 and 1978; Rust 1977; Stiles 1977; Bolten & Fensinger 1978; Ranta & Lundberg 1981b; Waddington *et al* 1981; Wells *et al* 1981; Zimmerman 1981a and b; Best & Bierzychudek 1982; Tepedino & Parker 1982; Baker & Baker 1983; Kevan & Baker 1983; and further references are given in these publications). Though the flexible foraging behaviour of the insects does not always follow that predicted by models of optimal foraging (Zimmerman 1981a), which may be too simple to cope with all the variables involved, it is evident from these studies that energetic considerations can be important in explaining patterns of flower visitation that cannot be attributed to flower-structure and tongue-length alone. I therefore speculate that the apparent differences between *florea* and *mellifera* in the number of plant species they utilized in Oman and in their ability to cope with dry years, as outlined in 4.1 above, can partly be interpreted on the basis of foraging energetics.

Having a smaller body size and crop, *florea* workers almost certainly need less nectar and/or pollen to obtain a full load on a foraging trip than do *mellifera* workers. In a temperate deciduous forest it has been shown that *mellifera* concentrate their foraging on just a few flower patches offering the best rewards, a mean of 9.7 patches accounting for 90% of each day's forage, and during times of poor forage many foragers remained inside the nest "conserving their flight energy and the energetic capital they themselves represent" (Visscher & Seeley 1982). So in Oman, *mellifera* may not exploit either small patches of forage, in which each flower offers a substantial reward, or larger patches with each flower yielding only a small reward; the smaller *florea* may be able to exploit both sources economically.

Some incidental, unquantified observations that I made on *florea* foragers visiting lucerne at Khabura in June/July of 1979 and 1980 I believe illustrate this principle. Amongst the other flower visitors were carpenter (*Xylocopa* sp.) and anthophorid bees *Amegilla crocea* Klug (det. D.B. Baker), considerably larger than *florea* and the *Xylocopa* sp. especially could "trip" the lucerne flowers with little difficulty. Sometimes *florea* were observed to trip the flowers, but a substantial proportion of workers just collected nectar, by sliding/forcing their tongue down by the side of the wing petals. Of significance was the fact that still other foragers of *florea* did collect pollen, but mainly from flowers that had already been tripped, most presumably by the larger insects, though a few possibly by plant movement in the wind. The *Xylocopa* sp. moved very quickly between flowers collecting both nectar and pollen. It cannot have been worth this large insect's time and energy to glean all the resources from each flower; instead it must have been profitable for it to move on and "cream off" the best of the crop from the next flower. Yet the quantity of nectar and pollen left behind was presumably sufficient for profitable collection by the smaller *florea* workers. Adey (1984) also reports such behaviour, including *mellifera* gleaning pollen from stamens of *Cytisus baeticus* (Leguminosae) previously tripped by a larger bumblebee.

Therefore, though under-recording may be a major explanation for the number of forage species recorded for *mellifera* in Oman being smaller than that for *florea*, it is also likely that at any one locality and time, *mellifera* may be exploiting fewer patches and species of forage than *florea*. This may explain why I recorded *florea*, but not *mellifera* though they were present in the area, using species such as *Sonchus oleraceus*, *Euphorbia helioscopia*, *Maerua crassifolia* and *Allium cepa* when only a few plants were available. Similarly, *florea* but no *mellifera* on plants which, though abundant in places, probably offered only small rewards eg *Vigna unguiculata* (extra-floral nectaries), *Cynodon dactylon* (pollen only). Comparative recordings on the foraging of *florea* and *mellifera*,like those of Visscher & Seeley (1982) or more simply determination of the number of different pollen types gathered by each colony on various days at several localities, would confirm or reject this hypothesis.

In contrast to the differences between *florea* and *mellifera* in Oman, analysis of the pollen in a few honeycombs of *florea* and *cerana* from Ceylon, showed that the mean number of pollen species present for each *Apis* sp. was approximately the same, 13 and 14 pollen types respectively (Koeniger & Vorwohl 1979). However, according to Sakagami (1959) introduced *mellifera* in Japan had a tendency to concentrate their foraging effort on a major nectar source, while similar-sized *cerana* tended to forage on numerous minor sources, as *florea* appears to in Oman for much of the year. Maybe different species, or even different races of the one species, have evolved different foraging strategies appropriate to their native flora and thus worker-size and tongue-length may only be one of the factors determining energy-efficient exploitation of floral resources and thus the number of species used in a country or region. Whatever the detailed foraging patterns and strategies for each *Apis* species prove to be in Oman, at the densities at which they exist, the consequences appear to be that colonies of *mellifera* fluctuate considerably in numbers and strength according to forage availability (determined by rainfall) but can produce relatively large yields of honey, while the productivity of colonies of *florea* tends to be more consistent from year to year.

D. CONCLUSION

This part of the study was mainly a practical exercise to identify from scratch the various sources of honeybee forage that occurred in Oman; thus an overall picture of the annual cycle of resource use by *florea*, and to a lesser extent by *mellifera*, has been obtained. Some conclusions can be drawn about the foraging strategies of the 2 species from the patterns observed, but they must remain speculative until the next phase of research has been undertaken, namely detailed investigations on the phenology, energetics and ecology of Omani plant-pollinator interactions in more limited areas like those of Heinrich (1975b, 1976a and b, 1979a), Moldenke (1976), Corbet (1978), Heithaus (1979a), Ranta (1981, 1983), Bauer (1982), Visscher & Seeley (1982), Pleasants (1983) and Thomas (1983).

In wild habitats it was during the cooler period of the year (mid-November to March) that most of the herbs and shrubs, which were negligible, minor and intermediate sources of honeybee forage, came into flower. There was considerable overlap in the flowering times of some of the plants, but a degree of floral succession was also evident. This pattern was probably mutually beneficial to both plants and insects with enough forage being provided to stimulate and maintain insect activity and reproduction (and therefore pollination), but maybe not so much overlap in flowering that there was intense competition for pollinators.

However, the blooming periods of the two most abundant trees, *Acacia tortilis* (April - May), *Ziziphus spina-christi* (end of September - beginning of November), were completely separate from each other and to a considerable extent from the winter-spring flowering period of most shrubs and herbs. Had these two species of tree flowered simultaneously I am certain there would have been detrimentally intense competition between them for pollinators, including honeybees. Furthermore, though insects such as honeybees would have thrived for a month or two in such a situation, their growth in numbers would not have been sufficiently quick for them to have exploited fully the temporary abundance of nectar and pollen and they would then be left devoid of any other <u>major</u> source of forage till the same time the following year; their numbers would decline and their survival might even be in doubt (at further disadvantage to the trees requiring pollination too). Therefore, having the flowering of these 2 dominant tree species at almost diametrically opposite times of year, which do not overlap with the main flowering periods of other shrubs and herbs, should be selectively advantageous to both the honeybees and plant species concerned.

Thus, though flowering in the middle of the summer has been avoided by most wild species in lowland northern Oman, either directly or indirectly because of the climatic stresses, it would appear that the phenology of flowering in the autumn, winter and spring has co-evolved with the requirements of pollinators, including honeybees. Bawa (1983) discusses how flowering times of plants can be influenced by pollinators, but what role honeybees have played in Oman and what role other pollinators, is not known.

Other than the few "intermediate" and "substantial" species of forage, it appeared that the honeybees in both wild habitats and gardens had to depend on a large number of "negligible" and "minor" sources (Table 7.5a). When these are abundant in wet years, both *mellifera* and *florea* probably thrive and prosper, but in dry years I speculate that the diminished resources are not sufficient for *mellifera* to exploit economically and many may often remain inactive in their nests (Visscher & Seeley 1982) and their numbers dwindle, while the smaller *florea* can maintain themselves satisfactorily on the large number of minor, though limited, forage sources available. This would be the result of (a) *florea* workers' smaller nectar and pollen carrying capacity and therefore need to visit relatively few flowers on one trip and (b) *florea*'s overall forage requirements for maintaining a viable colony, probably being considerably less than those of *mellifera*, there being more workers, 30-40,000 in a strong colony of *mellifera* in Europe (Butler 1974), and several combs, as opposed to 4-10,000 workers and a single comb for *florea* (Seeley *et al* 1982 and my own data).

In the dry years, the high density of *jemenitica* colonies in the Jabal al-Akhdār will seriously exacerbate the dearth situation and increase the mortality, but in wet years that follow there are probably insufficient colonies to exploit the sudden abundance of ephemerals and the large numbers of *Acacia tortilis* and *Ziziphus spina-christi*. Dispersed colonies of *florea*, with an ability to use many minor forage sources, may be better adapted to cope with this fluctuating environment. To speculate even further, perhaps the other tropical and sub-tropical species and races of *Apis* can also exploit many minor sources like *florea* in Oman, as studies of *florea* and *cerana* in Sri Lanka have suggested (Koeniger & Vorwohl 1979). In contrast, *mellifera* of European origin (as Sakagami (1959) indicated was the case in Japan), may not be able to exploit efficiently the greater plant diversity in tropical as compared to temperate regions (Krebs 1978) and therefore many minor sources of forage, but few major ones, may be one reason why temperate *mellifera* do not always prosper when introduced to tropical areas (Crane 1980).

As for the most suitable habitat category for bee-keeping, from the sources of forage available, their abundance and my observations on the quantities of honey stored, it was clear that interior oases were superior to Bātina gardens. This was primarily a result of the system of "falaj" irrigation in the former, with flood irrigation of large "galba" allowing ground vegetation (weeds and crops) to flourish and the closer spacing of tree crops. In dry years, with irrigation providing year round forage of one sort or another, oases and even Bātina gardens are likely to be better than wild habitats, but in wet years the latter, with a profusion of ephemerals and the full-flowering of indigenous trees and shrubs, are likely to provide the biggest crops of honey.

Either keeping colonies in oases close to wadis with an abundance of *Ziziphus spina-christi*, *Acacia tortilis* and other vegetation, or moving colonies from gardens to such wadis just for periods when these major species are flowering should make the best use of both types of habitat - as long as the nest site requirements of *florea* in particular (shade/exposure) are met. Ground surveys and particularly aerial photographs should facilitate identification of wadi sites with the greatest densities of trees. On the Bātina coast colonies will probably do best where wadis, with their associated concentration of vegetation, cut through the cultivated belt before reaching the sea.

In both Interior and Bātina gardens, many of the minor and negligible sources of forage which together were important to *florea* were weeds eg *Sonchus oleraceus*, *Pimpinella* ? sp. nov., *Euphorbia heterophylla*, *Vernonia cinerea*, *Cyperus rotunda*, *Launaea* spp., *Sporobolus spicatus*, *Cynodon dactylon*, some flowering for much of the year. In the U.K. weeds were excellent sources of nectar and pollen in both grassland and cereal crops, but have now been almost eliminated by herbicides (Sims 1984). Some of the weeds in Oman were used to sustain or supplement the diet of livestock, but many crops would no doubt have benefited from their partial or complete elimination. However, Omani farmers might want to bear in mind the consequences to their bees and honey crops when assessing the costs and benefits of increased crop hygiene.

Similarly, alternative systems of irrigation (eg Hillman 1983) may bring about more efficient use of water and higher crop yields (for bees too if the crops are melliferous) but may also result in loss of bee forage. For instance, *Phyla nodiflora* was particularly abundant in earthern irrigation channels, forming a protective mat that seemed to reduce erosion of the channel sides. Replacement of these with piping, concrete or other channels would diminish this valuable "intermediate" source of forage.

The overall composition of forage in Oman makes for interesting comparison with that recorded in Germany by Bauer (1982), where there was an interaction between the use of wild and crop plants; wild plants provided a fairly smooth sequence of forage, but the crop plants gave the main honey flows. In Oman too there was an interaction between the exploitation of wild plants and crops where both were available; each provided some sort of forage sequence for parts of the year, but the main flows came from the wild, native *Acacia tortilis, Prosopis cineraria* and *Ziziphus spina-christi*. In the areas of Germany Bauer (1982) studied there was a dearth period in July and August and the value of verges, hedges and waste ground, equivalent to fallow ground, useful weeds, shade trees in Oman, was stressed and the possibilities of providing additional bee forage by suitable plantings investigated.

Might bee forage be planted profitably in Oman? With water being so scarce, any plantings solely for bees that required large quantities of water should not be contemplated. *Acacia tortilis, Prosopis cineraria* and *Ziziphus spina-christi* might be encouraged in areas where their density is low but, where their density is already high, honeybee populations large enough to exploit such numbers of trees to the full would be difficult to maintain during intervening periods of low forage availability, and further plantings would be unnecessary. However, plantings of species to cover the dearth period following the *Acacia tortilis* honey flow, especially for July, August and September, and also to follow the *Ziziphus spina-christi* flow in the latter half of November and December, would be valuable if the plants concerned have other uses. Thus species good for honeybees should certainly be planted where shade or ornamental trees are required. Eucalypts that flower at the appropriate times could probably be found and species of *Acacia* from Africa, already adapted to arid and semi-arid conditions. Other leguminous trees and shrubs used in afforestation, to prevent desertification and for livestock browse, should be assessed for their potential as honeybee plants. In particular, good sources of pollen are required, since this appeared to be in short supply on the Bātina, especially for *mellifera* (see p.272-3). Of course any such introductions should be planted on a small, controlled scale first, to check their flowering seasons and attractiveness and value to honeybees under Omani conditions. The important world honey sources listed by Crane *et al* (1984) as drought tolerant would be the most promising to investigate, including those species (such as *Dalbergia sissoo*) which are already found in Oman, but are relatively scarce at present.

CHAPTER VIII

EXPERIMENTS AT HIVING *APIS FLOREA*, WITH OBSERVATIONS ON ASSOCIATED COLONY MANIPULATIONS

A. INTRODUCTION

The design of a hive for *Apis florea*, that facilitates the management of the species, could prove to be of particular importance both in Oman, where there is a strong preference for the locally produced honey of the Little Bee, and in other Asian countries wishing to exploit their honey potential to the full and maximise crop pollination. In an attempt to make *florea* a more rewarding prospect for established bee-keepers and casual honey gatherers alike, a number of different hives were made and tested that were intended to tackle various characteristics of the Little Bee that created drawbacks to its management by traditional methods (Chapters III and IV). The main difficulties were absconding and honeycomb removal/honey extraction. Though some Omani bee-keeping operations with *florea* were more successful than others, none of the methods employed, such as the choice of suitable nest sites, had overcome these problems entirely satisfactorily.

This chapter gives accounts of several series of observations made on colonies introduced to different hives and thus indicates some of the potential and problems of managing *florea* in such a way.
Several attempts at hiving *florea*, some opportunist following the arrival of a swarm in a bee-keeper's garden, others more deliberately planned, are recorded in the literature (Indian Bee Journal 1942; Millen 1943 and 1944; Das 1946; Bridgnell 1946: Muttoo 1956: Pundir 1971). However, as Free (1981) has pointed out, the methods used in some of these attempts have not been well documented and the results seem to have been

uncertain. For this reason, details of hive construction and bee behaviour are presented here, which may have been of significance in these trials in Oman and which could prove to be pertinent to the development of new hives and to the interpretation of their success or failure. In addition, various practical details of the handling of the bees and combs are given.

There is only space in this thesis to describe and discuss just a small proportion of the several hive-types constructed and the numerous hivings of colonies that were performed. I believe that those which are considered give a fair indication of the problems involved, but experience with the other hivings not portrayed is taken into account in the discussions. The total number of "hivings" conducted (c. 69) and the mixed success with which they met are evident from the sections on absconding and its seasonality presented in Chapter VI, much of which was based on hived colonies.

The account describing the initial use of Hive 2 is concerned particularly with the problems of absconding when first gathering and establishing a colony and is presented and discussed first (Part 1). Descriptions of further manipulations on this colony and accounts of other hivings, that were concerned more with the use of frames and with other problems, are then presented (Part 2) and the overall advantages and disadvantages of hives considered.

B. MATERIALS, THE HIVES

The hive (identifying code 2) used for the first series of observations is illustrated in Figure 8.1. It was one of several hives, of similar design, that had been constructed following 2 years of experimentation with a variety of different models. A cross-section is shown in Figure 8.2 and the main dimensions are given in Table 8.1; its principal features were:-

Table 8.1 Dimensions, in centimetres, of experimental hives (Nos. 2, 13 and 22) and frames for *Apis florea* under trial in Oman 1979, 1980. 1.75cm thick plywood was used for the sides, base and roof of each hive, but a thin (5mm) plywood for the removable front and back of each lower brood box. Hives 13 and 22 were "thinner" than Hive 2 (Depths/Lengths, ie front to back, 10, 10 and 15cm respectively) and both needed pieces of wood, 30 x 4cm, nailed to the bottom at each side as "feet". This prevented them from falling over; Hive 2 also had these feet though they were not essential. With Hive 2, deep frame (a) was replaced with (b) from another hive (No. 20) during the course of the observations. Figures 8.1,8.2,8.4,8.5 and 8.6 illustrate Hive 2 and its upper and lower frames, Figures 8.7 and 8.8 illustrate Hive 13 and its upper frame.

	Lower Box, Brood			Upper Box, Honey (Super)		
Hive Number	2	13	22	2	13	22
Height (External)	31	31	31	9.5	11.5	9.5
"Depth"/Length (Internal)	15	10	10	15	10	10
Width (Internal)	31	31	31	31	31	31

	Deep Frame, Brood				Shallow Frame, Honey		
Hive Number	2(a)	2(b)	13	22	2	13	22
Height (Internal)	27.8	27.8	27.8	27.8	7.5	9.5	7.5
Width (Internal)	27	24.5	24.5	27	27	24.5	27
Side Bar "Depth" -Tapering to	3 2	3 2	3 2	3 2	3 (Not Tapering)	3	3
Side Bar Thickness	1	1	1	1	1	1	1
Top Bar "Depth"	2	3	3	2	3	3	3
Bottom Bar "Depth"	2	2	2	2	2	3	2
Top and Bottom Bar Thickness	0.5	0.5	0.5	0.5	0.5	0.5	0.5

(a) A narrow, upright lower "brood" box, with a removable front and back to allow easy inspection of the colony without moving the frame inside.

(b) A shallow upper box (super) with a strip of mesh at the front and back, providing an "opening" of 31cm by 3cm to permit workers to forage while preventing the queen from escaping.

(c) A long, narrow (33cm by 2cm) removable entrance block, above the mesh; this could be removed , if absconding was considered unlikely, in order to facilitate the entrance/exit of the foragers.

(d) A roof extending beyond the front and back edges of the hive to give shade.

(e) A deep brood frame with a separate shallow honey frame nearly resting on top of it (ie no bee space between them). These were suspended from rebates in the side walls of the brood box and super respectively.

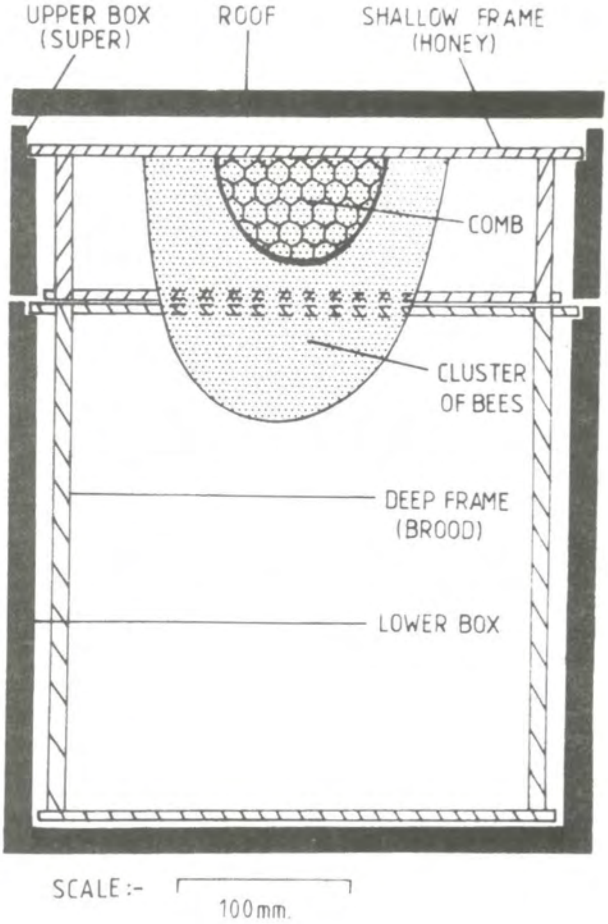
Finer details of the hive's construction are not given as the author does not want to give the impression that this design is a blue-print for success! However, the following points might be borne in mind. The top and bottom bars of the frames were thin so that the distance between the honey and brood combs was small; a large gap might affect the colony as the brood and honeycombs are united (a single comb) in wild colonies. However, the depth of the bottom bar of the shallow frame and the top bar of the deep frame (a) was 2cm (that of deep frame (b) was 3cm; see Table 8.1), ie a little deeper than the natural depth (approximately 1.8cm) of a *florea* brood comb. This was to discourage the bees from building beyond the edge of the bars, encircling them and thus actually joining the two frames together. This could have made the separation of the upper honeycomb, for extraction, difficult.

Figure 8.1 Experimental *Apis florea* hive No. 2 on a four-legged stand at Khabura, Oman on 17 March 1980, just after a colony of Little Bees had been installed. One of the mesh entrances in the upper box (super) is visible just below the protruding front edge of the roof. A frame sugar-syrup feeder is on top of the hive.

Figure 8.2 Cross-section through the centre of experimental *Apis florea* hive No. 2, as viewed from the front or back. The positions of the comb and cluster of bees are approximately those observed with a recently installed colony, at Khabura, Oman, on 18 March at 09.00h and 22 March at 23.30h, 1980 (see text). The hexagons representing the cells of the comb are not drawn to scale.

Figure 8.3 A 4-day old colony of *Apis florea* at Khabura, Sultanate of Oman, on 16 March 1980, just before it was collected and transferred to an experimental hive, No. 2. The cluster completely enclosed a small piece of comb and was hanging from the bottom edge of an inward-opening bathroom window; it was thus <u>inside</u> the building.

8.1


UPPER BOX (SUPER)
ROOF
SHALLOW FRAME (HONEY)
COMB
CLUSTER OF BEES
DEEP FRAME (BROOD)
LOWER BOX
SCALE:-
100mm.

8.2

8.3

The galvanised steel mesh, obtained in Oman, was woven with wire strands of diameter 1mm, leaving 3.5mm square apertures. The large *florea* queens were not able to squeeze through it, but the workers could, though sometimes with difficulty and particularly if they had large pollen loads. There is evidence (Narayanan *et al* 1960) to suggest that *florea* may vary in size in different parts of its range in Asia, as does *mellifera* with its several races in Africa and Europe, so close observations to determine the correct mesh size for a particular region will be needed. Meshes suitable for Omani *florea*, eg as cited above, will not necessarily be appropriate elsewhere.

The dimensions of two other hives (13 and 22) used in experiments described in this chapter are also given in Table 8.1. They were similar in principle to Hive 2 and their minor differences are considered in Methods and Results, Part 2. Most of the colonies came from Khabura and nearby villages and plains, and the majority of the hivings were performed in this locality. However, some colonies kept in hives at Khabura had been brought from other regions and a few others were kept in hives away from the Khabura district, eg at Rustaq.

C. METHODS AND DESCRIPTION OF RESULTS

PART 1

1. The colony of bees for Hive 2

The colony of *florea* put in Hive 2 had arrived as a swarm, including drones, on 12.iii.80 at a house 50m from the sea at Khabura on the Bātina coast of Oman. It had attached itself to the bottom edge of a small, inward-opening bathroom window, on the ground floor of the house and facing SSE into a courtyard. The window was hinged along the top and propped open; therefore the colony was inside the room, but visible from the outside (Figure 8.3). The main events in the subsequent history of this colony till 1.iv.80 are outlined in Table 8.2.

2. Collecting the "swarm"

The swarm was collected, at dusk, on 16.iii.80 by which time a small piece of comb had been built and it already contained eggs, some very young larvae and a little pollen and nectar/honey. The queen was found in the cluster and put in a plastic cage, the comb cut away and nearly all the bees were removed in a cotton sack to the hive. About 400 workers were still present at the window 16 days later on 1.iv.80; they were probably ones which had been left behind, though it is not inconceivable that some had returned here from their new site in the hive. The hive was on a small 4-legged stand under an open-sided shelter with a roof of date-palm leaves; this provided shade during most of the day. The shelter was approximately 1.25km SW (215^{o}) of the house from where the swarm was collected.

3. Hiving the "swarm"

The small piece of brood comb was fixed to the top bar of the shallow (honey) frame. Initially wire was used to tie the comb but this cut through the soft wax and the comb fell away; therefore the comb was re-attached using a date-palm leaflet which, being broader (width approximately 8mm), once it had been threaded through the comb did not tear it as much as the wire. Though two small pieces of the comb did fall away from the frame the following day (17.iii.80), the bees had attached the main piece to the palm leaflet by 18.iii.80 and subsequently fixed the comb firmly to the shallow frame's top bar.

Some of the bees were released around the comb in the hive after dark on 16.iii.80 and the remainder had all been released by 14.30hrs

Table 8.2 Outline of principal events in establishing a wild colony of *Apis florea* in an experimental hive (No. 2) at Khabura, Sultanate of Oman. See text for details.

12.iii.80	Swarm arrived in bathroom window
16.iii.80	Swarm collected and partly installed in Hive 2
17.iii.80	Remaining bees released
18.iii.80	Bees, with queen, absconded; queen caught and put back in hive; bees returned
19.iii.80	No observations
20.iii.80	Bees absconded, queen remained enclosed in hive; bees returned
24.iii.80	Comb being extended; queen laying; entrance block removed
1.iv.80	Comb extended further; eggs, larvae and pupae (sealed) present; ie colony established in hive

the following day. These last bees would all have been released early that morning (17.iii.80) had it not been for the occurrence of strong winds and rain which could have blown the bees away while trying to orientate on their new hive. The roof was left off the hive while the bees orientated, but the queen was unable to escape as she was still in her cage; this had been tied next to the comb (after she had been marked with paint on her thorax) the night before. A little honey was smeared on the top bar of the shallow frame and a small "frame feeder" with sugar syrup put next to the cluster in the "super" of the hive; the bees very quickly started to feed from these.

A little later, the queen was released from the cage, the roof put on the hive and the entrance blocks inserted. The frame feeder as it was effectively blocking one of the mesh entrances was removed from inside the hive and put on the roof; the bees continued to feed from it here. Thus at 09.00h on 18.iii.80 the colony appeared to be settling, with the workers using the mesh entrance and taking sugar syrup from the feeder; the bees had formed a cluster which covered the small piece of comb, the centre of the shallow frame and the top of the brood frame immediately below (Figure 8.2). The only sign of "distress" observed was that of the drones, many of which flew inside the hive in making unsuccessful attempts to get out through the mesh. Their exact periods of flight were not recorded, but observations on another colony on the same day indicated that this activity occurred approximately between 10.30h and 13.30h.

4. <u>First absconding attempt</u>

At 13.55h a few workers were observed flying round (not foraging) approximately 20m from the shelter. An inspection of the hive revealed that the bees had absconded and were starting to cluster in a small bush, *Conyza dioscoridis* (Compositae), 12m away at a bearing of 30° (approximately NNE). Despite the mesh, the queen had managed to find a way out of the hive - probably through a crack by a loose-fitting back or front of the brood box. About 100 drones were still in the hive and approximately $^2/_3$ of these flew out when it was opened, the remainder staying on the mesh.

The queen was caught at the bush and returned to the hive in the plastic cage which was again tied next to the small piece of comb in the shallow frame. By 14.55h approximately 5% of the bees had returned inside the hive, around the comb and queen cage, and approximately 80% were flying round the hive; the remainder were flying round the bush and between the two sites. By 16.00h nearly all the workers had settled again in the hive. Many of the drones were trying to enter the hive, with workers feeding some of them on the mesh; the entrance blocks were therefore opened and most drones had found their way into the hive by 17.00h. The bees were present the following morning (08.30h, 19.iii.80) but no further observations were made that day; it is not inconceivable, though, that another unsuccessful absconding attempt was made during the afternoon.

5. Second observed absconding attempt

On 20.iii.80 returning foragers were seen at 12.30h so the queen was released from the cage once it had been made certain that there were no exits from the hive except through the mesh on the upper box. "Figure of eight" dances were observed, but whether these indicated a source of forage or a new nest site could not be ascertained. At 13.50h the colony was still present but the bees in the cluster were more active than before; some workers on the surface were performing a form of "waggle dance", with longer runs and wing-flicking, which other observations had suggested took place prior to absconding; such "buzz-runners" were also seen by Seeley *et al* (1982) on a *florea* colony in Thailand before it absconded. At 14.55h the bees were seen to have absconded and were flying round the same bush as before, some of them forming a small cluster; the drones were again flying inside the hive, trying to get out, but this time the queen also remained enclosed in the hive.

There were eggs in most of the cells of the small deserted piece of comb (the eggs and larvae that were in the comb when the colony was first taken had disappeared earlier); therefore the queen had started laying in the 2 hours or so since her release from the cage. A small queen cell had also been started at the bottom of the comb, possibly a supersedure cell built by the workers as a result of the queen's inability to lay eggs when enclosed in the cage. This suggests that the lack of eggs and brood (one characteristic of a "failing" queen) might be involved in the induction of supersedure cell construction in *florea* as well as the absence of a queen and queen substance (Butler 1974) as in *mellifera*.

However by 16.45h on the same day all the bees, apart from a few still flying, had returned into the hive; only a few were on the comb, while the rest had formed a cluster just away from it on the underside of the hive roof, with the queen presumably in the middle. At 17.45h as only a few more bees had moved onto the comb - barely covering it - the roof was shifted so that the cluster was forced near to the comb. No more observations were made till 23.30h on 22.iii.80 when the bees were seen to have abandoned the roof and were again clustered, as desired, from the top bar of the lower frame as in Figure 8.2. In the bottom of the hive there were quite a few dead drones, some with genitalia everted; they could not have left the hive since 20.iii.80 so this would not be the consequence of a mating flight.

6. Successful establishment of the colony in the short term

On the following morning, 23.iii.80, at 07.30h a forager was seen to return with pollen and, later, bees were seen dancing on the protective "curtain" round the comb. At 18.00h on 24.iii.80 closer inspection revealed that the brood comb, in the upper frame, was being extended and more eggs were present in it, indicating oviposition by the queen since the second absconding attempt. There was good evidence, then, that the colony would now stay. The mesh, however, was seen to hinder the passage of workers (particularly those with large pollen loads, which were sometimes knocked off) and prevented completely the drones from leaving the hive. Therefore, to reduce this potential source of irritation to the colony and on the assumption that the colony was not now likely to abscond, the entrance blocks on either side of the super were removed. As a result the workers, drones and queen could leave and enter the hive unimpeded; in fact it took some of the bees a long time to learn this as on 5.iv.80 (09.00h) workers with pollen loads were still to be seen struggling through the mesh!

The supposition that the bees were not likely to abscond proved to be correct, at least in the short term, for at 13.15h on 1.iv.80 (12 days after the colony had made its last absconding attempt) the comb in the shallow frame had been extended further and sealed worker brood occupied most of its centre. This was surrounded by larvae and there were eggs at the very edge of the comb; the queen cell which had been started on 20.iii.80 had been destroyed.

D. DISCUSSION

PART 1

How this colony would have developed had it now been left undisturbed is a matter for speculation as the colony was next subjected to a considerable upheaval. The brood comb of a second colony was introduced in another deep frame (b) (Table 8.1), thus increasing the size of the colony very rapidly. This will be described in E. Part 2, but the implications of the results so far are considered here.

Two main points have been demonstrated. First, *florea* will use a frame in a hive which, except for a fairly narrow entrance, almost completely encloses the colony. Second, restricting the queen in such a hive with mesh can overcome the problem of absconding even when there is no brood or only eggs.

On the first point it has been suggested (in an editorial comment on a paper by Das (1946)) that it is "unnatural" for *florea* to nest in a dark hive or box, ie in enclosed spaces. This may generally be true but *florea* does nest in caves (albeit with large unrestricted entrances) and buildings in Oman, as well as in trees (Chapter II). The hive used here did enclose the bees more than they would be enclosed in these natural sites, but the sky was visible from within, and the workers appeared to be foraging successfully. Therefore, though such a site may not be preferred, as long as some direct light is available for communication dances (Lindauer 1957; Koeniger *et al* 1982; this thesis, Chapter II) and there is sufficient ventilation for effective thermoregulation of the brood nest, hives should not be totally dismissed as a means of keeping *florea*, particularly if they present other advantages. One such advantage, as demonstrated here, would be their ability to overcome absconding. In this example the mesh did not actually prevent the workers leaving the hive, but the enclosure of the queen twice induced the bees to return to it and subsequently stay. Presumably the workers (and queen?) made the "decision" to abscond and carried out this decision before they "realized" the queen was unable to escape. Whether the bees had tried to leave because the hive was not entirely suitable or because of the disturbance that was associated with the hiving process was not clear. Honey stores at the start were minimal so their loss in this case was unlikely to have been of great importance.

That this return of absconding workers of a colony to their enclosed queen was not a freak occurrence was apparent from other observations, including those of Hamoud Ali Sālim to whom I had lent similar hives, with mesh, for trial. Thus in the first half of December 1979 he reported that workers attempted to abscond twice from one such hive (unspecified), but on both occasions returned to the imprisoned queen. Then in the first half of February 1980 he said the workers of another colony (in Hive 26) absconded one morning to a tree maybe 100m or more distant. However, they returned in the afternoon, and shortly afterwards (presumably on another day) made a second attempt, but again returned to the queen and hive, apparently after c. 3 hours; a few days later I saw the colony and it was starting to rear brood. One final example was with an <u>un</u>enclosed colony (IC) that I had at Khabura; I noticed on 17.vii.80 at 09.00h that "buzz-runners" were "dancing" across the colony, indicating that absconding was imminent (see p. 378-9). I caged the queen immediately, but the workers still absconded at c. 09.30h, some travelling over 100m away and settling on vegetation, but never forming a compact cluster (that I could see). Nevertheless after 45 mins, c. 90% of the bees had returned to their nest. The queen was released the following day, oviposition started again and no further absconding attempts were recorded.

Therefore these various observations suggest that there is scope for keeping *florea* in hives. However, they have only provided evidence that two of the problems associated with hiving *florea* can be overcome and there are two others which I consider particularly important. One is the problem of inducing the bees to build their comb, probably in a frame, in such a way that it is not damaged, but can be returned to the bees when the honey is extracted. The other is coping with the bees during a swarming period when drones and queens are being produced (and the observations on this hive indicated that drones were a problem when mesh was being used) or preventing them from reaching this stage at all. These problems and possible modifications to the hive are considered in the remaining sections of the chapter.

E. METHODS AND DESCRIPTION OF RESULTS

PART 2

1. Natural comb structure and hive design

Wild colonies of *florea* build only one comb; it consists of an expanded upper portion of honey storage cells which are usually made deeper than the worker brood cells. Most honeycombs are usually built around a thin branch on a tree (Chapter II); viewed end-on they may be as much as 125mm across if attached to a relatively thick support (unpublished data). The honeycomb narrows to form a lower, vertical portion of uniform thickness, c. 18mm, for brood rearing; drone comb, below the worker comb, is thicker (25.8mm for empty cells of the colony in Hive 2). Pollen is usually stored in a zone of cells between the honey and brood comb. The experimental hives had been constructed with a "super" and brood box to test whether *florea* colonies could be induced to build their honey and brood combs separately, in the upper and lower frames respectively, as do colonies of *mellifera* and *cerana* in modern, movable-frame hives. The intention was to facilitate honey extraction (in a suitably adapted radial or tangential extractor) and allow the honeycomb to be re-used.

With all the techniques I had seen practised by Omanis, from honey-hunters to skilled *florea* keepers, the honeycomb was cut away just above the brood; the honey was squeezed and strained through a cloth and the wax discarded. Even with a managed colony that was carefully "perpetuated" by fixing the brood comb to the split mid-rib of a date-palm frond, a band of brood at least 20mm broad was usually squashed - as the top of the comb is clamped in the fork of the mid-rib. The waste of wax and damage to the brood must have reduced the potential honey yields and the disturbance to the colony must have increased the probability of absconding. Therefore Omani methods, though more successful than any other techniques recorded, were not entirely satisfactory and having the combs in movable frames might overcome some of the drawbacks.

As outlined on p. 374 and in Table 8.1, the top frames were nearly touching the lower frames (no bee space) and they had thin bottom and top bars respectively; thus the vertical gap between honey and brood comb was minimised (there being no gap at all in wild colonies). The bottom and top bars were, however, deeper than the usual depth (thickness) of *florea* brood comb, to deter the bees from encircling and thus joining the two frames in the way that a natural supporting branch would be encircled. It had been planned to test in these frames, wax foundation with cell bases of the correct dimensions for Omani *florea*; however, the manufacturer had problems in machining a mill embossed with hexagons of such a small size, and the equipment did not arrive in time.

Therefore, as no *florea* foundation was available, alternative trials to test the bees' use of the frames were performed. One such trial, a continuation of that just discussed with Hive No. 2, and the manipulations of *florea* associated with it, are here described in detail. Comparisons are made with the results of similar trials on two other colonies; these are described in brief. The problems of gathering wild *florea* and their swarming from these hives are also considered.

2. Continued manipulations with Hive 2, March-June 1980; addition of brood comb from another colony

2.1 Background

April is one of the best periods for *florea* in Oman with the important forage source, *Acacia tortilis*, coming into full flower in the middle of the month (Chapter VII). If this *florea* colony No. 2 had been left undisturbed for a month or more it is almost certain that the bees would have continued to build up rapidly and filled the upper frame with honey, pollen and brood. Whether the bees would also have built comb in the empty lower frame is difficult to judge, but experience with other colonies, 22 and 13, in similar situations the previous year (see sections 3.1 and 3.2) indicated that they might not have done. Had the lower frame contained a sheet of foundation with cell size appropriate to *florea* it is considered likely that the colony would have drawn out the foundation and expanded its brood rearing to this frame. In the absence of the required foundation, alternative action was taken.

On 31.iii.80 the weight of the colony was 164gm including the brood comb of estimated weight 30gm, and from measurements made by weighing, killing and counting the bees of another colony, it was calculated that there were approximately 4,400 worker bees. Other data (Whitcombe, unpublished), now supported by work in Thailand where 6,271 workers was measured to be the mean worker population of 12 colonies (Seeley *et al* 1982), suggested that this colony was still smaller than a "mature" colony. As it was needed later for experiments on nest temperature regulation (Chapter V), and a stronger colony was required, the opportunity was taken to increase the colony's size rapidly, and to test the bees' use of 2 frames, by adding the brood comb of another colony. The main features of the operation are described below and the principal events are outlined in Table 8.3.

2.2 Acquisition of the brood comb

The brood comb came from what must have been a fairly large colony at the bottom of a small "ghāf" tree, *Prosopis cineraria* (L.) Druce (Leguminosae), growing in a narrow wadi between date gardens at Khabura. The nest had been found by boys living nearby who, during the afternoon of 31.iii.80, had taken the honeycomb; however, they had dropped the brood comb amongst the twigs at the base of the tree, near to its original position.

At 17.00h most of the bees were clustered round the comb. Drone cells, with eggs, larvae and sealed pupae were present at the bottom of the comb and were cut away, as was an uneven section of worker cells at the top, so that the comb could be fitted into deep frame (b) (Figure 8.4 and Table 8.1). This main portion of the brood comb weighed approximately 135gm. Its maximum height was 14.5cm and width 18.0cm and it contained approximately 70% sealed brood and 30% eggs plus larvae. Its maximum height with drone comb included was 24.0cm.

Table 8.3 Outline of principal events during the continued manipulation of an *Apis florea* colony in an experimental hive (No. 2) at Khabura, Sultanate of Oman. See Table 8.2 and text for other details.

16.iii.80	Swarm collected from bathroom window and installed in Hive 2
24.iii.80	Comb being extended in upper frame. Eggs present
31.iii.80	Brood comb, from colony in "ghāf" tree, introduced to deep brood frame; put adjacent to upper, shallow frame
4. iv.80	More bees clustering round introduced than resident comb. Eggs and larvae have been removed from latter shallow comb but pupae (sealed) still present. Introduced comb, from which adult workers were emerging, put beneath shallow frame
9. iv.80	Queen ovipositing in lower, but not upper, comb
27. iv.80	Comb in upper frame extended and attached to top and bottom bars. Being used for nectar/honey and pollen storage. Introduced comb well attached to lower frame with worker brood at all stages, unsealed drone cells and queen cups
7. v.80	Drone comb extended further but with 3 queen cups destroyed; replaced by one new cup
8-9. v.80	Foraging activity and temperature regulation normal
c.25.v.80	Old queen left colony with primary swarm (Deduction)
c.1.vi.80	New queen left hive with remaining bees (Deduction)
2. vi.80	Deserted combs empty of food stores and worker brood; bees collecting wax for new nest

Despite a search (brushing the bees gently aside so they did not take wing), through the curtain of bees on the comb before it was removed, the queen could not be found. While the comb was being fixed in the frame, some of the bees clustered on twigs near their old nest site, and others circled in flight higher up the tree. The comb, held in the frame by 3 strips of date-palm leaflet tied round the top bar and also by 2 horizontal sticks, one on either side of the brood and stapled to the side bars (Figure 8.4), was put back in the original nest site. By this time, 17.25h, most of the bees had clustered round a twig, 4m from the ground, near the top of the tree. The queen presumably was with the cluster. The cluster was soon dislodged, 17.30h (by throwing a stone at its supporting twig!), but only approximately 200 bees returned to the brood comb, the majority re-clustering on the same twig. Persistent disturbance of this cluster by throwing objects, shaking the tree and finally a little smoke, failed to make the bees return to their brood comb. The brood comb, in its frame, was then moved at 18.00h even closer to the cluster (3m away) by putting it on a vehicle roof. The cluster was dislodged again but re-formed on another twig, slightly higher up, on the other side of the tree. Despite being knocked off this "new" twig several times, the bees could not be induced to return to the brood comb so were abandoned at 18.30h as dusk approached.

Therefore, so that the brood should not be chilled or starved, the brood comb and frame were moved to Hive 2.

2.3 Introduction of the brood comb to Hive 2 and acceptance by resident colony

By 19.00h on 31.iii.80 the brood comb from the "ghāf" tree was hung in the upper box of Hive 2 immediately adjacent to the frame

Figure 8.4 Section of deserted *Apis florea* brood comb, from a wild colony in a "ghāf" tree, tied into a lower frame (b) before introduction to Hive 2. Khabura, Sultanate of Oman, 31.iii.80.

Figure 8.5 The same *Apis florea* brood comb as in Figure 8.4, extended and sealed into frame (b) by the bees of Hive 2. Worker and drone brood is being reared in the comb and 4 queen cups/cells are visible along its lower edge. The bees have been brushed away. Khabura, Sultanate of Oman, 27.iv.80.

and comb covered by the resident bees. After 5 minutes a single layer of the resident bees had covered approximately 75% of the introduced brood comb. At 13.15h on 1.iv.80 a thin curtain of bees (1 to 2 bees thick) covered equally each of the combs and some dead or damaged larvae had been pulled from cells of the introduced comb. By 11.30h on 2.iv.80 it possessed a thicker curtain of bees than the original comb. Though the colony was actively gathering forage, it probably had an insufficient worker force and stores to feed and maintain at an optimal temperature this sudden influx of additional brood. On 4.iv.80, 09.10h, even fewer bees covered the original comb and it could be seen that the bees had nibbled away some of the wax of its peripheral cells and removed/consumed eggs and larvae which had been present on 1.iv.80. Sealed brood, however, still remained in the centre of the comb. Adult bees were emerging from the comb of introduced brood, which was being fixed more firmly with wax into the deep frame (b).

The resident bees had thus readily accepted the introduced comb, but to encourage the colony to use the deep frame (b) for brood comb and the shallow frame, once the pupae had emerged, for honey storage, the deep frame (b) was moved to the lower brood box. It was put directly below the shallow frame in place of the original brood frame (a) in which the bees had never built any comb.

An examination of the colony at 09.10h on 9.iv.80 indicated that this strategy was working. Adult workers had emerged from the sealed cells in the centre of the brood comb in the upper shallow frame and no eggs or larvae had replaced them there; no eggs or young larvae could be seen through the curtain at the edge of the comb. In the lower frame, adult workers (offspring of the "ghāf" colony queen) had emerged from sealed brood and these cells now contained eggs. It appeared therefore that the queen was ovipositing in the lower comb, but not the upper one. At approximately 10.00h on the same day, about 200 worker bees were seen flying around the hive and then gradually returning to it. Such behaviour has been observed on several occasions with other *florea* colonies, at similar times in the morning; it is almost certainly an orientation flight by young bees and in this case provided further evidence that the enlarged colony had settled. On 13.iv.80, 15.00h, nearly all the sealed brood was seen to have emerged from the upper comb and a little pollen was now stored in its centre. The lower comb contained eggs, larvae and pupae (sealed) with a little unsealed honey/nectar at the top. By weighing (with a Pesola balance) the frames plus combs, first with the bees and then without (by shaking and brushing them from the comb) it was estimated that the colony had a population of c. 5,250 adult workers.

2.4 Swarming phase

Up to this stage, the hive had proved fairly successful and the bees, despite becoming rather aggressive, had not absconded through the disturbances caused by inspections and the introduction of the brood comb. They had accepted the latter remarkably well and this had probably accelerated the colony's growth by at least one month. However, a season of relatively abundant forage had been reached, when many *florea* colonies produce drone and queen cells and swarm (Chapter VI). This colony also entered a swarming phase though the pattern of events did not appear to be entirely typical compared to those observed in other colonies. To reduce the risk of the bees absconding due to repeated disturbance, detailed examinations were made less frequently and some stages of the colony's later development were missed, but information worth recording was gathered.

On 22.iv.80 a brief inspection, without brushing the curtain of bees away to see the comb, suggested that the colony was still developing normally though ants, including *Camponotus sericeus*, were taking dead bees and pollen that had fallen to the bottom of the hive. However, at 09.15h on 26.iv.80 a dead, unmarked virgin queen, soft and with wings incompletely expanded, was found on the bottom board of the hive, presumably killed on or before emergence from a queen cell within the previous 48 hours.

(i) Situation at 16.45h, 27.iv.80

A more thorough examination of the colony on 27.iv.80, 16.45h, revealed 2 queen cells at the bottom outer edge of the upper comb (Figure 8.6). One was sealed and was cut away to reveal an unemerged, but fully developed, dead virgin queen; she was rather hard with inflexible legs so may have been killed by a sting through the cell 2 or 3 days previously. The second queen cell was open and must have contained the dead queen found on the hive floor. According to Sandhu & Singh (1970) the mean duration of *florea* queen development is 16.5 days from egg to adult emergence so these queens must have arisen from eggs laid on c. 9.iv.80 and their cells had not been noticed. There were also 8 sealed drone cells at the periphery of the comb and c. 14 unsealed cells with larvae (drones and/or workers).

The encouraging development was that the comb in the upper frame had been extended to the full height of the frame, 7.5cm, and was firmly attached along the top and bottom bars, as shown in Figure 8.6; its maximum width was 14.5cm. Nectar and honey, a little of it sealed, were stored in approximately 80% of the top half and pollen in approximately 25% of the cells of the bottom half.

Figure 8.6 Wax comb, constructed by *Apis florea* and well fixed into the upper frame of Hive 2, being used for storage of honey and pollen. Prior to the introduction of the brood comb from the "ghāf" colony (Figures 8.4 and 8.5), brood had been reared in this comb. 2 queen cells can be seen at the bottom left and 4 sealed drone cells at the bottom right. The bees have been brushed away. Khabura, Sultanate of Oman, 27.iv.80.

The brood comb, now 17.5cm high by 19.0cm wide, was well attached to the lower frame (Figure 8.5) along the top bar, one side bar and the two cross-bars; it contained no pollen or honey, but consisted of c. 85% worker brood (eggs, larvae and sealed pupae), c. 15% unsealed drone cells and 5 queen cups (ie small, open queen cells). Three of the queen cells were attached to the drone comb, 2 to the worker comb; 2 of the cups contained 2 eggs, 2 contained 1 egg and 1 cup contained no egg at all. There were several eggs/cell and 2 larvae/cell in parts of the drone comb. In the worker comb, no more than one egg or larva/cell was observed but there were a few (≤10/side), larger and protruding, scattered drone cells. Such egg laying patterns suggested the queen was failing and that laying workers may also have been present.

By weighing the combs with and without bees, as before, it was calculated that there was a total of 6,460 bees in the colony (2,180 were round the honeycomb, weight 85gm; 4,290 round the brood comb, weight 140gm). Before the inspection, the curtain of bees extended right down across the two combs covering the gap caused by the juxtaposed frames; a little wax had been squeezed between the two frames, but comb had not been built out around the adjoining bars so they were easily separated. The queen was seen to be present.

(ii) Final observations on Hive 2, 28.iv.80 to 2.vi.80

At 09.05h, 28.iv.80, the bees were rather aggressive following the disturbance of the previous day's inspection, but were still gathering pollen. Hanging below the lower brood comb was a cluster of bees, probably making new drone comb. Two or three days later the 3 queen cups at the bottom of the drone comb were empty (having had 0, 1 and 2 eggs before), but another queen cell had been started in the top frame in the position from which the sealed queen cell had been removed on 27.iv.80.

Apart from the series of observations on 8 and 9.v.80 (Chapter V) which indicated that the colony was foraging and regulating its temperature normally, the last full inspection with the bees present was made on 7.v.80. This showed that the new queen cell in the upper frame had disappeared and that the top part of this comb still contained, mostly, unsealed honey while the bottom half was nearly filled with pollen. There was little change in the brood of the lower comb, but the original queen cups on the drone comb had been destroyed, the drone comb extended and a new queen cup started.

It is deduced (from observations on other colonies) that the old queen probably left with a swarm in the latter half of the month (May) and the rest of the colony with a new queen left several days later. This would have been on or just before 2.vi.80, as the combs were deserted then except for workers collecting wax to take to their new, untraced nest site. The comb left behind contained no pollen, nectar, honey or brood (except for 2 unemerged drones) and wax had been taken especially from the perimeter of the combs and the cell tips, from both upper and lower frames. The brood comb, maximum height 20.0cm and maximum width 21.5cm, had an area of $340cm^2$ (84% worker and 16% drone cells). There were 8 empty queen cells on the comb; 4 attached to drone cells, 4 to worker cells. The 4 latter queen cells appeared to have been torn open at the apex and sides. Of the drone comb attached queen cells, which were shorter, 3 had neat round openings at the apex, while the cap had been re-sealed on the fourth. The honeycomb, having had much wax torn away from it for the new nest, was smaller (5.5cm high by 12.0cm wide, weight 4gm) than on 27.iv.80 and, because of the loss of wax, was becoming detached from the upper frame.

3. Use of frames by two other colonies

To show that the example detailed above is not exceptional and to confirm that *florea* will adapt to building its comb in a frame, two comparable cases of hiving *florea* colonies will be briefly cited. They emphasize how important it will be to test the use of *florea* foundation if this type of hive is to be developed further.

3.1 *Apis florea* colony in Hive 22; March - June 1979

The bees put in Hive 22 were originally a swarm that had left a colony installed in another hive of earlier design. The main features of the colony's subsequent development are outlined in Table 8.4. The queen was almost certainly the old one, though she had lost the paint marks put on her thorax, and the estimated one third to one half of the colony which went with her, on 27.iii.79, settled in a *Lantana camara* L. (Verbenaceae) bush due east and 19m away from the parent colony. By 8.iv.79 a small comb had been built containing unsealed nectar/honey, eggs, larvae and pupae (sealed) and an open queen cell with a small larva estimated to be 1 to 2 days old (confirming that it was the old queen in the swarm, which was now re-queening itself).

On 8.iv.79 the honeycomb and supporting stick were cut away and the bees and brood comb installed in Hive 22. On the following morning the hive was moved directly to its new site, 19m NE from the *Lantana*. The brood comb, however, had fallen from its frame overnight and when the hive lid was removed, the bees immediately flew back to the *Lantana*. The hive was taken back there too and the brood comb was re-installed in the upper frame, by wedging it between two slender (c. 0.5cm thick) wooden rods which were held up under the top bar by a loop of wire at either end. The bees clustered round the frame

Table 8.4 Outline of principal events in the development of an *Apis florea* colony that was introduced to an experimental hive (No. 22) at Khabura, Sultanate of Oman. Further details in text.

27.iii.79	Swarm arrived in *Lantana* bush
8.iv. 79	Small comb built with nectar/honey, eggs, larvae, pupae
10.iv. 79	Installation of colony in upper frame of Hive 22 completed
26.iv.79	Comb expanded; worker brood at all stages with honey region above
9.v. 79	Brood comb expanded laterally; now attached to bottom bar of frame as well as top bar. Eggs and young larvae at perimeter of comb, but queen dead
10.v. 79	Virgin queen introduced, mesh removed
17.v. 79	New eggs in comb (queen now mated)
30.v. 79	Upper frame nearly filled with comb; lower brood frame empty
18.vi.79	Upper frame completely filled with comb; brood rearing ceased (only a few pupae left). Lower brood frame empty
21.vi.79	Colony absconded

and after dark on 9.iv.79 the hive was moved again to the new site. This time the bees settled there.

Hive 22 was essentially similar to Hive 2, but it was thinner and, instead of having a removable entrance block, the whole mesh entrance (3.2 x 31cm) was on a wooden frame which could be removed. Details are given in Table 8.1 but the differences in the two hives are not considered to be of great significance. The queen was caged, from 8 to 11.iv.79, and was kept within the cluster except for being removed temporarily for marking. This enclosure and the age of the queen must have stimulated the workers to build emergency queen cells, in addition to the replacement queen cell already described, for 5 were recorded during inspections on 15 and 17.iv.79; they were all sealed by the latter date. Also, some worker cells, damaged when the comb was installed, had been expanded to drone cells and contained several eggs each, presumably from laying workers. However, the old queen released on 11.iv.79 was still present on 17.iv.79 and new comb built at the periphery was of normal worker cells with one egg each.

On 25.iv.79, all the queen cells had disappeared and one dead, still soft, virgin queen with shrivelled wings was on the hive bottom. The old queen, still present, and/or the workers must have been responsible for killing the one new queen and destroying the other emergency queen cells. On 26.iv.79 the frame was removed from the hive, the bees brushed gently away, and the comb photographed; it was 14.3cm wide by 7.2cm high, nearly touching the bottom bar. The honeycomb at the top had been extended on either side beyond the edge of the top bar (depth 3.0cm), but did not encircle it; the brood comb below contained eggs, larvae and sealed pupae. Thus development appeared normal and foragers crawled through the mesh satisfactorily on their return.

On 9.v.79, though eggs and young larvae were present in the outer part of the comb, the queen was found moribund on the floor of the hive. The brood comb, however, had been expanded laterally and was also attached to the bottom bar of the top frame, with cells rather larger than usual worker cells. A caged virgin queen from another colony was introduced that day and released on 10.v.79; the mesh was removed to allow the queen to leave for a mating flight. Eggs were seen in cells at the centre of the comb on 17.v.79, indicating the queen had mated successfully. On 30.v.79, the top frame was nearly filled with comb, but the bees were not building on the lower frame intended for brood. On 3.vi.79, clusters of workers were seen to be hanging from the top bar of this lower "brood" frame but no comb was being built.

By 18.vi.79, except for small gaps in the corners, the comb completely filled the upper frame, but still none had been built in the empty lower frame. Brood rearing, however, had ceased as there were only a few sealed cells (pupae) and no eggs or larvae in the comb. On 21.vi.79 the colony absconded and their new nest site could not be traced. No.brood was left and there was only a little sealed and unsealed honey in the top centre of the frame, where the comb had a maximum depth of 4.8cm and protruded beyond the top bar (depth 3.0cm) on each side. No comb had been built in the lower frame, though the crack between it and the upper frame had been partly filled with wax. The mesh, which might have inhibited their absconding had been removed earlier (to allow the introduced, virgin queen to mate) but not replaced as it could knock some of the larger pollen loads off the legs of returning foragers.

3.2 *Apis florea* colony in Hive 13; September - December 1979

This colony was obtained by dividing a very large colony in another hive (No. 9) on 13.ix.79. It was estimated visually that 45% of the bees plus the old queen formed the new colony in Hive 13, while 55% of the bees remained on the parent comb which had sealed queen cells and was removed to another site. The drop in weight (310gm) of colony 9 through the "loss" of bees to the new hive indicated that colony 13 consisted of approximately 10,200 workers. It was formed round a piece of empty brood comb, weight 16gm, from a third colony (in Hive 20) which had absconded on 12.ix.79. It was fitted into the upper (super) frame of Hive 13 which differed slightly in dimensions from Hive 2, the upper box and frame being taller (Table 8.1), but not in principle, having a mesh entrance (5.5 x 31cm), a separate removable entrance block etc. The initial dimensions of the empty brood comb were not recorded, but from its weight (and the weight of empty brood combs of known area) its area was calculated as approximately 140cm^2, thus filling 60% of the frame. The colony's subsequent development is outlined in Table 8.5 and explained in more detail below.

In the second half of September the colony was taken in my absence to a site several km away, where on 1.x.79 the colony did not appear to have grown, but the comb had been well attached to the frame by the bees and contained sealed brood. (In fact the bee-keeper who moved the hive had thought it contained a different colony of *florea* belonging to him; but the comb in the frame did not appear to be different from the one installed on 13.ix.79, and he had probably mistaken this colony for one of his in another hive, 20, which had absconded.) Being October, the "sidr" tree, *Ziziphus spina-christi* (Rhamnaceae), the major honey plant at this season, was in flower

Table 8.5 Outline of principal events in the development of an *Apis florea* colony in an experimental hive (No. 13) at Khabura. Further details in text.

13.ix.79	Colony 13 derived from division of hive 9
1. x.79	Colony not grown in size but comb well attached to frame; sealed brood present
26. x.79	Comb occupies $\geqslant$ 75% of upper frame
12.xi.79	Upper frame completely filled with comb. Honeycomb encircles top bar and its depth is approximately 90mm. No comb built in lower frame
4.xi.79	Empty piece of brood comb introduced to lower frame
21.xi.79	Honey extracted
22.xi.79	Brood comb in lower frame empty but seen to be attached better by bees. Queen no longer ovipositing in upper comb - only pupae present
1.xii.79	Bees absconded

(Chapter VII) and on 12.xi.79 the top frame was completely full of comb. Beneath the top bar the upper honey portion was greatly expanded, as these cells are in natural colonies, and was nearly touching the front and back of the hive; the hive's depth being 10cm, some of the individual honey cells on either side must have been 4.5cm deep. The comb was completely covered by a dense curtain of bees and both the comb and bees encircled the top bar (Figure 8.7) so the hive roof could not rest on top (for this reason the roof had been removed c.10 days earlier). No comb had been built in the empty lower frame, even though there were several clusters of bees hanging from its top bar; some wax in the crack between the upper and lower frames was holding them together. The comb, honey and bees together weighed almost exactly 1kg on 14.xi.79. To induce the bees to use the lower frame an empty piece of brood comb, from another colony, was introduced to it.

On 21.xi.79, it was reported that the hive had been knocked over and about half the honey was lost, but there was no evidence to support this. However, the protruding parts of the honey cells had been removed by the bee-keeper, leaving the remaining comb flush with the frame. The weight of honey and wax taken was 530gm and the bees and wax remaining the following day, 22.xi.79, weighed 485gm. Thus the total weight of the colony was 1,015gm, a little greater than the weight 8 days earlier (little growth would be expected at this time as the *Ziziphus* had passed its flowering peak).

On 22.xi.79 it was seen that the bees had themselves attached, with wax, the introduced piece of brood comb to the lower frame, but there were no eggs or larvae in it. No eggs or larvae could be seen in the comb in the upper frame either, but older brood (sealed and unsealed pupae) was present. With the disturbance and loss of honey,

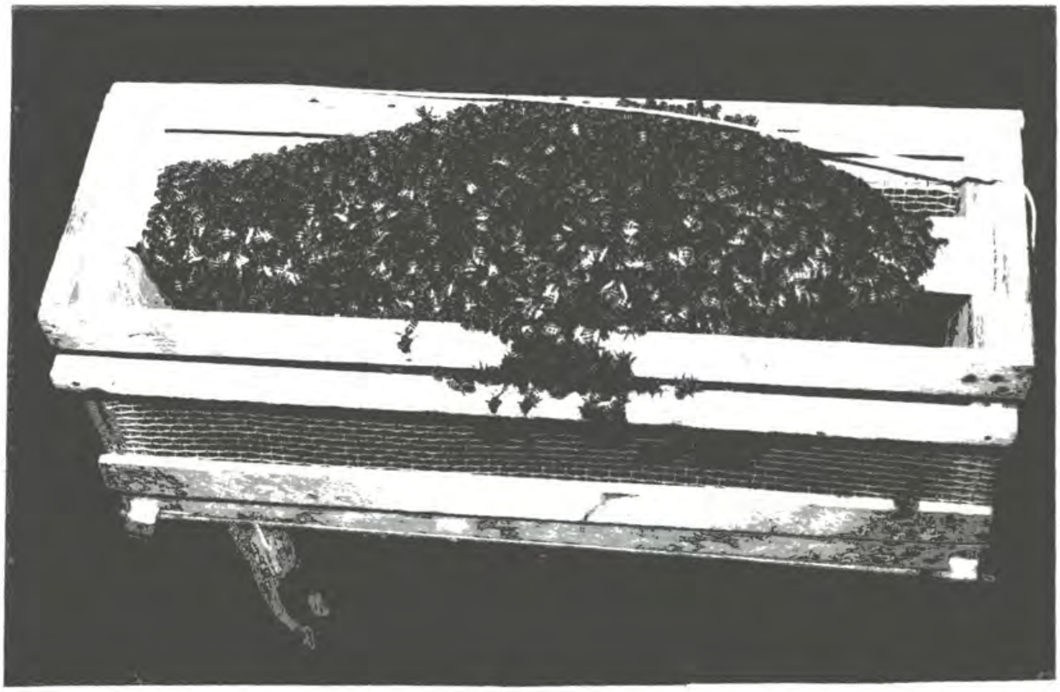


Figure 8.7 Top view of experimental *Apis florea* hive No. 13, at Qusabiat near Khabura, Sultanate of Oman, on 14.xi.79. A thick curtain of bees covers the whole comb, which had been built in the upper frame only. No comb was built in the empty lower frame below (not visible), even though the honeycomb was full and had been extended around the top bar of the top frame, so that it nearly touched the front and back of the hive. The bees appeared to be "overcrowded" and the roof could not have been fitted on the top without crushing some bees. The mesh entrance to the upper box is visible.

Figure 8.8 Upper frame from experimental *Apis florea* hive No. 13 (see Figure 8.7 and text) after the bees had absconded on 1.xii.79. The brood comb almost completely fills the frame; the top portion of the comb <u>had</u> been greatly expanded, partly around the top bar, for honey storage, but this was cut away on c.21.xi.79. The small piece of parallel comb, built subsequently, is visible in the centre.

brood rearing had ceased and, with little forage available in the immediate vicinity it was suspected that the bees might abscond. This they did, to an unknown site, 9 days later on 1.xi.79.

Apart from securing the introduced brood comb to the lower frame, the bees did not appear to have used it. However, after the honey had been taken they had built a small, half-moon shaped piece (7.3 x 4.1cm) of new comb, in the centre of and parallel to the upper comb (similar to parallel *mellifera* combs) and separated from it by a gap of 3 - 4mm, except for 4 horizontal supporting "struts" of wax. The way in which the main comb had been built within the shallow frame and how the small piece of parallel comb was attached are illustrated in Figure 8.8.

F. DISCUSSION

PART 2

1. "Gathering" wild swarms and colonies

In gathering wild *florea* colonies for management, the immediate problem is that of inducing the bees to re-settle on their comb after it has been removed from the natural site and placed in a hive, frame or split stick. Factors that may be important in preventing or inducing clustering and in determining the site selected, based partly on unpublished observations but particularly on experience with the colonies detailed in previous pages, are discussed here:-

(a) Damage to the comb and brood. This does not appear to inhibit *florea* from returning to their nest, as the parent bees of the "ghāf" tree colony at first re-clustered on their brood comb (Section E. 2.2). The greater size and/or damage or chilling in fact appeared to render the brood comb attractive to the bees of the colony (Hive 2) to which it was successfully introduced (Section E. 2.3).

(b) Memory of nest site. The evidence does not suggest that disturbed bees forget their original nest site in the short period during which the brood comb is removed. Workers will collect wax from a comb several days after they have deserted it (eg Hive 2 on 2.vi.80, p. 392). Also, the bees in the *Lantana* bush, when first moved to a new position 19m away, returned immediately to their original nest site (p. 393).

(c) Presence or absence of the queen. In the case of the "ghāf" tree colony, the queen had escaped detection among the bees on the comb before it was put in the frame and had apparently settled higher up the tree, where workers assembled around her in preference to the brood comb and associated disturbance at the old nest site. Part I gave a case of an absconding colony being twice induced to return to its nest site (Hive 2) by enclosure of the queen there. However, in another case (not detailed here), an attempt was made to settle a swarm of bees without a brood comb, by enclosing its queen in a cage attached to a frame (Hive 9) at the nest site first chosen by the swarm. Instead of joining the caged queen, the workers avoided the scene of interference and proceeded to cluster at another site several metres away.

Overall then and taking other trials into account, it appeared that the presence of a queen could be a deciding attractant force in settling a colony but was not consistently so, even when deserting her would lead to its demise.

In South America, queen excluders placed over the entrances of hives of Africanized *mellifera* bees straight after their acquisition (as swarms/feral colonies) generally prevented absconding. Some colonies attempted to abscond for up to a week, but only a few colonies actually absconded without their queen (Winston *et al* 1979). Morse (1977) gives the need for the worker bees to ascertain the presence of their queen as one explanation for the temporary settling of a swarm of *mellifera* close to the parent colony. If the queen does not join the cluster within a few minutes, the bees detect her absence and return to their original colony. Most swarming and absconding *florea* are thought not to have temporary cluster sites (Chapter VI, p.296-8) and possibly their queens take wing and join swarms more readily and reliably than queens of *mellifera*. Perhaps this is one reason why *florea* workers have not evolved such a strong attraction to an enclosed queen and will sometimes abandon her, to their own detriment, or take considerably longer than a few minutes to rejoin her (p.381-2). Nevertheless, despite this tendency of workers to desert their queen, if she does need to be enclosed for longer than an hour or two during a hiving operation and provided there is brood comb present, a hive with mesh (that allows the queen to move over the comb and continue oviposition) is to be preferred to a small queen cage that would prevent oviposition and create a temporary break in brood rearing. Such a break for 2 or 3 days might enhance the workers' desire to abscond still further.

(d) Presence or absence of the brood comb at the old or new site. Although initially attractive in the case of the "ghāf" tree colony cited above, presence of the brood comb was not sufficient to retain the workers under the conditions prevailing.

(e) Availability of alternative sites and their suitability relative to the old one. Again in the case of the "ghāf" tree colony, it was shown that once the bees, after the disturbance/"predation" at their original site, had assembled at a new site, persistent disturbance was needed to induce them to move. When they did move they did not return to their old site or to their brood comb nearby.

Building their nests on twigs and thus having numerous potential sites in areas with trees, from which a selection can be made, it appears that *florea* are reluctant to return in the short term to sites which have proved unsuitable. This behaviour of *florea* is likely to be different from that of *cerana* and *mellifera*, which nest in cavities such as tree trunks, as *florea* may have 100s of alternative nest sites available within a radius of a few hundred metres, whereas the other two species may have none.

The above evidence shows that a bee-keeper must act swiftly when gathering a *florea* colony, using the re-sited brood comb as intact as possible, caging the queen if found and causing the minimum disturbance. The use of synthetic pheromones in lures could prove valuable at this critical first stage in hiving wild *florea* colonies by providing an additional and more reliable way of attracting the bees quickly to the new site. *Mellifera* use their Nasonov pheromone in attracting swarm members to the entrance of a new nest site (Seeley *et al* 1979). Unpublished observations in the present work in Oman confirmed on several occasions the fact recorded by Free & Williams (1979) that *florea* workers also expose their Nasonov glands at new nest sites and after they have been disturbed at an existing site. In England a synthetic formulation of components of the Nasonov pheromone mixed with (E)-9-OXO-2-decenoic acid (the main queen mandibular gland pheromone) has been used with some success to attract *mellifera* swarms (Free *et al* 1981); further trials suggest that the proportions and purity of the components used are not critical for that species (Free *et al* 1982, 1983). Until the components of the *florea* Nasanov pheromone are elucidated, trials using *mellifera* formulations are indicated for *florea*, as the review by Free (1981) shows that the main components of the queen mandibular gland and alarm pheromones are the same in the two species. The lure should be attached to the frame, split stick etc to which the bees are to be attracted.

2. The use of movable frames by *Apis florea*

Little information exists on how *florea* will build a comb or combs when installed in frames similar to those used in modern *mellifera* hives. Pundir (1971) describes how a *florea* colony occupied 3 frames of a *cerana* (named *indica*) hive. Its original comb was tied to a central frame and was used for honey, pollen and brood; the bees built no comb in one of the adjacent frames, which was empty, but the third frame already contained empty *cerana* comb and was used for honey storage.

Dutton & Free (1979) demonstrated with a colony of *florea* that bees would continue to occupy the honey storage section of a comb when it was placed on the bottom bar of a wooden frame immediately above another frame supporting the brood section. The photographs in their article indicate that the bees did not actually expand the honeycomb in the upper frame in order to attach it to the top bar, but instead extended the brood comb in the lower frame. The colony absconded before honey extraction was attempted, but it would have been difficult without damage to the comb. Early experiments with frames by the author (unpublished) met with similar problems, in that bees showed a reluctance to extend a brood or honeycomb upwards into the empty space provided in an upper frame. Their natural behaviour appears to be to store most surplus honey in extended, empty brood cells below the support (which is all they can do when the support is the roof of a cave) and the remainder in the relatively small amount of comb that they build above it.

I have evidence that bees occupying a comb in a lower frame will use a frame placed above if it already contains comb. For instance a colony in Hive 6 given the old upper frame from Hive 13, which already had comb built in it as described here (p.396-8, Figure 8.8), started to clean and repair it and fill it with nectar/honey, a proportion of the bees moving up from the frame and comb below. The colony, however, already had queen cells and was in a rather poor site for forage in a very dry year. It swarmed, eventually leaving no bees behind, before the upper comb was filled with the quantities of honey hoped for and which might have been expected with more abundant forage and with a colony that was not about to swarm. This concurred with Pundir's (1971) observations that *florea* will use empty, nearby comb if surplus honey needs to be stored.

Circumstances prevented proper trials with wax foundation placed in shallow frames above hived colonies with brood in a lower frame. The intention was to see if *florea* would draw out the wax foundation and fill the resulting upper comb with surplus, extractable honey while the brood comb was extended downwards in the lower frame. In the three trials described here, the initial piece of brood comb was always tied into the upper frame with the intention that each colony should extend this brood comb downwards, as in nature, and eventually into the lower frame. It was hoped that the brood in the upper frame would be replaced, by the bees, with stored honey which would then be readily available for extraction, without damage to the brood that was to be reared in the lower frame. The colonies in Hives 22 and 13 both filled their upper frames completely with comb, replacing the brood in the uppermost portion with honey as they grew. However, neither of these colonies built comb in the empty frame below them, even though clusters of bees would hang from the top bar and they appeared "overcrowded" while occupying the shallow frame alone. Eventually both absconded, though whether this was of a seasonal nature (through changes in microclimate and forage - see Chapter VI), or due to their self-inflicted overcrowding, or to the re-queening (Hive 22) and honey extraction (Hive 13) disturbances to which they were subjected, is not clear. The re-queening did not appear to be important in Hive 22 as the bees started rearing brood again afterwards. The bees in Hive 22 and also Hive 2 absconded after the weather had become hotter (21.vi.79 and 2.vi.80 respectively), but those in Hive 13 absconded when it was getting colder (1.xii.79). The colonies could therefore have been searching for nest sites with a microclimate more favourable to the changed temperature regimes. June and December both follow periods of major honey flows (from "samur", *Acacia tortilis* (Forssk) Hayne and "sidr", *Ziziphus spina-christi* (L.) Willd. respectively - see Chapter VII) so the sudden dearth of forage might also/instead have been responsible for the bees absconding.

Whatever the cause or causes of absconding, there did appear to be a certain reluctance on the part of the bees to build comb of their own accord around and below the wooden bars partitioning the upper and lower frames; yet they inserted wax in the crack between the frames, joining them together. It was considered possible that the bees would not build comb and rear brood in the lower half of the hive because, without mesh in front of it, the light levels were too low. But the bees in Hive 2 readily reared brood in and extended the comb which was introduced to the dark, lower region of the hive, discounting this hypothesis. In any case the bees must be able to care for their brood when it is dark at night and under a thick outer curtain of workers so, as long as light is available for the forage communication dances on the honeycomb above, the light levels at the brood comb should not be important.

Though the results with Hives 22 and 13 were disappointing (nevertheless the latter did produce c. 0.5kg of honey in a poor year) in that the lower frames were not used, the results with Hive 2 were encouraging. With the stimulus of a comb already in the lower frame, brood rearing was abandoned in the upper frame in favour of honey and pollen storage. It is justifiable to speculate that at a site and season with abundant forage and a colony with a younger queen (see Section 3) a repeat of the experiment with Hive 2 would have produced an upper frame completely filled with comb and extractable honey and a brood comb that occupied most of the lower frame before drone and queen cells were started.

Though the colony "hived" by Dutton & Free (1979) did not appear to have attached its combs very satisfactorily to either frame, the 3 colonies described here and the one by Pundir (1971) all attached their combs securely to the insides of their frames. Therefore, it seems that *florea* will adapt to using frames assuming they are of suitable dimensions and have combs, or preferably foundation, carefully installed within. If no combs or foundation are available to stimulate downward extension of a colony from the upper to the lower frame, perhaps a reduction in the depth of the upper frame's bottom-bar and the lower frame's top-bar (which are juxtapposed) from 2 - 3cm (Table 8.1) to 1 - 1.5cm might remove this "barrier" for the bees and encourage the required downward comb construction. Even if the honey and brood frames are joined with wax, they should be easily separable with a sharp knife which would cause little if any damage to either comb, brood or stores. The honey could be extracted from the upper frame with an appropriately sized extractor and the comb returned to the hive. This should minimize disturbance to the colony and greatly reduce the concomitant risk of absconding, a frequent occurrence after honey is removed when *florea* is kept according to Omani systems.

What constitutes an appropriate frame size for the honeycomb and what for the brood comb? The fact that the honeycomb did not fill the upper frame of Hive 2 before the bees swarmed and that the bees in Hives 22 and 13 used the upper frames alone for both brood rearing and honey storage suggests that these frames were rather larger than was necessary. This was probably the case in the arid period during which the experiments were carried out, though had the bees in Hive 13 built a comb in the lower frame they need not have extended their honey cells to such a depth (c. 45mm on each side of the comb rather than the c. 9mm depth of brood cells) and the honey alone, if evenly distributed, might have filled much of the upper frame.

The size of the frames chosen was based on early measurements of *florea* combs, both wild (Chapter VI) and those kept by Omanis (Chapters III and IV), that had attained what was considered to be a large size. In a good season Omanis reckon that in the order of 1kg can be harvested from a single colony and it was estimated that the upper frames of Hives 2, 22 and 13 (areas 202.5, 202.5 and 232.75cm^2 respectively) would be able to hold such a yield. In view of the fact that harvests will not always be of this size and that some honey and all the pollen should be stored at the top of the brood frame (so that some food reserves are left for the bees after the honey in the upper frame has been taken), in future rather shallower frames - say 6cm high - should be considered and tested. With Hive 2, all the honey plus pollen beneath it were stored in the upper frame and no stores would have been left for the brood had it been removed. In seasons when copious honey was being produced these smaller frames could be used more than once; even two frames at a time, next to each other or to the lower comb (cf Pundir 1971), could be tried.

What is a suitable size for the lower brood frame? The brood comb in Hive 2 did not completely fill the lower frame before the colony swarmed but, as explained in the next section (3), it was considered that the colony swarmed prematurely because of a failing queen. Colonies with a brood comb area greater than the internal area, 681.1cm^2 of this frame (b) in Hive 2, were recorded during the present studies and a colony put in a similar frame (internal area c. 740cm^2) in an earlier model of hive filled it completely with honey and brood comb (worker and drone) before swarming, so such a size is not unrealistic.

If a colony were to fill a rather smaller, lower frame entirely with worker brood cells, of its own accord or perhaps encouraged by worker-sized wax foundation, whether it would then be inhibited from producing drone and queen cells and thus from swarming and would instead concentrate on honey production, cannot be predicted. The colonies 13 and 22 in very small upper frames intended for honey storage did not construct drone cells, but absconded. Possibly a brood frame intermediate in size between the upper and lower frames used would deter swarming but not induce absconding. This could be tested, bearing in mind the possibility that a medium-sized colony, restricted in such a way, might not have reached the full complement of workers necessary to maximize honey production. For this purpose, the area of the brood frame should be diminished by reducing the height, as drone cells are usually built along the bottom of a comb, not at the edges. However, if the upper honey frames are also made smaller as just suggested (p.406), enough space should be "allocated" to the brood frames for storage of a certain amount of pollen and honey at the top; therefore only a slight reduction in internal brood frame height would be necessary, eg to between 20 and 25cm.

Other suggestions for frame dimensions that would be worth testing, based on measurements of the size and shape of colonies kept by Nāsr Ahmad al-Ghaythi (Chapter IV) and of natural colonies, are given in Chapter VI.

3. Swarming and absconding from the experimental hives

Certain events in the development of both colonies 2 and 22 suggested that their queens were relatively old and, with the actual death of one queen (22), this appeared to bring about premature swarming and absconding; this was unfortunate for the hiving tests. Soon (approximately 10 days) after the introduction of the brood comb to Hive 2, queen cells were started (c. 9.iv.80) in the upper frame. Though the resultant queens did not survive, the colony was probably trying to re-queen itself because of a failing queen; the new queen cells etc (p. 390) observed on 27.iv.80 supported such a conclusion. This re-queening behaviour then developed into a swarming sequence which, from observations on "normal" colonies, the author believes does not usually occur till a colony is larger.

Likewise the colony in the *Lantana* bush, even before it was put in Hive 22, was about to re-queen itself - having a queen cell on a very small comb within 10 days of arriving at the bush. In this colony too, queen cells were started and eventually the old queen died or was killed. The queen which replaced her eventually absconded as did the queen or queens finally produced in Hive 2. Therefore, though it cannot be entirely discounted, I do not believe the bees in Hive 2 entered the swarming/absconding sequence because they were affected by the hive and/or the frames, but because they had an old queen.

Similar behaviour shown by *mellifera* colonies, termed "queen-loss swarming", supports this conclusion on *florea*, viz colonies of African (Fletcher & Tribe 1977) and Africanized (Winston 1979b) *mellifera* often swarm following loss of their queen even though their population size may be less than that at which reproductive swarming usually occurs. Indeed, contrary to popular belief, queen-loss swarming is also frequent in *mellifera* colonies of European origin, but not so frequent as in the tropical races (Punnett & Winston 1983).

The final absconding by the bees in Hives 2, 13 and 22, leaving large quantities of energy-rich wax behind, is not fully understood and occurs in some wild colonies of *florea* as well. As has already been mentioned in the previous section (p.403-4 and discussed in Chapter VI), such absconding may be due to seasonal changes in temperature and forage availability and not necessarily to unsuitable hives or frames, although the severe disturbance some hive inspections entailed (similar to an attack from a predator) could have been, in part, responsible.

How well could a hive with a mesh entrance cope with swarming? Before a large colony starts producing new queens it usually starts to produce drones in considerable numbers. As pointed out on p. 378 and 383 drones could not pass through the mesh used and their buzzing round inside a hive at certain hours every day is likely to disturb a colony. Therefore leaving the mesh on, in order to prevent the old queen leaving with a swarm, might not be advisable because of the drone problem alone. How the old queen and incipient swarm members would react to temporary enclosure of just the queen, when she was due to leave, was not tested here.

Even if the old queen did leave with a swarm or was removed prematurely to encourage the bees to remain as one large colony with a new queen, the mesh would have to be removed for a while (a few days) to allow one of the virgin queens to mate, and I suspect the first to emerge would then leave with a swarm - and possibly others - till none were left. Maybe removal of all queen cells except one and of the old queen shortly before her estimated date of departure would delay swarming, at least until the new queen was ovipositing and capable of participating in another swarming episode.

Swarm control is an area ripe for experimentation but the chances of hives of the design used being able actually to stop swarming are not good. Modern hives for *cerana* and *mellifera* do not stop large colonies swarming either, but they do allow preventative measures to be taken. The principles and practices of these measures, and also those of colony division, applied to large *florea* colonies (hived or unhived) before or as swarming is initiated,could produce similar methods of swarm control. These hives with mesh, however, should not be dismissed as they could still be effective in preventing absconding after a new queen has mated and returned to the hive, and after honey has been extracted - in addition to being effective at the initial hiving of *florea*, as was demonstrated with Hive 2 in Part I.

4. Other possible improvements to the hives

On the basis of the experiments described here, alterations to the frame sizes have already been suggested. These and other hiving trials not described have indicated that further modifications to the basic hive type would be worth testing. Some of these will be listed here to encourage people in Oman, India and wherever *florea* is found that there is much scope and need for further experimentation, requiring little investment in terms of materials.

(a) The mesh excluder (really "encloser") acted rather like a pollen trap, knocking larger pollen loads off foragers' legs. A "mesh" of horizontal slits, with only a few vertical bars, should be preferable eg a specially made queen excluder with the right spacing for the race of *florea* concerned, or "expanded metal" meshes which are produced commercially in many standard sizes.

(b) As bees using a fixed mesh entrance continued to use it, even after an adjacent entrance block had been removed, creating an "easier" entrance, it would be better to have hives with the mesh itself being removable.

(c) Instead of, or in addition to, having mesh as an entrance on the vertical front and back faces of the hive, as returning foragers usually land on top of the honeycomb the roof of the hive could be made of mesh - rather than of wood as here. Such a horizontal sheet of mesh could even be put between the upper honey and lower brood frames so that, with no roof, foragers could take off and land on the nest top directly, while the queen was restricted to the brood frame - just like a queen excluder in a *mellifera* hive.

(d) The roof was removed from Hive 13 to make room for the small amount of comb that was built round the top bar of the top frame and the bees on top of it; this created a satisfactory horizontal "dance platform" for the foragers. If a hive has a roof, enough space should be left above the top bar for dances to be performed there; *florea* will dance on a vertical surface, but studies in Oman and elsewhere have not determined whether dances on the vertical can communicate the position of sources of forage accurately (Chapter II, C.5, p. 53-56).

(e) A certain amount of debris, especially dead adults and immature bees, fragments of wax and pollen loads, usually accumulated in the bottom of the experimental hives. As they do not usually live in enclosed spaces like this, *florea* workers do not appear to have developed the "house-cleaning" activities, such as carrying dead bees out of the hive, practised by *mellifera*. This debris was frequented by various scavengers including cockroaches, crickets, ants and even the black-widow spider, *Latrodectus mactans* (Appendix I). Some, such as the ants, were potential predators or honey thieves, so to discourage these animals a hive from which the bottom can be easily removed and cleaned would be advantageous. A grid (with apertures too small for the queen to escape through!) would allow smaller particles to fall through, but dead bees would still need to be discarded.

(f) Some experimenters might find that a hive with mesh, along the lines described, despite its advantages is too complicated or expensive for the return of honey. They might therefore consider developing further the techniques used by skilled Omani bee-keepers that were examined in Chapters III and IV. One line I had wanted to follow if the *florea* foundation had been available involved use of the shallow frames designed for the hives. Fitted with a sheet of foundation, such a frame could be tied on top of a split palm frond mid-rib, "zoora", containing the brood comb of a colony; the bees might then store their surplus honey in the frame rather than around the split "zoora". The "zoora" or other stick used should be thin, as a thick support would result in much of the honey being stored below and at the sides of the "zoora"/stick and not in the frame above. Absconding could not be prevented this way, but colonies could be handled and even divided in the manner already practised successfully by some Omanis (Chapters III and IV). Most important, the frame could be easily removed for honey extraction without disturbance to the brood and returned to the colony with the comb intact.

G. CONCLUSION

These hiving experiments have demonstrated certain points about the possible "domestication" of *florea*. (i) A colony will develop enclosed inside a hive with a fairly narrow entrance made of mesh. (ii) Enclosing the queen within a cage or a hive will, but not always, deter the workers from deserting their nest. (iii) That *florea* will build their honey and brood combs in frames, one above the other, that can be separated. (iv) In a good season honey could probably be stored in a frame of an appropriate size in such a way that it could be extracted with little damage to the comb, which could then be returned in the frame to the hive. (v) The tendency of *florea* colonies to develop rapidly to a swarming stage and, when conditions are apparently not right, for all the swarms to depart (leaving the comb abandoned) is problematical. These hives provide no immediate answer as their mesh must be removed at such times to allow new queens to mate. To understand this last problem better, closer examination of the ways in which bee-keepers such as Nāsr bin Ahmad al-Ghaythi (Chapter IV) deal with swarming, eg by dividing colonies, should be rewarding.

The causes of absconding, its seasonal nature and preventative measures to reduce the likelihood of its occurrence have been considered in detail already (Chapter VI). Such preventative measures should be applied to colonies kept in hives, to further the chances of their successful usage, and also to colonies managed along more traditional lines. Again, closer examination of Omani practices to prevent absconding (Chapters III and IV), such as the movement of colonies from shady gardens in summer to more exposed sites in winter , should be helpful. Choosing nest/hive sites similar to those selected by wild colonies (Chapter II) is also commended; for instance, hives could be placed against S/SE facing walls (except in the hottest months) providing there is sufficient shady foliage to prevent too much direct insolation falling on the colony. If it seemed necessary to increase exposure or ventilation in such a situation, the front boards of the hives might be removed, though the colonies and queens, no longer enclosed, could not then be physically prevented from absconding.

Another point these experiments have indicated, of relevance to anyone conducting studies on *florea,* is that separate colonies should be kept for biological and hiving investigations. Regular inspections of or recordings on hived colonies, as were often performed here, constituted unnecessary interference liable to affect the outcome of a colony's use of a hive, as I discovered to my cost when bees absconded after weighings and other disturbances. Likewise, the natural swarming cycles, re-queening and other behavioural traits may be distorted through mis-handling in those colonies kept in hives, so biological studies should, in general, be conducted on "natural" colonies.

Finally, it must be stated that these observations were based on only one or two types of hive out of several that were built and tested at different seasons and under a variety of circumstances and there has not been space to detail and consider all the results here. Controlled conditions were impossible to obtain so it was difficult to make direct comparisons of success and a balanced assessment of each hive type. The outcome of the hivings was by no means consistent and there were many failures, as demonstrated by the data on absconding in Chapter VI. However, signs of progress were sufficiently encouraging to indicate that there was still scope for much improvement in hive materials and design and in management techniques and that the search for a hive for *florea* should be intensified and not abandoned. Success could mean increased crop pollination, more honey and an extra source of income for people in Oman, India and south-east Asia.

CHAPTER IX

FINAL DISCUSSION : ECOLOGY AND MANAGEMENT OF *APIS* IN HOT REGIONS

1. Introduction

This thesis has not been a detailed investigation of a single aspect of the biology of *Apis florea* in Oman but a broad study of the natural history of the species, which should provide a framework for and indicate the direction of future research. Some conclusions may require modification when results emerge from studies based on larger sample sizes or performed during wetter periods. Nevertheless, I hope these findings will make a small contribution to the fund of knowledge on the ecology of honeybees in the wild, which was so limited until recently (see p. 1).

The individual topics covered in the thesis have already been discussed at length in the appropriate chapters; in this section I will try to highlight and draw together some of the main points concerning the adaptations of *Apis* to warm environments. Seeley (1983) and Winston *et al* (1983) have already examined some of the differences between species and races of honeybees that have evolved in temperate and in tropical areas and Koeniger (1982) some of the interactions among the 4 *Apis* species; results from Oman will be discussed in relation to their findings.

2. Foraging strategies

Conclusive information on foraging strategies in Oman was lacking but the implications were of significance. The data in Chapter VII showed that there was considerable niche overlap between *florea* and *mellifera* in terms of the plant species exploited, while the ability of the larger *mellifera* to forage at lower temperatures than *florea* might result in exploitative competition detrimental to the latter (Chapter V, p. 237-8) when the bees are visiting the same patch of flowers (cf Linsley *et al* 1955; Roubik 1978, 1982). However, in Chapter VII it was also suggested (p.366) that *florea* might forage on a larger number of plant species than *mellifera* in a given location, because its smaller size enables it to exploit smaller flower patches and species yielding smaller rewards of nectar and pollen. Thus *florea* were recorded gleaning pollen from previously tripped lucerne flowers (p.362-3) and often seen foraging for nectar and pollen on the tiny florets (corolla 2.25 - 2.5mm long) of *Phyla nodiflora* (Verbenaceae) while *mellifera* were not, though they were known to use this species elsewhere in times of dearth (Eisikowitch & Masad 1982). Analyses of honey samples from *Trigona iridipennis*, *florea*, *cerana* and *dorsata* in Sri Lanka also showed that the number of different pollens and thus forage species used was highest for *Trigona*, the smallest of the 4 honeybees, and greatest for *dorsata* (Koeniger & Vorwohl 1979; Koeniger 1982). Differences in body size, eg in ability to trip papilionaceous flowers, and tongue-length (cf *Bombus* spp., Ranta 1983 and discussed on p.360-1) may also have resulted in *florea* and *mellifera* showing distinct floral preferences.

According to Heithaus (1979a) highly eusocial species comprise a larger proportion of Neotropical bee faunas than of New World temperate faunas and this is presumably the case in the Old World too. The climate being less seasonally severe it may be particularly advantageous to be polytropic, social and consequently active all year round. In contrast, oligotropy and limited periods of activity (ie a few months/ year) as exhibited by many Megachilidae and Andrenidae (see p. 315

and p. 337 for references) may by and large be a better adaptation to temperate climates than the all-year activity of honeybees, which can survive winter only when nests are well stocked and insulated.

Hot arid areas like Oman, however, have temperatures permitting honeybee activity nearly all the year round, but tend to be seasonal or erratic from year to year as far as forage is concerned. What is the best foraging strategy under such conditions, with a few major sources of forage (*Acacia tortilis, Ziziphus spina-christi*) flowering for limited periods and a large number of minor species at other times? As Baker & Hurd (1968) said "in arid or desert environments one might assume that (use of) the broadest possible range of pollen sources would favour the survival of polylectic bees." Yet they go on to point out that "the overwhelming majority of desert bees, at least in continental areas, appear to be oligolectic ..." Such a strategy is no doubt well-suited to univoltine, solitary bees but where social, perennially active honeybees do occur in arid regions, as Baker & Hurd first suggested, survival is likely to be enhanced if many flower species can be exploited. Indeed, the successful build-up of *florea* colonies in spring in Oman to exploit the main *Acacia tortilis/Prosopis cineraria* nectar flow seemed to depend on their utilization of many "minor" and "negligible" sources (p. 347-9).

Yet honeybees (*mellifera*) in temperate regions have been shown to focus their forager force on a few high-quality patches (Visscher & Seeley 1982; Seeley 1983) and seem to produce most honey when large areas of a single crop are available (eg oil-seed rape in the U.K., eucalypts in Australia). This strategy may be less appropriate for a diverse tropical flora or for arid areas where forage patches may be of low quality. If tropical *mellifera* do exploit more species in an area than do temperate *mellifera* and *florea* even more species still as the limited evidence suggests, I speculate that these differences in foraging strategy may be one reason why (i) introductions of temperate *mellifera* to the tropics have not always been successful (Crane 1980, 1982) and why (ii) in Oman, *florea* is more widespread than *mellifera* and is relatively productive in dry years (p. 356) even though the smaller bee may be at a competitive disadvantage when temperatures are low.

3. Nest-site selection : a response to microclimate and predation

In Thailand Seeley *et al* (1982) concluded that predation was a "pervasive and powerful force in the evolution of tropical bee (*Apis*) societies" and that this was a major determinant of the nest sites chosen by *florea*. Yet in Oman, though predation pressure from man was high (Appendix I) much evidence suggested that appropriate microclimate at the nest site was more important. The decline or cessation of brood rearing by *florea* at high altitude (Chapter V) and in winter, particularly in small colonies (Chapter VI), their less effective (than *mellifera*) brood-nest thermoregulation (Chapter V) and their preference for nest-sites in the SE sector of trees, but avoidance of over-exposed sites in date-palms (Chapter II) all pointed to this conclusion. Flight activity patterns (Chapter V), the seasonal pattern of absconding (Chapter VI), circumstantial evidence for some seasonal variation in nest-site choice (Chapter II) and the use of different apiary sites in summer and winter by Omani bee-keepers (Chapters III and IV) were further indicators of the critical role of temperature in the biology of *florea*.

Perhaps the large diurnal and annual ranges of ambient temperature in Oman (Appendix II) put a premium on temperature relations, while such influences are less important in tropical areas like Thailand.

However, even in these tropical environments, I believe more attention should be paid to the role of colony temperature regulation and nest microclimate in the biology of all 4 *Apis* species, especially *florea* and *dorsata* which nest in the open, and measurements of characteristics that indicate their importance, such as seasonal absconding, tree sector of nest and so on, should be made. Nevertheless, in Oman and elsewhere, dearth and predation cannot be dismissed as important causes of absconding. The fairly well concealed nest sites usually chosen by *florea* must reduce the risk of attacks from man, if not from other predators, such as ants, which do not use visual cues to locate colonies.

4. Evolution of warm-climate honeybees

Seeley *et al* (1982) present a hypothesis on the evolution of interspecific differences among the 3 species of honeybee in Thailand. The observations just made (p.415 - 418) on probable differences in the foraging patterns of *florea* and *mellifera* are consistent with their first proposal that interspecific foraging competition could have led to worker size differences. However, I am not convinced by their second proposal that competition for nest cavities led to nest site differences (open-air or cavity). They and Koeniger (1982) assume that cavity-nesting in *Apis* is ancestral and open-air nesting is more advanced, even though *florea* and *dorsata* are considered to be the more primitive of the living honeybees and similar to the ancestral type (Culliney 1983). I suggest an alternative hypothesis.

Perhaps both open-air and cavity nest-sites were used by ancestral *Apis*, but cavities were not favoured all year round for microclimatic reasons, as in Oman (Chapter II), because colonies with a single comb (the primitive condition?) were unable to regulate the temperature inside. Sympatric speciation may then have started when colonies in cavities (but not in the open-air) began to build multiple combs, making cavity thermoregulation a possibility and the site therefore potentially suitable all year round.

Having developed the multiple-comb habit, *cerana/mellifera* were able to spread to temperate areas where the increased honey storage capacity of cavities and their insulatory properties enabled them to survive the long winters. Meanwhile the two open-air nesting species diverged (foraging competition?) but maintained their migratory tendencies over long (*dorsata*) and short (*florea*) distances, so that they could take advantage of sites with the best microclimate and foraging opportunities. This mobility would be made possible by an abundance of nest sites, not guaranteed to cavity-nesting honeybees.

In temperate areas, large winter food stores are necessary for honeybees and nesting in the open or in sub-standard cavities is liable to prove fatal, while in warm-climates the need to stay in one high-quality cavity to build up food reserves is less. Thus the *mellifera* that have evolved in the tropics now use a wider range of nest-sites (p. 16 - 17) and store less honey (Winston *et al* 1983) than their temperate counterparts. They have also retained in warm-climates, as an optional strategy, the ancestral trait of absconding which is useful when forage or microclimate change or predation occurs (Fletcher 1975 and 1976; Winston *et al* 1979); the consequences of moving to a sub-optimal site are likely to be less severe than in a temperate climate. Thus absconding still occurs in tropical *mellifera* and *cerana*, as well as in *florea* and *dorsata*, because of seasonal factors, but perhaps to a lesser extent because their multiple combs allow better control of nest microclimate (except at very high ambient temperatures?) and a small nest entrance to a cavity does afford more reliable protection from predators.

One other attribute that cavity-nesting bees had to acquire was the more sophisticated communication dance that transposes the position of the sun, invisible from the nest, to the direction of gravity. That *florea* and *dorsata* cannot dance effectively if the sky is obscured (Lindauer 1957), is further evidence that cavity-nesting is an advanced feature, open-air nesting ancestral, and lends support to my hypothesis.

5. Management of warm-climate honeybees

Though the contrasting hypotheses of evolution described above are speculative, I believe they are important to help our understanding of the selective pressures which have shaped temperate and tropical honeybee societies. Knowing these environmental pressures and the corresponding adaptations of honeybees, appropriate bee-keeping practices can be developed on a sound basis.

Absconding is one of the main problems facing keepers of *florea* and other *Apis* in the tropics and in the past it has been attributed primarily as an adaptation to predation (Seeley 1983) and to climatic factors that cause a local floral dearth (Winston *et al* 1983). The findings in this thesis point to poor nest microclimate as another important cause, at least in *florea* and by implication in the other tropical *Apis*. Knowing this bee-keepers can at least try to control the microclimate for colonies at an apiary, according to the season, by providing well-insulated hives, shade and so on. Where the absconding tendency is seasonal, it may even be better to simulate the trait by actually moving colonies to another site.

However, that the absconding tendency is seasonal and varies between races indicates that it is genetically as well as environmentally controlled, as are other ecological and behavioural traits (Cornuet &

Louveaux 1981). Therefore there is also likely to be genetic variability within races which would provide a basis for selecting lines of *florea* and tropical *mellifera* and *cerana* with a low absconding rate. Perhaps this has already happened with the *jemenitica* of Yemen and northern Oman, which have a long history of domestication (p. 11 - 13), as the latter population did not show strong absconding tendencies in my experience. Selective breeding in the long-term may be a better option than importing temperate bees to the tropics. Though already well-adapted to management and to storing large quantities of honey for winter, the observations on p.415 - 418 do suggest that temperate honeybees may not always be so well adapted to a warm-climate flora and to other features of tropical environments such as predation (Winston *et al* 1983).

So *florea*, as demonstrated by the problems of keeping them in experimental hives (Chapter VI and Chapter VIII) appears to be similar to other tropical *Apis* in being poorly adapted to management, but well-adapted to cope with its environment. There are no easy solutions to this predicament for *florea* keepers and all credit must go to those Omanis (Chapters III and IV), such as Nāsr Ahmad al-Ghaythi, who coped with the vicissitudes of this species to produce small, but marketable quantities of honey. Their success and the indications that *florea* would use combs in movable-frames that would facilitate honey extraction (Chapter VIII), signify that bee-keeping with *florea* can be developed further. Continued biological and practical research, for which suggestions were made in the various chapters and especially on p. 409-414, is definitely warranted.

SUMMARY

1. *Apis florea* is found in natural and cultivated habitats throughout northern Oman and in most regions there are specialists managing colonies for their honey. *Apis mellifera jemenitica* occurs wild in Dhofar and is kept in log hives in the central Jabal al-Akhdār, where it is reported to have been introduced between 1688 - 1711 A.D.
2. In cultivated areas wild *florea* selected nest sites in well-foliaged trees such as *Citrus*, avoiding over-exposed positions in the more abundant date-palms.
3. The mean diameter of nest support branches was 13.6mm. Nest height distribution was bi-modal, matching the availability of sites. The primary mode was 0 - 1.0m, the secondary one 3.0 - 4.0m and the mean height from the ground 3.28m.
4. There was significant selection by *florea* for nest sites in the SE sector of trees (mean angular position, 155^o) and on the SE side of walls. A mean colony shade value of 75.1% was determined and it was concluded that sites partially exposed to insolation, particularly in the morning, were being selected to facilitate colony thermoregulation and foraging.
5. There was some evidence for seasonal variation in the types of nest-site selected; the microclimate of natural and man-made cavities may be particularly suitable at one season, but unfavourable at another.
6. The sites chosen for managed *florea* colonies by bee-keepers were partly for their own convenience, eg mean height 1.84m, but were also selected to meet the supposed requirements of colonies for warmth or shade. The widespread siting in *Citrus* trees probably

suited both bee-keepers and bees. Natural and man-made cavities were popular with some bee-keepers and their orientation was often taken into account. Some bee-keepers used different sites according to time of year.

7. There was much variation in the skills and techniques of *florea* keepers, but the use of a split palm-frond midrib was a common feature. Several practices are described, including methods of honeycomb removal and of hunting for wild colonies; the survival of colonies away from cultivation is discussed.

8. The apiaries and bee-keeping practices of Nāsr Ahmad al-Ghaythi are described in detail. He kept successfully up to 30 *florea* colonies; such numbers under management have not been recorded before. A key feature was Nāsr's "migration" of colonies between shady date garden in the hotter months and tree sites in the nearby plain ("sayḥ", p. 136) for exposure to some insolation in winter.

9. The annual cycle of *florea* under Nāsr's management is related and discussed. The main honey flows came from *Acacia tortilis* in April/May and *Ziziphus spina-christi* in October. A summer absconding season was apparent. Nāsr divided colonies, particularly in April, and so compensated for such losses.

10. *Jemenitica* kept brood temperature (T_B) near 35°C at ambient temperatures (T_A) of 7°- 37°C; *florea* maintained T_B near 35°C at high T_A but thermoregulated less effectively than *jemenitica* at $T_A < 30^{\circ}$C. At 1950m, *florea* brood rearing ceased with T_A 7° - 20°C, but cluster temperature was kept above 20°C. *Florea* exerted little thermoregulatory control over the honeycomb.

11. *Jemenitica* flight activity started at lower T_A (12°C) than *florea* (18°C) and peak activities occurred at about 22°C and 30°C respectively. At 1950m in winter, *florea* foraged for only a

short period in the warmest part of the day. At 10m in summer, *jemenitica* foraging peaked at dawn before *florea* had started; *florea* activity was greater than that of *jemenitica* in the hotter part of the day. In both species flight activity, though modified by acclimatization and other factors, showed significant correlations with T_A and hypothetical curves of flight activity against T_A (0^o - 50^oC) are presented. The adaptation of *florea* to a higher range of T_A than *mellifera* and the ecological consequences are discussed.

12. Maximum worker brood production by *florea* was in March - May and October - November. 8 - 17% of colonies stopped rearing brood in summer (June, July, August). 45 - 50% stopped in winter (January - December), particularly the smaller colonies; this was attributed primarily to poor colony thermoregulation at low T_A and secondarily to floral dearth.
13. Adult *florea* drones were recorded in all months but their production appeared to be seasonal, February - August and especially April (60% of colonies) and October - November (30% of colonies) and mainly in response to forage. The main *florea* swarming season was March - July, peaking in May, with a small episode in October - November.
14. After initial downward extension, brood comb construction is greatest horizontally, probably to prevent it tearing away under its own weight. Frame shapes and sizes for *florea* combs are suggested.
15. Information on absconding was obtained from monthly records of the failure rate of "hiving" *florea* and from the absconding rate of successfully hived colonies. The mean residence time of successively hived colonies was 101.6 days, range 17 - 493 days. Absconding was attributed to (i) Predation/Disturbance, (ii) Inappropriate nest sites and (iii) Dearth of forage or water.

Microclimate (ii) was thought to be a major cause in Oman, but with absconding most frequent in summer a seasonal trend, probably with a genetic basis, was evident.

16. Seven absconding colonies that were re-located had moved only 4 - 65m to their new sites, while 7 reproductive swarms had moved 25 - 800m or more. There was no evidence for long distance migration; such reports are better explained in terms of local movements and/or population fluctuations. Except in one instance, no interim cluster sites were recorded.

17. Field observations, pollen analysis and the literature provided data for "Floral Calendars" of *florea* forage in 3 broad habitat types:- 1. Oases in the interior of Oman. 2. Coastal Bātina gardens. 3. Wild. In terms of number of forage species the habitats were ranked 1>2>3. The tree and ground flora density were greatest in 1, but 3 of the 4 most important forage sources, *Acacia tortilis*, *Prosopis cineraria* and *Ziziphus spina-christi* were most abundant in 3. The 4th, *Citrus*, occurred only in 1 and 2.

18. It appeared that *florea* and *mellifera* in 1, 2 and 3 depended on a large number of "minor" and "negligible" forage sources and that high honey yields from the main *Acacia/Prosopis* flow required an abundance of early spring flowers for colony build-up. *Florea* seemed to fare better in dry years and was recorded using more plant species in Oman than *mellifera*. This was attributable to either (i) under-recording for *mellifera* or (ii) *florea*'s ability to exploit small flower patches and/or flowers yielding less nectar/pollen.

19. Flowering patterns and phenology in Oman are discussed. The majority of bee species exhibited a restricted flowering pattern, with flowering in summer more scarce than winter flowering. The separate flowering periods of the dominant trees *Acacia tortilis* (April - May) and *Ziziphus* (October - November) may have co-evolved with the requirements of insect pollinators such as *florea.*

20. Three experimental hives for *florea* are described. Principal features were a lower brood and a shallow upper box (super), each with a frame. The supers had mesh entrances which allowed workers to forage but enclosed the queen.

21. A swarm installed in one hive, after absconding twice and returning each time as the queen was enclosed, settled to rear brood. An abandoned brood comb from a wild colony was introduced; honey was then stored in the upper frame and brood reared in the lower one. Colonies put in shallow upper frames in the other 2 hives completely filled them with comb, using the 1 frame for both honey and brood. All 3 colonies eventually absconded, one following a swarming sequence.

22. These and other results demonstrated that *florea* could adapt to using a honeycomb, suitable for extraction, in a frame separate from the brood comb, but starter comb or foundation was needed to initiate such usage. Drawbacks to the hives, possible improvements and other *florea* management techniques are discussed.

23. Adaptations of *Apis,* particularly *florea,* to warm environments in terms of foraging strategies and nest-site selection are discussed. Other than from man, predation pressure on *florea* in Oman seemed relatively low. Predation has been considered a major factor determining nest-site selection in Thailand, but in Oman micro-climate was thought to be of equal or greater importance for

florea. On this basis a hypothesis is put forward concerning the evolution of cavity and open-air nesting habits in *Apis*.

24. Absconding in response to poor microclimate, predation and dearth though a valuable adaptation in warm environments makes tropical *Apis* hard to manage; preventative measures and selective breeding are indicated, and for *florea* management further research and development.

APPENDIX I HONEYBEE PESTS AND PREDATORS IN OMAN

These are listed, with comments, in an order corresponding to that of Morse (1978). Specimens of nearly all the organisms were collected in Oman; various taxonomists, most at the British Museum (Natural History), kindly helped with identifications. Pests of honeybees mentioned in the literature and known to occur in Oman eg rats, mice, lizards, have been excluded if there was no local evidence indicating they were a problem. It is hoped to publish at a later date further details of the information on which this summary is based, including provenances and some discussion. Morse (1978) has reviewed the biology and control of most of the species concerned and Fry (1983) that of bee-eaters in particular. No microscopical examinations of bees were undertaken, but many examinations of colonies of both honeybee species and their brood revealed no signs of disease or of parasitic mites such as *Varroa*.

Scientific and common names	Comments
I INSECTS	
LEPIDOPTERA	
Galleria mellonella (L.) (Greater Wax Moth)	Not recorded in any *Apis florea* colonies, but a serious pest of *Apis mellifera jemenitica* in log hives.
Acherontia styx styx Westwood (Death's Head Hawk-moth)	Northern Oman. Found adjacent to some *florea* colonies, probably taking nectar/honey at night, and in *jemenitica* hives (Langstroths).
Acherontia atropos (L.) (Death's Head Hawk-moth)	Dhofar. In *mellifera* hives (Langstroths).
DIPTERA	
Asilidae (Robber flies) esp. *Promachus laciniosus* Becker	Seen to prey on adult *florea* workers and drones and *mellifera* (Australian origin) workers - usually foragers close to colonies were taken.

Scientific and common names	Comments
Braula sp. (Bee Louse)	Reported on *mellifera* in Dhofar (Jan Karpowicz, pers. comm.)
HYMENOPTERA	
Formicidae (Ants) Including:- *Pachycondyla sennaarensis* (Mayr) *Monomorium* spp. *Crematogaster* spp. *Camponotus hova* Forel *Camponotus fellah* Emery	See Whitcombe (1982c) for details. I recorded c. 24 species in Oman and many were clearly irritants to colonies of both *Apis* species, but none appeared to be major predators as was *Oecophylla smaragdina* on *florea* in Thailand (Seeley *et al* 1982). Weak colonies, of *florea* in experimental hives and of *mellifera* in log and modern hives, were evidently more susceptible to attacks than stronger colonies and wild *florea* (to which ants have limited access). Several ant species scavenged on abandoned combs and their prior activities may have been a stimulus to absconding. Sticky ant barriers on nest-supporting branches were absent, presumably because not required rather than due to raw material shortage.
Vespa orientalis (L.) (Oriental Hornet)	Preyed on adult *florea* and *mellifera*, sometimes picking off individuals at or near the nest/hive. Could probably deplete a weak colony's field force, eventually leading to its demise.
Polistes indicus Stolfa) *Polistes wattii* Cameron) (Paper Wasps)	Not actually seen to take bees in Oman, but flew in close proximity to their colonies and this genus is listed in Morse (1978) as attacking honeybees.
Liris haemorrhoidalis (Fab.) (Sphecid Wasp)	Seen flying in front of *florea* colonies and inducing synchronised shimmering defence response (cf Seeley *et al* 1982) by workers in the protective curtain. No actual predation recorded.
Philanthus triangulum Fab. (Bee Wolf)	Recorded in northern Oman and Dhofar near to *mellifera* colonies and foragers, though not seen to capture any. Probably of minor or negligible importance only, though can be serious elsewhere.

Scientific name and Common Name	Comments
ORTHOPTERA	
Symploce persica Bei-Bienko *Blatella* sp. (Cockroaches) *Acheta* sp. (Cricket)	In experimental hives of *florea*. Not predatory, but probably feed on colony debris (wax, pollen, dead bees). Unhygienic and may irritate bees.
PSOCOPTERA	
Liposcelis ? bostrychophilus (Psocid or Book House)	As above.
II ARACHNIDS	
ARANEIDA	
Latrodectus mactans (Black Widow Spider)	Web built, with egg sac, in experimental *florea* hives catching adult workers and drones.
Plexippus paykulli (Jumping Spider)	One male seen to catch *florea* worker near managed colony.
Argiope sp. (Orb Weaver)	Webs occasionally found near *florea* colonies and to have caught adult workers.
Sporassidae indet. (Heteropodidae) (Giant Crab Spider)	Seen running over *jemenitica* Langstroth hive at night.
Araneida indet.	Small (<5mm), fast-moving spider. Ensnared *florea* worker, on table next to colony, by running round it and wrapping it in thread.
SOLIFUGIDA	
sp. indet. (Camel or Sun Spider)	Seen attacking *florea* colony transferred to a box and taking individual adults; workers also attacked the spider before it was removed (Mjeni, pers. comm.). The bees absconded the next day, but had been subjected to other disturbances.

Scientific and Common name	Comments
III AMPHIBIANS	
Bufo orientalis Werner (Oriental Toad)	Seen on supporting branch of one very weak *florea* colony near ground and assumed to be in part responsible for its decline. Also claimed by Nāsr (Chapter IV) to be a problem in his *florea* apiary.
IV BIRDS	
Merops orientalis muscatensis (Little Green Bee-eater)	Resident and partial migrant. Pairs and small family parties sometimes perched near *florea* colonies and would take bees leaving and/or returning to the nest, depleting the number of foragers. Also prey on *mellifera* foragers. Minor but regular pest.
Merops apiaster Linn. (European Bee-eater)	Both species were summer breeding visitors, but more abundant as passage migrants; *M.s.p.* was the most common. Flocks, some mixed, of up to 40 birds, were recorded feeding at apiaries of *mellifera* (Australian origin, in Langstroth hives) and weakened the colonies present. *M.s.p.* and probably *M.a.* also preyed on *florea.* See Gallagher & Woodcock (1980) for further details of these 3 *Merops* in Oman. N.B. Bee-eaters can be beneficial to bees and agriculture as they feed on ants (winged forms), myiasis causing flies and other harmful insects, so bee-eater predation of honeybees should not be tackled by killing the birds.
Merops superciliosus persicus (Blue-checked Bee-eater)	

Scientific and Common name	Comments
V MAMMALS	
Mellivora capensis (Ratel or Honey-badger)	Predator of *mellifera* in modern hives in Dhofar (Berkeley 1979).
Homo sapiens (Man)	By far and away the most important "predator" of *florea* in northern Oman. Colonies with brood combs re-established by bee-keepers/hunters, rather than discarded, would be more likely to survive. However, their subsequent fecundity might be reduced by further honey removal and swarm control measures.

SUMMARY:- There is a need to quantify further the effects of pests and predators on *florea* in Oman to allow comparison with predation levels in other countries, such as Thailand (Seeley *et al* 1982). However, briefly assessed, this data indicates that, though there are a number of organisms that may irritate colonies, steal their stores or destroy comparatively small numbers of individual bees, other than by man, predation is not by and large a major pressure on *florea* in Oman. The predation by man is unusual in that it may result in the perpetuation of a colony and its protection from other predators, despite subsequent losses of honey; nevertheless man is the predator whose activities can most easily lead to the greatest drop in fecundity of *florea* colonies and to their complete destruction. Keeping *florea* in hives increased exposure to various pests (ants, spiders, cockroaches etc) but may have given some protection against the death's head hawk-moth and toads.

APPENDIX II

TEMPERATURE AND RELATIVE HUMIDITY ON THE BĀTINA COAST

To give an indication of the meteorological conditions experienced by *Apis florea* in Oman, temperature and relative humidity data from the National Meteorological Service at Seeb Airport (23° 35' N, 58° 16' E. Alt. 14m) for 1979 and 1980 have been graphed as follows:-

Figure A.1 :	Maximum temperatures
Figure A.2 :	Minimum temperatures
Figure A.3 :	Mean temperatures
Figure A.4 :	Relative humidity

The temperature and humidity regime at Khabura (c. 130km to the WNW and also on the Bātina Coast), where much of this research was performed, was similar to that at Seeb but conditions in the interior of Oman were more extreme; see Whitcombe (1982d) for additional graphs and detailed comparisons. Further climatic information, including records of rainfall, can be found in Horn *et al* (1977), Horn & Nielsen (1977a and b) and Gallagher & Woodcock (1980).

Fig A.1 SEEB. Monthly means of daily maximum temperature; range for each month indicated.

(Data from Sultanate of Oman National Meteorological Service)

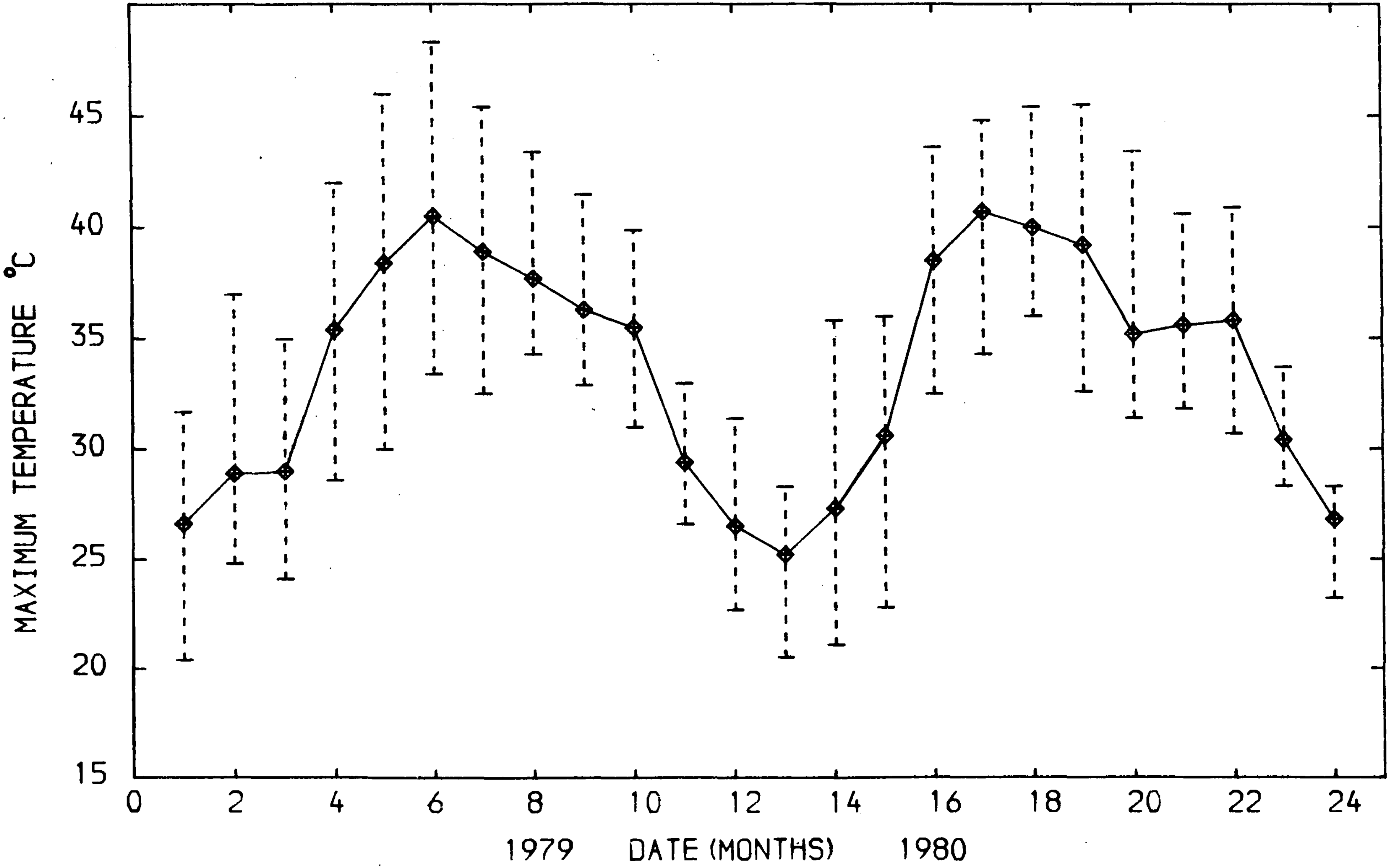


Fig A.2 SEEB. Means of daily minimum temperature ; range for each month indicated.

(Data from Sultanate of Oman National Meteorological Service)

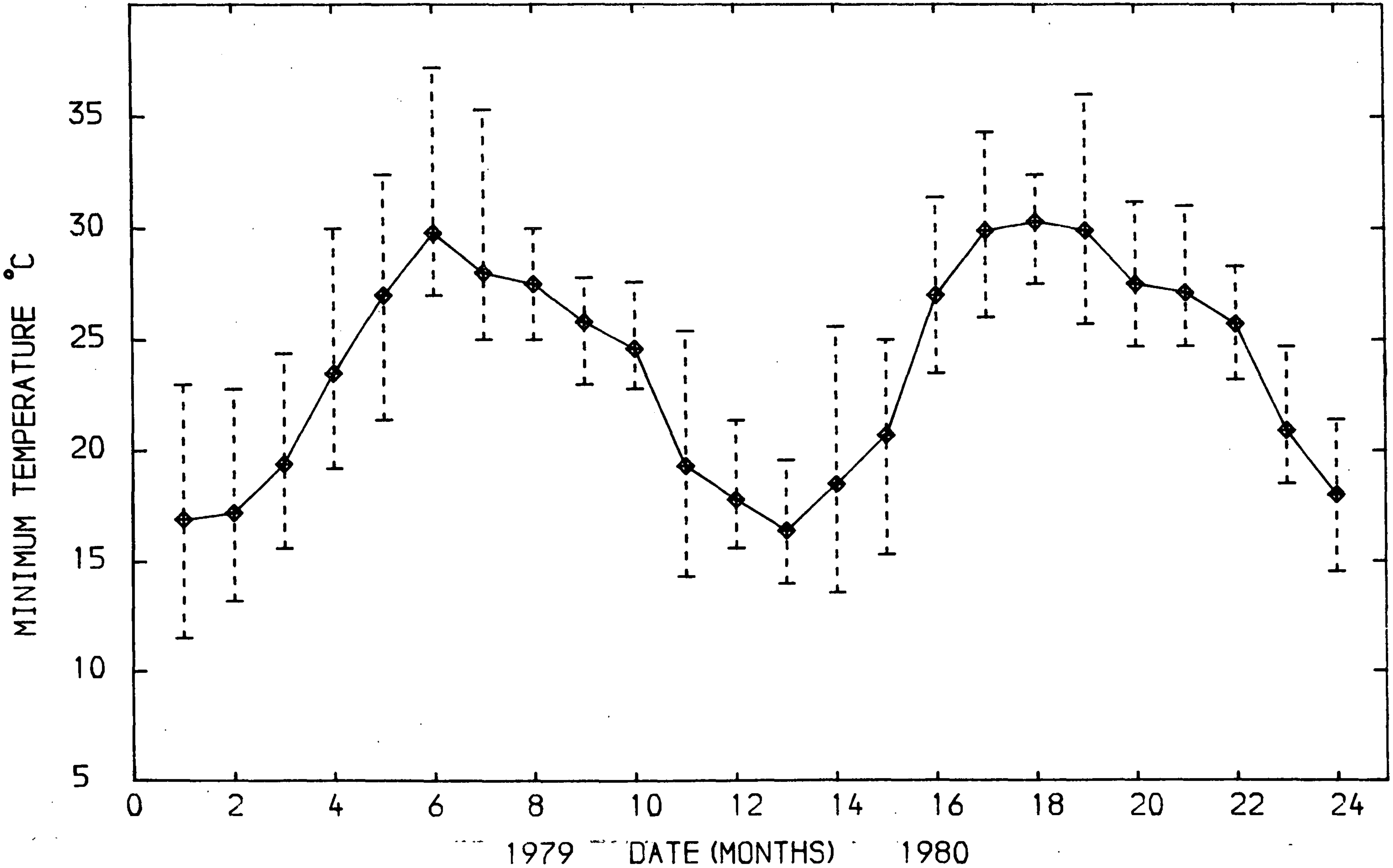


Fig A.3 SEEB. Monthly means of daily mean temperature; range for each month indicated.

(Data from Sultanate of Oman National Meteorological Service)

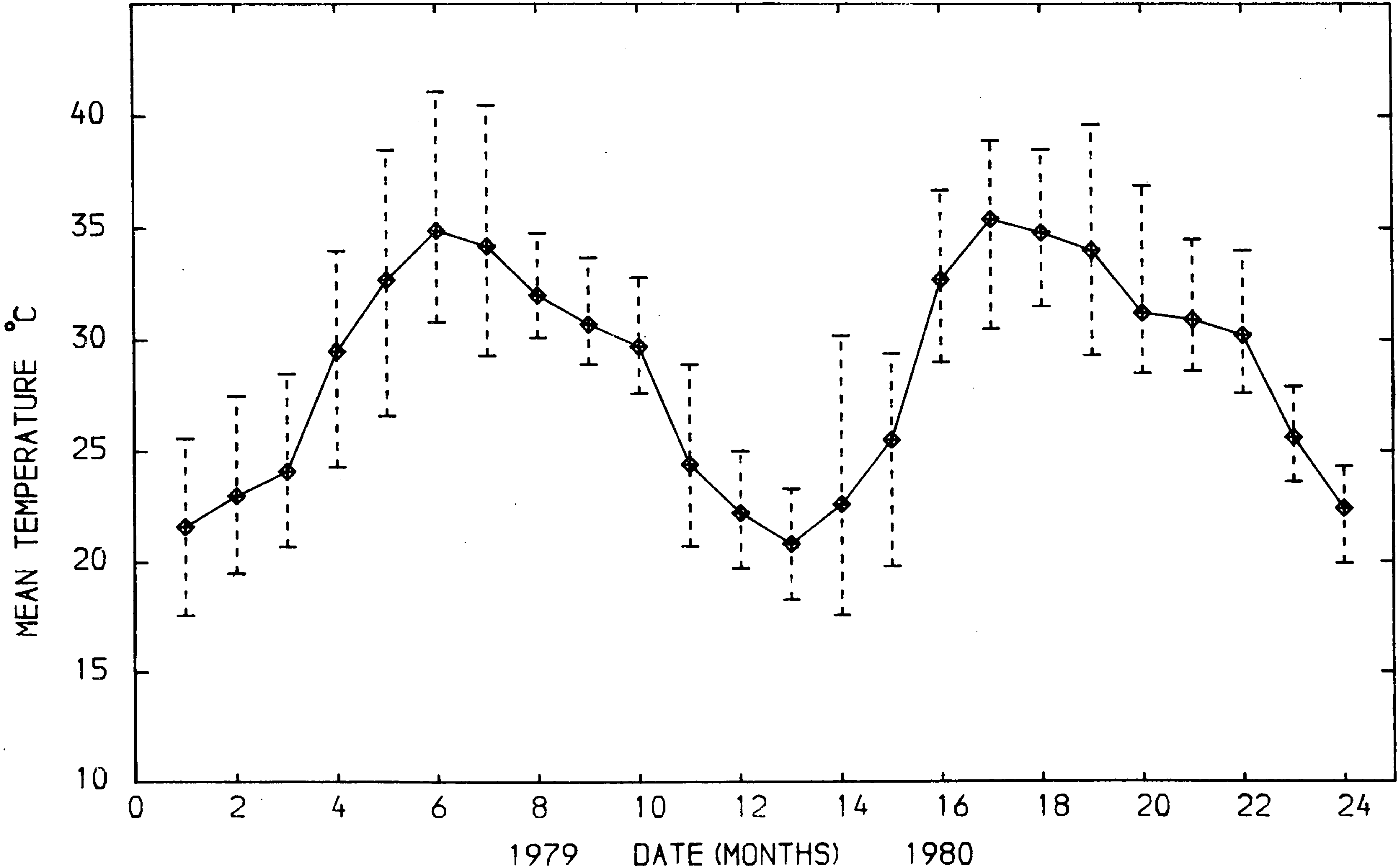
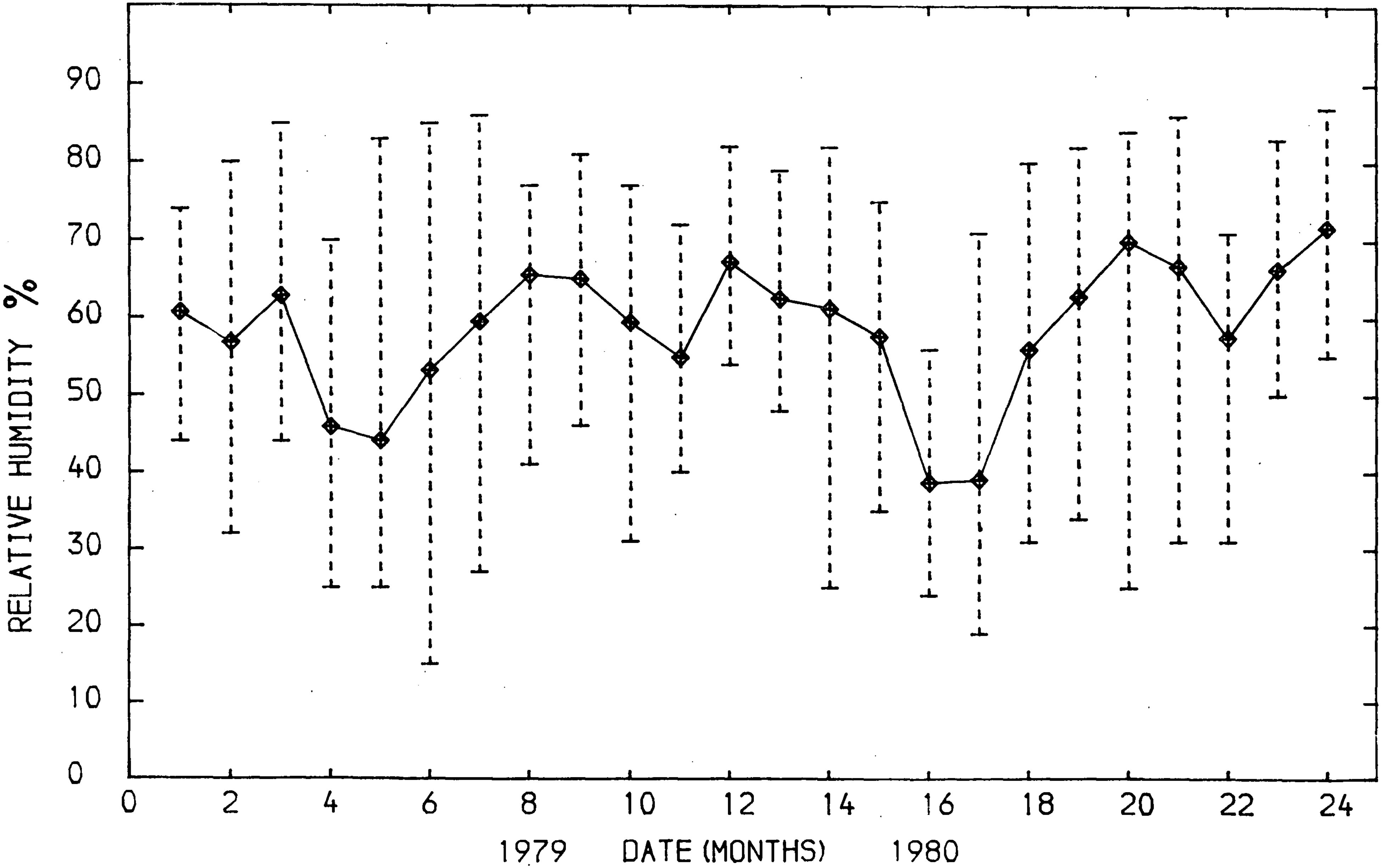


Fig A.4 SEEB. Monthly means of daily mean relative humidity; range for each month indicated.
(Data from Sultanate of Oman National Meteorological Service)



APPENDIX III

ANNOTATED CHECKLIST OF THE FLORA OF NORTHERN OMAN

This is a list of as many of the plant species recorded in northern Oman as I have been able to trace, with authorities and brief notes on status, habitat and distribution. It is based on my own plant collections and records but has been supplemented by those of other biologists; its main function is to provide a minimum of information on those plants mentioned in the thesis and particularly the honeybee plants (Chapter VII). The "non-honeybee plants" have been included as a full checklist for the region has not been prepared before and because further research may yet show that a good number of them are in fact used by honeybees.

The plants are listed in alphabetical order by family, genus and species. A number of synonyms amd names that have been used incorrectly in the past are also given, but numerous inaccuracies will still be present since a considerable amount of work still needs to be done on the Arabian flora to sort out many taxonomic and nomenclatural problems.

LEGEND

(i) Symbols immediately preceding and following the plant names and authorities:-

The numbers (1-93) before the family names are the "FAMILY NUMBERS" used as abbreviations in Tables 7.1-3.

P: Colour photograph taken of the species; where written after a collecting number, a photograph of that specimen was taken.

PO: Plant recorded by colour photograph only, no specimen collected.

B&W: Black and white photograph taken.

RO: Record only of plant, no specimen collected.

?: Identification, synonym, numbering or other detail needs confirmation.

The numbers after the species name (eg in Acanthaceae, for *Blepharis ciliaris* 315, 337) refer to my collecting numbers and, except in a few cases where the plants have been lost or were of poor quality, indicate that the numbered specimens are in the herbarium of the Royal Botanic Garden, Edinburgh.

[JRE]: record from J.R. Edmondson (1980)

[JPM]: record from list in J.P. Mandaville (1977). JPM* are plants below 450m and JPM** are plants around cultivated areas or disturbed habitats.

[PM]: record from P. Munton (198?, in press).

[AR-S] : record from A. Radcliffe-Smith (1978).

N.B. In this amalgamated list of my own records and those of others, it is likely that some species have been included at least twice under different names.

(ii) Symbols in the columns to the right of the species list:-

STATUS/ORIGIN

E : Endemic
N : Native
Nd: Naturalised - established introductions, including most crops
C : Casual - an introduction, but not well established; includes recently introduced ornamentals

N.B. The origin of many weeds (N or Nd) was not certain

NATURE/"HABITAT" (in its broadest sense)

W : Wild
R : Ruderal weed - disturbed ground, including deserted farmland. Also includes "rupestrals", plants growing on walls (in Oman, falaj walls especially). Plants growing by roadsides have been put in this category too, even though some may effectively be in their "natural" habitat of rocky, stony or sandy slopes
S : Segetal weed - of crops under cultivation (not deserted farmland) ie particularly weeds which require regular irrigation for their survival and reproduction. Includes many annuals
Cr: Crop-cultivated fruit trees, vegetables, fodder crops etc
O : Ornamental-cultivated species, including hedge plants

DISTRIBUTION

1 : Musandam - no records included here
2 : Mountains (Jabal) > 1500m. Probably close to the frost line ie no/few frosts below this altitude.
3 : Mountains (Jabal) < 1500m. Some species included in this category may occur only in the flatter, sandier areas within the mountains and ecologically are closer to category 5, eg *Calligonum* cf *tetrapterum* 174 and *Pennisetum divisum* 175
4 : Bātina, both the sandy/gravel/rock plain and the cultivated coastal strip
4̲ : Bātina, where the plants are found only in the villages irrigated by falaj in the Bātina plain eg Diqāl, and not in the coastal strip. The weed flora of these gardens is more akin to that of mountain villages because of the flood irrigation pattern (p. 331).
4* : Where plants are found only on rocky outcrops in the Bātina region and are not recorded from the plains eg "Sohār Peak" (Edmondson 1980) and the low coastal hills at Mīna al-Fahal, Ras al-Hamra and Qurum. These are geographically associated with the Bātina, but ecologically are closer to category 3
5 : Desert plains of north and central Oman, including Ras al Hadd, Haima, Masīrah.
5̲ : Plants found only in the oases of the desert plains, irrigated by aflaj from mountain and wadi aquifers eg Adam, Buraymi, Zāhib. Geographically these are 5 but ecologically are most similar to the oases of 3.

A few examples, showing how these data/symbols on the plants can be interpreted are given in Chapter VII, p. 329.

Through his help with identifications this checklist must be attributed to A.G. Miller as well as myself, but the compilation was primarily my undertaking and all mistakes remain my responsibility.

PRELIMINARY CHECKLIST OF THE PLANTS OF NORTHERN OMAN

BY

R.P. WHITCOMBE AND A.G. MILLER

I SPERMATOPHYTA

ANGIOSPERMAE

(a) DICOTYLEDONES

			NATURE/ "HABITAT"						DISTRIB -UTION				
			STATUS	WILD	RUDERAL	SEGETAL	CROP	ORNAMENTAL	MUSANDAM	JABAL>1500M	JABAL<1500M	BATINA	DESERT PLAINS
1	ACANTHACEAE												
	Barleria aucherana Nees [JRE 3205]		N	W							3		
	Barleria cf. candida Nees in DC [JPM]												
	Barleria hochstetteri Nees [JPM]												
P	Blepharis ciliaris (L.) B.L. Burtt	315, 337	N	W							3	4	5
	Ecbolium viride (Forssk.) Alston	768	N/	W	R						3		
	?syn. Ecbolium linnaearum Kurz.		Nd										
2	AIZOACEAE												
P	Aizoon canariense L.	35*, 157, 312, 660P(B&W), 821	N	W	R						3	4	
P	Gisekia pharnaceoides L.	689P	N	W								4	
P	Mesembryanthemum nodiflorum L.	745	N?		R							4	
	?Mollugo cerviana (L.) Ser. in DC.		?										
	Zaleya pentandram (L.) Jeffrey	219, 574, 589, 808, 892	N?		R	S					3	4	
	(syn. Trianthema pentandrum L.)		Nd										
3	AMARANTHACEAE												
P	Achyranthes aspera L. var. pubescens (Moq.) C.C. Townsend	296, 637, 811, 837	N		R	S				2	3	4	
	Aerva javanica (Burm.f.) Juss. ex Schultes	8, 358	N	W	R						3	4	5
	(syn. A. persica (Burm.f.) Merrill)												
	Amaranthus graecizans L.	187A, 190, 454, 640	N?		R	S					3	4	
	? some A. graecizans L. subsp. sylvestris (Vill.) Brenan [JPM]		Nd										
	Amaranthus hybridus L.	524, 693(probably)	N?		?R	S					3?	4	
	(syn. Amaranthus hypochondriacus L.)		Nd										
	Amaranthus viridis L.	289, 462	N?			S					3	4	
			Nd										
P	Pupalia lappacea (L.) Juss.	864P	N?	W?	?R					2			
4	ANARCADIACEAE												
PO	Mangifera indica L.		Nd				Cr				3	4	5
P	Rhus aucheri Boiss.	218, 432	E	W							3		
5	ANNONACEAE												
	Annona squamosa L. (Custard Apple)		Nd				Cr				3		

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

6 APOCYNACEAE

P	Catharanthus roseus (L.) G. Don cult. 551	C				O	4
	(syn. Vinca rosea L.)						
	(syn. Lachnera rosea....) - ?Lochnera rosea (L.) Reichb.						
PO	Nerium mascatense DC.	E?	W			O	2 3
	Plumeria alba Griseb. non L. (Frangipani)	C				O	3 4
	Rhazya stricta Decne. 18, 708	N	W				3 4 5
	Thevetia peruviana (Pers.) Schum. (Yellow Oleander)	C				O	4

7 ARISTOLOCHIACEAE

P	Aristolochia bracteolata Lam. 580	N?			S		3

8 ASCLEPIADACEAE

P	Calotropis procera (Willd.) R.Br. 207*?, 282, 836	N	W	R			3 4 5
P	Caralluma aucheriana (Decne.) N.E.Br. 142P	E?	W				3 4*
	Glossonema edule N.E. Br. [JPM]						
P	Leptadenia pyrotechnica (Forssk.) Decne. 431P	N	W				4 5
	Pentatropis nivalis (J.F. Gmel.) D.V. Field & J.R.I. Wood	N	W				3?4*
	(syn. P. spiralis (Forssk.) Decne) (on Acacia ehrenbergiana 173)						
	Pergularia tomentosa L. 373	N	W	R?			3 4
P	Periploca aphylla Decne. 63, 120, 221	N	W				2 3
P	Periploca aff. visciformis (Vatke) L. Schuman 380P	N	W				2 3

9 AVICENNIACEAE

	Avicennia marina (Forssk.) Alston ? or Vierh? - or VERBENACEAE?	N	W				4

10 BERBERIDACEAE

	Berberis sp. 246	N/ E?	W				2

11 BIGNONIACEAE

PO	Tecoma stans (L.) Juss. ex HBK ?or (L.) H.B.K.	C				O	3 4
	Tecomella undulata (G.Don.) Seem. 162	N?	W			O	3

12 BORAGINACEAE

	Arnebia hispidissima (Lehm.) DC. 107, 360, 622, 760	N	W	R			3 4 5
	Cordia myxa L. 217	Nd			Cr		3 4
	Echiochilon thesigeri Johnst. [JPM N. Oman]						
P	Ehretia obtusifolia Hochst. ex DC. 874, 903P	N?	W	R			2
	Gastrocotyle hispida (Forssk.) Bunge 716 (not 715), 900	N?		R			2
P	Heliotropium bacciferum Forssk. (incl. subsp. lignosum) 105, 117P, 253 306, 332, 804, 805	N	W	R			3 4 5
	(?syn. H. ramosissium Sieb. and Lehm. [JPM])						
	Heliotropium calcarium Stocks 76, 164, 334	N	W				3?4*5
	Heliotropium cf. calcarium Stocks 803	N	W				4
	?Heliotropium europaeum L. [R.C. Maxwell-Darling 406 Quryat (Kew]						
	Heliotropium lasiocarpum Fisch. and Mey. 890	N		R			3
	Heliotropium rariflorum Stocks - [JPM N. Oman]						

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Heliotropium spp. 159, 160, 453, 535							
	Heliotropium strigosum (Forssk.) Willd. [A.R-S 3718; Fernandez 390, 393, 402]	N	W			3		
	Heliotropium tuberculosum (Boiss.) Boiss. syn. kotschyi (Bunge) Gurke	N	W				4	5
	Lappula spinocarpos (Forssk.) Aschers. [JPM N. Oman]							
	Megastoma pusillum Coss. & Dur. [JRE 3321, 3324]							
	Trichodesma africanum (L.) Lehm. [JRE 3456]	?	?				?*	
	Trichodesma ehrenbergii Schweinf. [JRE 3256]							
	Trichodesma stocksii Boiss. [JRE 3475]	N?	W?			?3		
13 BURSERACEAE								
	Boswellia sacra Flueck.	N	W	O			4	
PO	Commiphora ?myrrha (Nees) Engl.	N	W			3		
P	Commiphora quadricincta Schweinf. 316P	N	W			?3	4*	
	Commiphora cf. quadricincta Schweinf. 132, 591					3		
14 CACTACEAE								
PO	Opuntia	Nd	R	O			4	
15 CAMPANULACEAE								
P	Campanula akhdarensis Miller & Whitcombe 379P	E	W		2	3		
16 CAPPARACEAE								
	Capparis cartilaginea Decne. [JRE 3391]							
	Capparis decidua (Forssk.) Edgew. 540	C		?O			4	
	Capparis droserifolia (Forssk.) Del. [JRE 3361] ?same as our aff. droserifolia 2033 etc?							
PO	Capparis mucronifolia Boiss.	N	W			3		
	Capparis spinosa L.	N	W				4*	
	Capparis spinosa var. pubescens Zoh. [JPM]							
	Cleome amblyocarpa Barr. and Murb. 361	N	W					5
	Cleome brachycarpa Vahl ex DC. 295, 314, 329, 368	N	W			3		5
	Cleome aff. droserifolia (Forssk.) Del	N	W R					5
	Cleome glaucescens DC. (? Present/Absent/Synonym) [JRE 3246,3267]							
	Cleome gynandra L. 371P	N/ Nd	R?S				4	5
	Cleome oxypetala var. micrantha Boiss. [JPM]							
	Cleome cf. quinquenervia DC. 327, 372, 471	N	W?R			3		5
	Cleome rupicola Vicary 78, 642	N	W?R			3		
	Cleome scaposa DC. 328, 367, 703	N	W			3		5
P	Dipterygium glaucum Decne. 118P, 252	N	W R				4	5
B&W	Maerua crassifolia Forssk. 4B&W	N	W			3	4	?
17 CAPRIFOLIACEAE								
B&W	Lonicera aucheri Jaub. and Spach 243, 410B&W	E?	W		2			
18 CARICACEAE								
	Carica papaya L.	Nd		Cr		3	4	

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

19	CARYOPHYLLACEAE						
	Arenaria leptoclados (Reichb.) Juss. [JPM]						
P	Dianthus aff. crinitus (possibly sp. nov.) 237P	E?	W	2			
	Dianthus cyri Fisch. & Mey. [JRE 3050]						
	Gypsophila bellidifolia Boiss. 163, 661, 704, 775	N	W		3	4	
	(syn. Saponaria barbata Barkoudah)						
	Polycarpaea repens (Forssk.) Asch. and Schweinf. 364	N	W			4	5
P	Polycarpaea spicata Wright and Arn. 308, 786P	N	W		3		5
P	Robbairea delileana Milne-Redhead 341, 609, 668P, 774, 790	N	W			4	5
	Silene apetala Willd. 724	N?	S	2			
P	Silene burchellii Otth. ex DC. ?257 ?not found in Herb.,721, 861	N	W R	2			
	(syn. Silene schweinfurthii Rohrb.)						
	Silene conoidea L. [**JPM]						
	Spergula fallax (Lowe) E.H.L. Krause 666	N?	W R		?3	4	
	(syn. Spergula flaccida (Roxb.) Asch.)						
P	Spergularia bocconii (Sol. ex Scheele) Asch. et Graebn. 186 Not found in herb. 198, 746	N	R S			4	
	Stellaria media (L.) Vill. RO [JPM**]	Nd	S	2			
20	CHENOPODIACEAE						
	Chenopodium album L. 877	N? Nd	R?S?	2		4	
	Chenopodium murale L. 638, ?670, 673, 725	N/ Nd	R S	2	3	4	
	Chenopodium vulvaria L. 734, 872	?Nd	S	2			
	Cornulaca amblyacantha Burge [JPM]						
	Cornulaca monacantha Del. 570	N	W			4	
	Cornulaca sp. [R-S; JRE 3159; JPM]						
	Halocnemum strobilaceum (Pall.) Bieb. [JRE 3436]						
	Haloxylon salicornium (Moq.) Bunge [JRE 3372 + JPM?]						
P	?Salsola baryosma (Roem. et Schult.) Dandy 545P	N	W S			4	
	Salsola bottae Jaub. & Spach. [JPM]						
	Salsola forsskalii Schweinf. 331	N	W				5
	Salsola rubescens Franch. 21, 338	N	W				5
	Salsola schweinfurthii Solms-Laub. [JPM*]						
	Salsola spp. 9, 569a, 569b						
	Halopeplis perfoliata (Forssk.) Bge. ex Schweinf. (Wild Fls. of N. Oman)						
	?Schanginia aegyptiaca (Hasselq.) Aellen 199*	N	S			4	
	Schanginia hortensis (Forssk.) Moq. Tand. [JPM*]						
	Chenopodiaceae indet. 590, 634, 735 (? or Rumex)						
21	CISTACEAE						
P	Helianthemum lippii (L.) Pers. 270, 413	N	W	2	3?		
22	COMBRETACEAE						
	Terminalia catappa L. RO	Nd	Cr O		3	4	5?
23	COMPOSITAE						
	Anthemis odontostephana Boiss. [JPM]						

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Bidens biternata (Lour.) Merr. 579 ?	Nd			S				3		
PO	Blumea aurita....	C? Nd			S						5
	Blumea bovei (DC.) Vatke 40, 303, 429, 674	N	W	R					3		
P	Carthamus tinctorius L. 115	Nd				Cr			3	4	
P	Centaurea pseudosinaica Czerep. subsp. pseudosinaica 630, 756 [JPM]	N	W						3	4	
	(non Centaurea sinaica DC.)										
	(non Centaurea solstitialis L.)										
	?Chrysanthemum sp. 740	C					O	2			
	Cichorium intybus L. 882	C			S					4	
P	Conyza dioscorides (L.) Desf. 448P	Nd		R						4	
	Conyza stricta Willd. 414, 684	N	W	R				2			
	Crepis foetida L. [JRE 3452] subsp. commutata (Spreng.) Badcock	N	W							4*	
	Crepis sp. 857	N	W					2			
	Echinops sp. cf. abyssinica [JPM] (Wild Fls. of N. Oman)										
	Echinops spinosus L. 769	N?		R					3		
	? = E. spinosissimus Turra										
P	Eclipta alba (L.) Hausskn. 442, 832, 884	N		R	S				3		5
	(syn. E. prostrata (L.) L.)										
P	Euryops arabicus Steud. 54, 61*, 233, 240, 680	N	W					2			
	(syn.= E. pinifolius A. Rich.)										
	Filago pyramidata L. [JRE 3314, JPM]										
P	Flaveria trinervia (Spreng.) Mohr. 32, 375	N/ Nd		R	S				3	4	5
	Gnaphalium luteo-album L. 883 at edge of falaj	N? Nd		?R	?S				3		
	Grantia arachnoides Boiss. 355, 593	N	W								5
PO	Grantia aucheri Boiss.	N	W						3		
	Helianthus annuus L.	C					O			4	5
P	Helichrysum sp. nov. aff. makranicum 140, 265, 404, 412, 607, 845, 852	N	W					2	3		
	Ifloga spicata (Forssk.) Sch.-Bip. 820	N/ Nd	?	R??						4	
	Inula sp. 67	N	W						3		
	Iphiona horrida Boiss. 834	N	W						3		
	Iphiona sp. 290	N	W						3		
	Lactuca capensis Thunb. [JRE 3269]	?	?						3		
	Lactuca dissecta D. Don. [JPM]										
	Lactuca sativa L. RO	C?				Cr			3	4	
	Lasiopogon muscoides (Desf.) DC. [JPM]										
	Launaea capitata (Spreng.) Dandy [JPM]										
	Launaea itybacea (Jacq.) Beauverd [JPM*]										
	Launaea massauensis (Fres.) Ktze. [JPM, AR-S Dhofar]										
	Launaea mucronata (Forssk.) Muschl. 649, 741, 810	N	W	R					3	4	
	Launaea nudicaulis (L.) Hook. [JRE 3217]										
	Launaea cf. nudicaulis (L.) Hook. 581	N/ Nd			S				3		
P	Launaea procumbens (Roxb.) Dandy 197*, 213, 283 ?Jabal too?	N			S				3?4		
	? or Launaea procumbens (Roxb.) Ramayya and Rajagopal which sp is 877										
	Launaea cf. remotiflora (DC. in Wight) Amin ex Rech.f. 266	N	W					2			
P	Launaea spinosa (Forssk.) Schultz Bip. 605P, 656	N	W						3		
	Launaea sp. 613 (immature), 887										
	Osteospermum vaillantii (Decne.) T. Norl. [JPM; R-S (Dhofar)]							2			
	(syn. Tripteris vaillantii Decne)										
	Phagnalon aff. nitidum Fres. 409	N	W					2			

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Phagnalon viridifolium Decne. 421	N	W		2			
	Pulicaria edmondsonii Gamal-Eldin	E	W		3			
	Pulicaria foliosa DC. [JRE 3214]							
	Pulicaria glutinosa (Boiss.) Jaub. and Spach 70, 156, 359, 827	N	W			3		5
	Pulicaria inuloides (Poir) DC. 68	N	W			3		
	(syn. P. arabica (L.) Cass. subsp. inuloides (Poir.) Maire)							
	Pulicaria orientalis Jaub. and Spach [JPM***]							
	?Pulicaria schimperi DC. [JRE 3161]							
	Pulicaria undulata (L.) C.A. Meyer ?or Kostel 10, 273	N	W R			3		5
	(?syn. or different from Francoeuria crispa (Forssk.) Cass.							
	which is synonymous with Pulicaria crispa (Forssk.) Benth.							
	ex Oliver subsp. crispa)							
	Reichardia tingitana (L.) Roth. 147, 650	N	W			3	4	
	Senecio abyssinicus A. Rich [JRE 3225, 3258]							
	Senecio flavus (Decne.) Schultz Bip. [JPM]							
	Sonchus maritimus L. 907	N	W		2			
	Sonchus oleraceus (L.) Gouan 50*, 51, 185, 467, 529, 714(not 715)	N/ Nd		S	2	3	4	
	Urospermum picroides (L.) ?F.W. Schmidt/Desf? [JRE 3051, 3185, 3422 & JPM]					3	4	5
	Vernonia arabica F.G. Davies 130, 335, 348, 597, 764	N	W			3	4	5
	Veronia cinerascens Schultz Bip. [JPM]							
	Vernonia cinerea (L.) Less. 167, 525, 582	N?		S		3	4	5
	Volutaria sp. [JPM]							
	Zoegea purpurea Fresen. [JRE 3454 and JPM]						4*	

24 CONVOLVULACEAE

	Convolvulus acanthocladus Boiss. [JPM]	N	W				4	
P	Convolvulus arvensis L. 126*, 200, 284, 285, 463	N/ Nd		S	2	3	4	5
	Convolvulus cephalopodus Boiss. [JPM] (Wild Flowers of N. Oman)							
	Convolvulus nr. glomeratus Choisy 72 [cf. C. virgatus, 604, but more pubescent]	N	W?R			3?		5?
PO	Convolvulus aff. hystrix Vahl	N	W			3		5
	Convolvulus pilosellaefolius Desr. in Lam. 742, 807	N?	W?R?			3	4	
	?or Convolvulus prostratus Forssk. [JPM]							
	(syn. Convolvulus microphyllus Sieb.)							
	Convolvulus ulicinus Boiss. [JRE 3285 and JPM]							
P	Convolvulus virgatus Boiss. 340, 604P, 641 [JPM]	N	W			3		5
	Convolvulus virgatus var. subaphyllus Boiss. [JPM]							
	Cressa cretica L. 286, 378	N/ Nd		S			4	
PO	Ipomoea batatas (L.) Lam. (cultivated Sweet Potato) ?15*	Nd		Cr		3	4	5?
P	Ipomoea cairica (L.) Sweet 206	C		O		3	4	
	(syn. Ipomoea palmata Forssk.)							
P	Ipomoea ?carnea Jacq. 553 (pollen different from I. batatas)	C		O		3	4	
	Ipomoea obscura (L.) Ker-Gawl.	N/ Nd		S			4	
P	Ipomoea pes-caprae (L.) Roth 205*	?C Nd		O		3	4	
	Seddera latifolia Hochst. & Steud. [JRE 3183]							

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

25 CRUCIFERAE

	Anastatica hierochuntica L. 677, 806	N	W	R?					3	4
	Brassica oleracea var. capitata L. (Cabbage)	Nd				Cr			3	4
P	Brassica sp. or Sinapis arvensis L. 548, 752	C		R	S					4
	Cardaria draba (L.) Desv. 839, 870	N/		R	S			2		
		Nd								
	Diplotaxis harra (Forssk.) Boiss. 106, 619	N	W	R					3	4
	Diplotaxis harra var. subglabra (DC.) O.E. Shultz [JPM]	N	W					2		
	?Enarthrocarpus sp.? [JRE 3442]									
	Eruca sativa L. ?or Miller 549*, 550*, 871) not found in	C		R			O	2		4
	? = E. lativalvis (Boiss.) Boiss. [JPM]) herbarium under this name									
	Erucastrum arabicum Fisch. & Mey. 712, 733	? Nd			S			2		
	(syn. Brassica arabica (Fisch. & Mey.) Fiori)									
P	Farsetia aegyptia Turra 396P, 685	N	W	R				2		
	Farsetia cf. linearis Dcne. 772	N	W?	R?						4
	Morettia parviflora Boiss. 125	N	W						3	
	(syn. Morettia canescens Boiss. var. parviflora Boiss.)									
	Morettia philaeana (Del.) DC. 74	N	W						3	
	(syn. Morettia asperrima Boiss.)									
	Morettia sp. 828, ?829									
	Notoceras bicorne (Aiton) Amo 646	N	W?	R?					3	
B&W	Physorrhyncus chamaerapistum (Boiss.) Boiss 11*, 112, 538	N	W	R					3	4
	Raphanus raphanistrum L. 468	N/			S				3	
		Nd								
PO	Raphanus sativus L.	Nd				Cr			3	4
	Sisymbrium erysimoides Desf. 47, 644, 715, 823	N	W	R				2	3	4
	Cruciferae indet. 668	N?	W?	R?					3	

26 CUCURBITACEAE

	Citrullus colocynthis (L.) Schrad. 104 Wild Form	N	W						3	?
	? = C. lanatus (Thunb.) Mansf. Cultivated Var.	Nd				Cr			3	4
	(syn. Citrullus vulgaris Schrad.) (Water melon; only wild form collected).									
	Corallocarpus schimperi (Naud.) Hook. f. 875	N	W					2		
	Cucumis melo L. ssp. melo 562 (friut only), 572 Wild Form	N/			S				3	4
	Cultivated Forms	Nd				CR				4
	Cucumis prophetarum L. 17*, 299, 888	N	W	R					3	?
	? = C. sativus L. ssp. prophetarum									
	?Lagenaria "Gourds"	Nd				Cr			3	4
	Luffa acutangula (L.) Roxb. 484	N	W							

27 CUSCUTACEAE

	Cuscuta cf. epithymum..... 744	N?			S					4
	Cuscuta spp. 69, 671	N	W						3	

28 DIPSACACEAE

	Scabiosa olivieri Coult. [JPM]									

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	29 EUPHORBIACEAE							
	Acalypha indica L. 578	N/ Nd	S			3		
	Andrachne aspera Spreng. 276, 647, 838, 893	N	W?R		2	3		
	Andrachne telephoides L. 126*	N	W			3		
	Andrachne sp. ?623							
P	Chrozophora oblongifolia (Del.) Juss. 12, 428	N	W R			3	4	
	Chrozophora sabulosa Kar. & Kir. 365	N	W					5
	Euphorbia arabica (Hochst. and Steud.) Boiss. 624	N	W			3	4	
	Euphorbia falcata L. [JPM]							
	Euphorbia granulata Forssk. ?345, 614, 657, 694, 878	N	W ??S			3	4	5
	Euphorbia helioscopia L. 45, 466, 672, 710	N/ Nd	S		2	3		
B&W	Euphorbia heterophylla L. 440	N/ Nd	S			3	4	
PO	Euphorbia hirta L.	N/ Nd	S			3		5
	Euphorbia indica Lam. 33, 187B(on sheet with Amaranthus graecizans L., 187A), 288, 298, ?313, 793, 833 (? &/or Euphorbia prostrata Ait.)	N	W S			3	4	5
P	Euphorbia larica Boiss. 324	N	W		2	3	4	
	Euphorbia peplus L. 170, 465	N/ Nd	S			3		
	Euphorbia schimperiana Scheele 717	N/ Nd	S		2			
P	Euphorbia sp. ?aff. penicillata.... 792P (tree-like, Khabura)	?Nd	R	?O			4	
	Manihot esculenta Crantz (Cassava)	Nd	Cr					5
P	Phyllanthus maderaspatensis L. 39, 447, 588, 886 (syn. P. niruri L.)	N	W R S			3		5
	Ricinus communis L.	Nd	W R			3	4	
	30 FRANKENIACEAE							
P	Frankenia pulverulenta L. 193,749	N/ Nd	R S				4	
	31 FUMARIACEAE/PAPAVERACEAE							
	Fumaria parviflora Lam. 726	N/ Nd	S		2			
	32 GENTIANACEAE							
	Centaurium erythraea Rafn. [JRE 3234, 3273a, 3397]					3		
	?syn. Centaurium pulchellum (Sw.) Druce 743, 771	N/ Nd	S				4	
	33 GERANIACEAE							
	Erodium circutarium (L.) L'Her. ex Aiton. 44, 727, 862	N?	R S		2			
	Erodium laciniatum (Cav.) Willd. [JPM] (Wild Fls. of N. Oman)							
	Erodium malacoides (L.) L'Herit. [JPM]							
	Erodium neuradifolium Del. ex Godr. [JRE 3428]							
	Geranium mascatense Boiss. ?46, 100	N	W?R S		2			
	Monsonia heliotropoides (Cav.) Boiss. [JPM]							
	Monsonia nivea (Decne.) Decne. ex Webb							

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Monsonia sp. 818		N?	W?R?	4
34	ILLECEBRACEAE				
	Cometes surattensis Burm.f. ?or L. ?129, 351, 536, 780		N	W	3 4 5
	Gymnocarpos decander Forssk. 133, (not 427, which is Jaubertia aucheri), 537		N	W	3
	Herniaria hirsuta L. [JPM]				
	Herniaria muscatensis Bornm. 346, 623, 779	?E	N	W	3 4 5
	Paronychia arabica (L.) DC 787, 814		N	W	3 4
	Sclerocephalus arabicus (Decne.) Boiss [JRE 3168 & JPM]				3
	Sphaerocoma aucheri Boiss. 675, 701		N	W	3 4*
35	JUGLANDACEAE				
RO	Juglans regia L. [JPM]				
36	LABIATAE				
P	Endostemon tenuiflorus (Benth.) Ashby 902P		N	W	2
P	Lavandula subnuda Benth. 152, 254, 435, 606P, 662		N	W	2 3 4*
P	Leucas inflata Benth. 139P, 602P, 867		N	W	2 3 4*
	= Physoleucas inflata (Benth.) Jaub. and Spach				
	syn. Physoleucas arabica Jaub. and Spach				
P	Mentha longifolia (L.) Huds. 879		N/ Nd	R S Cr	2 3
	Micromeria biflora (Buch.-Ham.) Benth. 387, 395, 863		N	W	2
P	Ocimum basilicum var. 1 (rihan) 216		Nd	Cr	4
P	Ocimum basilicum var. 2 (sawma) 474, 531		N/ Nd	S Cr	3 4
	?=Ocimum forskolei Benth.				
	(syn. Ocimum hadiense sensu E.A. Bruce [JRE 3042, 3262, 3395]				
	non Ocimum hadiense Forssk.)				
P	Plectranthus rugosus Wall. ex Benth. 390		N	W	2
P	Salvia aegyptiaca L. 388, 844P		N	W R	2 3
	Salvia macilenta Boiss. 434, 784		N	W	3 4
	Salvia schimperi Benth. [JPM]				
	?Salvia sp. 561				
P	Teucrium mascatense Boiss ?62, ?247, 385, 397, 420, ?854, ?905		E?	W	2 3
	Teucrium stocksii var. incana (Aitch & Hemsl.) Hedge and Lamond [JPM]				
	?syn Teucrium stocksianum Boiss. [JRE 3222, 3498]				
	Thymus sp. [PM 1400m Jabal Aswad]				
	?Labiatae indet. 229, 239				
37	LEGUMINOSAE				
P	Acacia ehrenbergiana Hayne 173, 182		N	W	3 4 5
	Acacia gerardii Benth. 58, 230, 896		N	W	2 3
	(syn. Acacia iraqensis Rech. f.)				
	= Acacia eburnea Willd.				
P	Acacia nilotica Willd. 3		Nd	R ? O	3 4
P	Acacia tortilis (Forssk.) Hayne 215, 539		N	W R	3 4 5
	Albizzia lebbeck (L.) Bent [R-S]		Nd	O	4
PO	Alhagi maurorum Medic.	?	Nd	W R	4
	(syns. A. camelorum Fisch. & A. pseudalhagi Desv.)				

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Alysicarpus sp. [R-S]								
	Argyrolobium crotalarioides Jaub. [R-S & JPM & PM]					2		4	
	Argyrolobium roseum Jaub. & Spach 73, 128, 627	N	W				3	4	
	?Argyrolobium sp. or Rhynchosia sp. 789	N?	W?R					4	
	Astragalus corrugatus Bert. [R-S]							4	
	Astragalus cf. eromophilus Boiss. [R-S & JPM]							4	
	Astragalus fasciculifolius Boiss. [R-S & JRE 3152 (?UAE) & JPM]							4	
	Astragalus fatmensis Hochst. [R-S, JPM]							4	
	Astragalus hauarensis Boiss. 801 [R- S]	N?	W?R?					4	
	?syn A. gyzensis Del.								
	Astragalus schimperi Boiss. 455	N?	W?R					4	
	Astragalus tribuloides Del. 759 not found in herbarium	N?	W?R				3	4	
	Astragalus tribuloides var. minutus Boiss. [JPM]								
	Astragalus vogelii (Webb) Bornm. 610, 825	N	W R					4	
	Astragalus sp. 851 not found in herbarium	N	W R?			2			
P	Caesalpinia bonduc (L.) Roxb. 568, 631	N/ Nd	R		O		?3	4	
	Cajanus cajan (L.) Millsp. 449	Nd		Cr			3	4	
	Cassia italica (Mill.) Lam. 122, 158, 645, ?817	N	W R				3	4	
P	Cassia senna L. 357P	N	W R?						5
P	Cassia ?sophera L. 168, 438P [JPM]	N/ Nd	R S				3		
	Ceratonia oreothauma Hillcoat,Lewis & Verdc. [JPM; PM]	N	W			2	3		
	?Cicer arietinum L. [R-S] Chick Pea or Phaseolus aureus							4	
P	Clitoria terneata L. (? ternatea) 552	C			O			4	
P	Crotalaria aegyptiaca Benth. 123, 445, 575, 592, 643	N	W				3	4	5
	(syn. Crotalaria wissmanii Schwartz)								
	Crotalaria persica (Burm.f.) Merr. 342	N	W						5
	Crotalaria retusa L. [JRE 3235]								
	Dalbergia sissoo Roxb. [JPM]	?	W?				3		
	Delonix regia (Boj. ex Hook) Raf. (Flame Tree)	C			O			4	
P	Ebenus stellata Boiss. 250, 393, 850P [R-S records on coastal plain]	N	W			2			
	Hippocrepis unisiliquosa L. subsp. bisiliqua (Forssk.) Bornm. [R-S]							4	
	Indigofera argentea Burm.f. [R-S]							4	
	Indigofera arabica Jaub. and Spach 144, ?232 [not found in herbarium] 278	N	W				3	4*	
P	Indigofera articulata Gouan 697, 866P	N	W			2	3		
	Indigofera coerulea Roxb. 223, 917 [R-S: var. occidentalis Gillet & Ali-Batina]	N/ Nd	W	Cr			3		
	Indigofera hochstetteri Bak. 802	N	W?R					4	
	Indigofera cf. insularis Chiov.							4	
P	Indigofera intricata Boiss. 77	N	W				3	4	5
	Indigofera ?n/hephrocarpa Balf.f. [R-S]							4	
P	Indigofera oblongifolia Forssk. 209	N	W R					4	
	Lotononis platycarpus (Viv.) P.-Sermoli [JPM]								
	Lotus sp.cf. arabicus L. [R-S]							4	
	Lotus brachycarpus Hochst. & Steud. 350	N	W					4	5
	Lotus garcinii DC. 305, 336	N	W					4	5
P	Lotus schimperi Steud. ?ex Benth. 452, 707, 800	N	W?R?S					4	
	Medicago laciniata (L.) Mill. [R-S] & var. brachycantha Boiss. [JRE 3173]							4	
	Medicago orbicularis (L.) Gart ?664, 690, 711	N	W R			2		4	

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Medicago polymorpha L. var. vulgaris (Benth.) Shinn. [R-S]				4
PO	Medicago sativa L.	Nd		Cr	2 3 4 5
	Melilotus indicus (L.) All. 116, 184, 719	N/ Nd	R S		2 3 4
	Melilotus officinalis (L.) Desr. 544 (grown from imported seed)	C		Cr	4
	Ononis sicula Guss. [R-S]				4
P	Parkinsonia aculeata L. 773P	Nd	R	O	4
P	?Phaseolus aureus Roxb. 541P (syn. Vigna radiata (L.) Wilczek)	Nd		Cr	4
P	Pithecellobium dulce (Roxb.) Benth. 30*, 113	Nd /C		Cr O	3 4 5
P	Prosopis cineraria (L.) Druce 189, 356 = Prosopis spicigera L.	N	W R		3 4 5
	Prosopis juliflora (Siv.) DC [R-S]				4
	?Ptycholobium plicatum (Oliv.) Harms or Tephrosia sp. 391 [JPM]	N	W		2
	Rhynchosia minima (L.) DC. var memnonia (Del.) Cooke [R-S] ?RPW 789				4
	Rhynchosia schimperi Boiss. [R-S, JPM]				4
P	Sesbania sesban (L.) Merrill 2	Nd	R	Cr	4
	Tamarindus indica L. 566	Nd		Cr O	3 4
P	Taverniera glabra Boiss. 339, 436, ?766	N	W R		3 4 5
	Taverniera spartea DC. [R-S]				4
	Tephrosia sp. [AGM & RPW 2012 Mina al Fahal]	N	W		4
P	Tephrosia apollinea (Del.) DC. ?or Link 121, 325, 556, 594P	N	W R		3 4 5
	Tephrosia nubica (Boiss.) Baker [-JRE] subsp. nubica (Boiss.) Gillett [R-S; JPM]				
	Tephrosia pentaphylla Roxb. [JPM]	N	W		3
P	Tephrosia persica Boiss. 476, 632, ?762 (not found in herbarium) (?syn. Tephrosia haussknechtii Bornm.)	N	W R		3 4 5
	Tephrosia purpurea (L.) Pers. [JPM]				4
	Tephrosia quartiniana Cuf. [R-S]				4
	Tephrosia subtriflora Hochst. ex Bak.				4
	Trifolium alexandrinum L. 880 (grown from imported seed)	C		Cr	4
	Trifolium resupinatum L. 824 (grown from imported seed)	C		Cr	4
	Trigonella foenum-graecum L. 23, 451	Nd		Cr	3 4
	Trigonella hamosa L. [R-S]				4
	Vicia faba L. var.?minor 461	Nd		Cr	3
	Vicia sativa L. 720 var. angustifolia L. [R.S.]	?Nd	R		2 4
P	?Vigna unguiculata (L.) Walp. 543 ?syn. Lablab purpureus (L.) Sweet [R-S Batina]	Nd		Cr	4
	Leguminosae indet. 349, 611, 612, 658 B&W, 748(not found in herbarium)				
	38 LINACEAE				
	Linum corymbulosum Reichb. [JPM]				
	Linum strictum L. 842	N/ Nd	W?R?		2
	Linum usitatissimum L. [JPM] (Wild fls. of N. Oman)	?			2
	39 LYTHRACEAE				
	Ammania baccifera L. 558	N	W		3
B&W	Lawsonia inermis L. 29	Nd		Cr	3 4 5

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

40 MALPIGHIACEAE

P	Acridocarpus orientalis A. Juss.	161, 222P, 291		N	W					2	3		

41 MALVACEAE

	Abelmoschus esculentus (L.) Moench.			Nd		R						4	
	Abutilon fruticosum Guill. & Perr. [JPM]										3		
	Abutilon sp. cf. fruticosum Guill. & Perr.	475		N/ Nd	W?R							4	
	Abutilon muticum (Del.) Webb.	127		N/ Nd		R	S					4	
	? = A. pannosum (but no purple centre to flowers) [JPM]												
	Althaea rosea (L.) Cav.			C					O	2		4	
P	Gossypium sp.	791P		N/ Nd		R						4	
	Gossypium herbaceum L.			Nd				Cr			3	4	
	Gossypium hirsutum var. punctatum (Schumach.) J.B. Hutch.		[JPM**]										
	Hibiscus micranthus L.f.	600, 709		N	W						3		
PO	Hibiscus rosa-sinensis L. vars.			C					O			4	
	Hibiscus trionum L.	898		N/ Nd			S			2			
	Hibiscus vitifolius L.	481		N	W								
	Malvaviscus arboreus Cav.			C					O			4	
	Malva neglecta Wallr. [JPM] (Wild Fls. of N. Oman)					R							
P	Malva parviflora L.	188, 651, 665, 718, 722		N/ Nd	W	R	S			2	?	4	
	Malvastrum coromandelianum (L.) Garcke	49, 636		N/ Nd		R	S			2	3		
P	Pavonia arabica Steud. & Hochst. ex Boiss.	143P		N	W						3		
	Sida spinosa L.	377, 443		N/ Nd			S					4	5
	Sida sp. cf. urens L.	576		N/ Nd			S				3		5
	(?syn. Sida cordata (Burm. f.) Boiss-Waalk) [JPM ***]												

42 MELIACEAE

P	Azadirachta indica Juss.	555		Nd					O			4	

43 MENISPERMACEAE

	Cocculus pendulus (J.R. and G. Forst.) Diels	281		N	W						3		

44 MORACEAE

	Ficus carica L.	?135, 422, 423, 424, 586	cultivated	Nd				Cr			3	4	5
	&/or Ficus pseudosycomorus Decne.		wild	N/	W					2	3		
	(syn. Ficus palmatus Forssk.)			Nd									
P	Ficus salicifolia Vahl.	153		N	W	R					3	4	
	Ficus sycomorus L.	430		Nd				?	O		3		
	Ficus sp.	894		Nd				?	O		3	4	

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

RO	Morus ?nigra or alba L. Mulberry	Nd		Cr	3 4
45	MORINGACEAE				
P	Moringa aptera (Forssk.) Gaertn. 22, 114, 470, 554 (505, 520 Dhofar)	N	W		3
	(syn. M. peregrina (Forssk.) Fiori)				
	Moringa pterygosperma Gaertn. 522 (Fruits only; prob. from introduced ornamental)	C		O	4
46	MYRTACEAE				
	Eucalyptus spp. [eg JRE 3348]	C		O	3 4
		N/			
P	Myrtus communis L. 908	Nd	R	Cr	2
RO	Psidium guajava L.	Nd		Cr	3 4
47	NYCTAGINACEAE				
P	Boerhavia diffusa L. 220, 626, 639, 818a, 819, 868P	N	W R		2 3 4
	syn. Boerhavia repens L. (incl. var. viscosa Choisy) [JPM]				
	Boerhavia elegans Choisy 179, 274, 599	N	W		3
	Boerhavia elegans Choisy var. stenophylla Boiss. [JPM]				
	?Boerhavia 891(not found in herbarium)				
	Bougainvillea glabra Choisy	C		O	?3 4
	(syn. Bougainvillea spectabilis (non Willd.) Guest)				
	Commicarpus stenocarpus (Chiov.) Cufod. 699	N	W		4*
48	OLEACEAE				
	Jasminum sambac (L.) Ait. 916	Nd		O	3
P	Olea europaea L. subsp.A 268, 405 (496 Dhofar)	N	W		2 3
	(syn. Olea africana Mill.)				
49	OROBANCHACEAE				
	Cistanche phelypaea (L.) Cout. [JPM] (Wild Fls. of N. Oman)				
	Cistanche tubulosa (Schrenk.) R. Wright 155	N	W		4
P	Orobanche cernua Loefl. 853P	N	W?R?		2
	Orobanche poss. cernua Loefl. 180 (Fls. paler than 853)	N	R		3
	Orobanche ramosa L. [JPM]				
50	OXALIDACEAE				
		N/			
P	Oxalis corniculata L. 103, 263, 577	Nd	W R S		2 3
51	PEDALIACEAE				
	Sesamum indicum L. 564	Nd		Cr	3
52	PLANTAGINACEAE				
		N/			
	Plantago afra L. 729	Nd	S		2
	Plantago amplexicaulis Cav. 477, 669, 816	N	W R S?		3 4
	Plantago ciliata Desf. [JRE 3167, 3316]				
		N/			

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Plantago major L.	841, 885	Nd	R	2	3		
	Plantago ovata Forssk.	667, 691	N	W			4	
53	PLUMBAGINACEAE							
	Dyerophytum indicum (Gibs ex Wight) Kuntze (syn. Vogelia indica Wight and Gibs)	15, 292	N	W	2	3		
P	Limonium arabicum.....	344	N	W				5
54	POLYGALACEAE							
	Polygala abyssinica R. Br. ex Fresen. [JPM]							
P	?Polygala erioptera DC.	145, 211, 758, 782, 822 [check dets.]	N	W R	2	3	4	
P	Polygala mascatensis Boiss.	224, 596	N	W		3		
55	POLYGONACEAE							
P	Calligonum comosum L'Herit.	1P	N	W			4	
P	Calligonum crinitum Boiss. subsp. arabicum (Sosk.) Sosk.	696P	N	W?R?			4	
	Calligonum cf. tetrapterum Jaub. & Spach	174	N	W		3		
	Calligonum sp. (?not kept. Growing in 8m Ziziphus tree - sterile, but almost certainly differerent from above species)		N	W		3		
	Emex spinosa (L.) Campd.	?809	N/ Nd	W?R?		?3	4	
	Pteropyrum scoparium Jaub. & Spach	148, 433	N	W		3	4	
	Rumex dentatus L.	635 (poss. introduced with imported seed)	C	S			4	
	Rumex vesicarius L.	149, 178	N	W		3	?	
	Rumex sp.	735 (or Chenopodiaceae?)	Nd C	S	2			
56	PORTULACACEAE							
P	Portulaca oleracea L. var. oleracea	192	N/ Nd	S		?	4	
P	Portulaca quadrifida L.	533, 573	N/ Nd	S		3	4	
57	PRIMULACEAE							
	Anagallis arvensis L. subsp. arvensis	813	N/ Nd	R S		3	4	
	Anagallis arvensis L. var. (? subsp.) caerulea	28, 102, 171	N/ Nd	S	2	3	4	
P	Dionysia mira Wendelbo	235, 408	E	W	2			
58	PUNICACEAE							
	Punica granatum L.		Nd	Cr	2	3	4	5
59	RANUNCULACEAE							
P	Clematis orientalis L.	?238, 255, 384	N	W R	2			
	Ranunculus muricatus L.	169, 528	N/ Nd	S		3		
	Ranunculus sp.	53	N?	W	2			

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

60 RESEDACEAE

P	Ochradenus aucheri Boiss. subsp. aucheri 108, 293, 437, 767	N	W R		3 4
P	Ochradenus arabicus Chaudary,Hillcoat & Miller (sp. nov.) 5, 450	N	W R		2 3 4
	(non Ochradenus baccatus Del.)				
P	Oligomeris linifolia (Vahl.) J.F. Macbr. 212, 747, 865	N/ Nd	R		2 3 4
	Reseda aucheri ?var. bracteata (Boiss.) Abd. 109, 700, 778	N	W		3 4

61 RHAMNACEAE

P	Sagaretia thea (Osbeck) M.C. Johnst. subsp. thea 59, 241, 394, 686P	N	W		2 3
	(syn. Sagaretia spiciflora (A. Rich.) Hutch & Bruce)				
P	Ziziphus spina-christi (L.) Willd. 55, 374, 565	N	W R	Cr	2 3 4
P	Ziziphus sp. nov. 60*, 269, 403, ?683P	N	W		2 3

62 ROSACEAE

	Amygdalus arbica Oliv. [JPM; PM]				2
	Cotoneaster sp. 242	N	W		2
	Malus pumila (non. Mill.) Shneid. (Apple)	Nd		Cr	3
	(syn. Pyrus malus L.)				
	Neurada procumbens L. 757	N	W?R		3 4
	Prunus amygdalus Batsch (Almond) 736	Nd		Cr	2
	(syn. Amygdalus communis L.)				
	Prunus armeniaca L. (Apricot) 738	Nd		Cr	2
P	Prunus domestica L. (Plum) 737	Nd		Cr	2
P	Prunus persica (L.) Batsch (Peach) 739	Nd		Cr	2?3
	(syn. Amygdalus persica L.)				
PO	Rosa sp.	Nd		Cr	2 3 4

63 RUBIACEAE

	Callipeltis cucullaria var. aperta Boiss. & Buhse [JPM]				
	?Coffea arabica L. (Coffee. Mentioned by J.R. Wellsted in 1830's - now absent?)	Nd		Cr	3
	Galium aparine L. 48, 730	N/ Nd		S	2?3
	Galium cf. ceratopodum Boiss. 713 [also JPM]	N	R		2
	Galium ?setaceum Lam. subsp. decaisnei (Boiss.) Ehrendf. 629	N	W		3 4*
	Jaubertia aucheri Guill. 427, 676, 755	N	W		3 4
	(syn. Gaillonia aucheri (Guill.) Jaub. & Spach)				
	Kohautia caespitosa [JRE 3327]				
	Kohautia retrorsa (Boiss.) Brzem. Dhof. [ARS] N. Oman [JPM]				
P	Pseudogaillonia hymenostephana (Jaub. & Spach) Lincz 138P, 598	N	W		3
	(syn. Gaillonia hymenostephana Jaub. & Spach)				
	Pterogaillonia calycoptera (Dcne.) Lincz 398P				
	(syn. Gaillonia calycoptera (Decne.) Jaub. & Spach)	N	W		2
	Rubiaceae indet. 411 ?= [JPM] gen. nov.	N	W		2

64 RUTACEAE

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Taxon	Numbers	Status	Habitat	Regions
PO	Citrus aurantifolia (Christm.) Swingle (Lime)		Nd	Cr	3 4 5
RO	Citrus ?aurantium L. (Sour or Seville orange - "noring")		Nd	Cr	3
RO	Citrus ?xlimon (?cf Rough lemon or Citron - "sfargil")		Nd	Cr	3
RO	Citrus ?medica (?cf. Citron - "mashink/q")		Nd	Cr	5
RO	Citrus paradisi Macf. (Grapefruit)		Nd	Cr	3
P	Haplophyllum tuberculatum (Forssk.) A. Juss.	14, 119P, 473	N	R S	3 4 5
	Ruta chalepensis [JPM] var. bracteosa (DC.) Boiss	753	N/Nd	R	2?3?

65 SALICACEAE

	Taxon	Numbers	Status	Habitat	Regions
P	Salix ?wilhelmsiana	849	?	R?	2
	Salix sp.	294	N	W	3

66 SALVADORACEAE

	Taxon	Numbers	Status	Habitat	Regions
P	Salvadora persica L.	352	N	W R	3 4 5

67 SAPINDACEAE

	Taxon	Numbers	Status	Habitat	Regions
	Cardiospermum halicacabum L.	[JRE 3278] - Habitat?		S	3 4
	Dodonaea viscosa Jacq.	56, 386, 687 (485, 492 Dhofar)	N	W	2 ?

68 SAPOTACEAE

	Taxon	Numbers	Status	Habitat	Regions
P	Monotheca buxifolia (Falconer) A.DC.	406, 754	N	W	2 3
	(syn. Reptonia mascatensis (A. DC.) Radlk. ex O. Schwartz)				

69 SCROPHULARIACEAE

	Taxon	Numbers	Status	Habitat	Regions
B&W	Anticharis arabica Endl.	654B&W, 763	N	W R	3
P	Bacopa monnieri (L.) Pennell	41, 302, 560	N	W R	3
P	Kickxia elatine subsp. crinata (Mabille) Greuter	899P	N/Nd	R	2
	Kickxia hastata (R. Br.) Dandy	625, ?777, 879	N	W	3 4
P	Kickxia ramosissima (Wall.) Janchen	389P, ?846	N	W R	2 3?
P	Leptorhabdos parviflora (Benth.) Benth.	418P	N	W	2
	Linaria micrantha (Cav.) Hoffm. & Link	728	N/Nd	R?	2
	Lindenbergia fruticosa Benth.	[JRE 3472 alt & habitat? & JPM]			?
	Lindenbergia indica O. Kuntz	[JPM] (Wild Fls. of N. Oman)			?
	Misopates orontium (L.) Raf.	705	N	W	3
	Omania arabica Sp. Moore	[JPM]			
P	Schweinfurthia imbricata Miller & Sutton (ined.)	347, 354	E	W	3 5
	Schweinfurthia papilionaceae (Burm.f.) Boiss.	770, ?812	N	W R	3 4 5
	Scrophularia arguta Ait.	[JPM]			
	Verbascum akdarense (Murb.) Hub.-Mor.	150	E?	W	3
	(syn. Celsia akdarensis Murb.)				
	Verbascum cedreti Boiss. var.	[JPM Wild Fls. of Oman - incorrect det.?]			
	Verbascum omanense Hub.-Mor.	472	E	? R ?	3
	Veronica polita Fres.	101, 731	N/Nd	R S	2

70 SOLANACEAE

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Brugmansia candida Pers. RO (syn. Datura candida (Pers.) Safford	C	O	3 4
	Capsicum frutescens L.	Nd	Cr	? 4
	Datura metel L. [JPM]			
	Hyoscyamus insanus Stocks [JRE 3466]			3
	Hyoscyamus muticus L. [JPM] (Wild Fls. of N. Oman)		R	
P	Lycium shawii Roem and Schultes 227P	N	W R	? 3 4 ?
	Lycopersicon esculentum Mill.	Nd	Cr	3 4
	Nicotiana tabacum L.	Nd	Cr	3
P	Solanum incanum L. 64, (?287 ?Aubergine! S. melongena?)	N/ Nd	W R	2 3 4
	Solanum ?luteum Mill. 873	N/ Nd	S	2 ?
	Solanum melongena L. var. esculentum Nees.	Nd	Cr	? 4
	Solanum nigrum L. 183, 203, 464, 815	N/ Nd	S	3 4
	Withania somnifera (L.) Dunal 25, 444	N/ Nd	R	3 4 5
71	STERCULIACEAE			
	Melhania muricata Balf.f. [JPM]			
72	TAMARICACEAE			
	Tamarix aphylla (L.) Karst. 172	N	W	3?4*
	Tamarix arabica Bge. 323	N	W	3 ? 5
	Tamarix sp. 65			
73	THYMELAEACEAE			
B&W	Daphne mucronata Royle 244B&W, 264	N	W	2 ?
74	TILIACEAE			
	Corchorus depressus (L.) Christens 362	N	W	5
	?Corchorus olitorius L. 564A (fruit only)	Nd	Cr	3
	Corchorus trilocularis L. 446, ?532, 571, 706	N/ Nd	S	3 4 5
P	Grewia erythraea Schweinf. 57, 426, 603P	N	W	2 3
75	UMBELLIFERAE			
	Ammi majus L. 181, 523, 527	N/ Nd	W R S	3 4
P	?Anethum graveolens L. 546, 830, 881P - not found in Herbarium	N/ Nd	S Cr	4 5
	Apium graveolens L. 166, 469	N/ Nd	S	3
	Coriandrum sativum L. 24	N/ Nd	S	3
	Daucus carota L.	C	Cr	4
	Ducrosia anethifolia (DC.) Boiss. [JRE 3451]			4*
	Ducrosia sp. 277, 310, 330, 534, 776	N	W	3 4 5
	Pimpinella sp. 165, 831	N/ Nd	S	3 5

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

P	Pycnocycla aucherana Decne. ex Boiss. 297, 835P	E?	W		3
	Pyconcycla sp. nov.? [JPM]				
	Scandix pecten-veneris L. [JPM**]				
	Umbelliferae indet. 333	N	W		5

76 URTICACEAE

B&W	Forskohlea tenacissima L. 659B&W	N	W R		3 4
	Parietaria alsinifolia Del. 154	N	W		3
	Parietaria sp. 628	N	W		3

77 VERBENACEAE

PO	Clerodendrum inerme (L.) Gaertn.	C		O	4
P	Lantana camara L. 214, 279 (introduced ornamental)	C		O	3 4
P	Lantana petitiana A. Rich. 681, 860	N	W		2
P	Phyla nodiflora (L.) Green 20, 43	N/	R S		3 4 5
	(syn. Lippia nodiflora (L.) A. Rich.)	Nd			
P	Verbena officinalis L. 52, 858P	N/	W R		2
		Nd			

78 VIOLACEAE

P	Viola cinerea Boiss. 381, 678	N	W		2
B&W	Viola ?sp. nov. aff. stocksii 653B&W, 781, 826 [JRE 3303]	N	W		3 4
	(?Lowland annual form of V. cinerea)				

79 VITACEAE

RO	Vitis vinifera L.	Nd		Cr	2 3 ?

80 ZYGOPHYLLACEAE

	Fagonia bruguieri DC. 137, 177	N	W		3
	(?syn. Fagonia schweinfurthii....)				
	Fagonia indica Burm.f. [R-S] nr Rustaq (3) & [JPM]				
P	Fagonia sp. 7, 234	N			
	Tribulus bimucronatus.... 901(untypical)	N	W R		2 3 ?
P	Tribulus parvispinos.... &/or pentandrus Forssk. 456, 620 [JPM]	N	W R		3 4
	Tribulus pterocarpus Ehrenb. ex Koern ?176	N	W		3
	Tribulus sp. 225				
	Zygophyllum coccineum L. 608, 698	N	W		4 5
P	Zygophyllum simplex L. 110, 307, 353, 761	N	W R		3 4 5

DICOTYLEDONS; FAMILIES INDET.

66, 304 (water weed ?Najas), 326 (?Boraginaceae/Cleome),
567 (aromatic), 652, 692P, 695 (?Fagonia seedling)

(b) MONOCOTYLEDONES

81 COMMELINACEAE

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Commelina albescens Hassk. [JPM]				

82 CYPERACEAE

	Cyperus aucheri Jaub. & Spach `forma depauperata' 309	N	W		5
	(or Cyperus conglomeratus var. socotranus Balf.f.)				
	Cyperus conglomeratus Rottb. 320, 702	N	W R		4 5
	?var. aucheri (Jaub. & Spach) C.B. Clarke or f. pumilus (Boeck.) Kukenthal				
	Cyperus laevigatus L. 31, 280B	N	W R		3
P	Cyperus rotundus L. 201	N/Nd	S		? 4
	Fimbristylis cymosa R.Br. [JPM]	N/Nd	R S		4 5
	Fimbristylis ferruginea (L.) Vahl var. sieberiana (Kunth)Boeck. 42, 280A,911	N	W		2 3
	Scirpus litoralis Schrad. 557	N	W		3
	Schoenus sp. [JRE 3248]	N	W		3

83 GRAMINEAE

	Aeluropus lagopoides (L.) Trin. ex Thwaites 204, 363	N	W R		4 5
	Agrostis viridis.... 617A, 843	N	W R		2 4
	(syn. Agrostis semiverticillata (Forssk). A. Chr.)				
	Aristida abnormis Chiov. [JPM]				
	Aristida adscensionis L. 141, 260, 343, 399, 458, 648A, 655, 785, 795	N	W R		2 3 4 5
	Aristida caerulescens Desf. 300	N	W		3
	Aristida mutabilis Trin. and Rups. 318, 370	N	W		5
	Aristida protensa Heurd. forma [JPM]				
	Aristida pumila Decne. [JRE 3163]				
	Avena barbata Pott ex Link [JPM**]				
	Bothriochloa ischaemum (L.) Keng. [JPM]				
	Brachiaria deflexa (Schumach.) Hubbard and Robins [JPM]				
	Brachiaria eruciformis (J.E.Sm.) Griseb. 191	N/Nd	S		4
	Brachiaria leesiodies (Hochst.) Stapf [JPM]				
	Bromus fasciculatus C.Presl [PM at 1390m, Jabal Aswad]				
	Bromus japonicus Thunb. [JRE 3378] [JPM]				
	Bromus madritensis L. [JRE 3228, 3447)	N?	W?		3 4*
	Bromus pectinatus Thunb. [PM at 1390m, Jabal Aswad]				
	Catapodium rigidum (L.) C.E. Hubbard 869	N/Nd	S		
	(?Catapodium tuberculatus/m Moris)				
	Cenchrus ciliaris L. 13, 75, 131, ?459, 859	N	W R	Cr	2 3 4
	Cenchrus pennisetiformis Steud. & Hochst. 210, 366	N	W		5
	Cenchrus setigerus Vahl. 615, 783	N	W		3 4
	Centropodia forsskalii (Vahl) T.A. Cope				
	(syn. Asthenatherum forsskalii (Vahl) Nevski)				
P	Chloris barbata Swartz. 194, 547P	N/Nd	S		4
P	Chrysopogon aucheri (Boiss.) Stapf. 146, 595P	N	W		3
	Chrysopogon gryllus (L.) Trin. [PM]				2 3
	Coelachyrum brevifoloim Nees [JPM]				
P	Cymbopogon schoenanthus (L.) Spreng. 236, 261, 663B&W, 682	N	W		2 3 4
	?Cymbopogon spp. 228, 855, 906 ?in herbarium				

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Cynodon dactylon (L.) Pers. 208, 584	N/Nd		R	S			3	4	
	Dactyloctenium aegyptium (L.) P. Beauv. 195, 798	N/Nd		R	S	Cr		3	4	
	?D. aeyptiacum (L.) P. Beauv.									
	Dactyloctenium aristatum Link [JPM*]									
	Dactyloctenium scindicum Boiss. [JPM]									
	Dichanthium annulatum (Forssk.) Stapf. 301 (502, Dhofar)	N	W					3		
	Digitaria nodosa Parl. [JPM]									
	Echinochloa colonum (L.) Link. 530, 796	N/Nd			S			3	4	
	Enneapogon desvauxii P. Beauv. [JPM]									
	Enneapogon persicus Boiss. 124, 134	N	W					3		
	Enneapogon schimperiana (Hochst. ex A. Richb.) Renv. [JPM]									
	Eragrostis aspera (Jacq.) Nees 585	N/Nd			S			3		
	Eragrostis barrelieri Daveau. 369, 618	N	W					?	4	5
	Eragrostis cilianensis (All.) Vign. ex Hubb. 460	N/Nd		R					4	
	Eragrostis ciliaris (L.) R.Br. 751	N/Nd		R					4	
	Eragrostis minor Host. 401, 416	N	W				2			5
	Eragrostis papposa ?(Roem. & Schult.) Steud. 258	N	W				2			
	or E. papposa ?(Dufour) Steud.									
	Eragrostis pilosa (L.) P. Beauv. 231	N	W					?	?	
	Eragrostis poaeoides P. Beauv. [JRE 3184]									
	Eragrostis spp. 559, 750, 799									
	Eremopogon foveolatus (Del.) Stapf. 311, 322	N	W					?		5
	syn Dichanthium foveolatum (Del.) Roberty [JPM]									
	Fingerhuthia africana Lehm. 402, 856	N	W				2			
	Heteropogon contortus (L.) Beauv. ?var. glabra 262, 417	N	W				2			
	Hordeum vulgare L. ?26*, 876	N/Nd			?S	Cr		3	4	
	Hyparrhenia hirta (L.) Stapf. 136, 392, 415	N	W				2	3		
	Lasiurus scindicus Henr. 321, 439	N	W	R						5
	(syn. Lasiurus hirsutus (Forssk.) Boiss.)									
	Lophochloa phleoides (Vill.) Bor [JPM**]									
	Lophochloa pumila (Vill.) Bor [JPM]									
P	Panicum antidotale Retz. 542P	C				Cr			4	
	?Panicum coloratum L. 441 [JRE 3052]	N/Nd				Cr		3		<u>5</u>
?P	?syn. Panicum maximum Jacq. 583	N/Nd				Cr		3		
	Panicum sp. 648B (inflorescence only)	N/Nd		R				3		
	Paspalidium desertorum (A. Rich.) Stapf. [JRE 3206]									
	Paspalum sp. [JRE 3296]								4	
	Pennisetum divisum (J. Gmel.) Henrard 175	N	W					3		
?P	Pennisetum orientale (?L.C.) Rich. 407P? [JRE 3471]	N	W				2	?		
	Pennisetum setaceum (Forssk.) Chiov. [JPM]									
PO	?Pennisetum sp. 1 (cultivated fodder grass - "musaybilu")	Nd				Cr		3	4	
	?Pennisetum sp. 2 889 (cultivated millet - "sahuwi")	N/Nd				Cr		3		
	Phalaris minor Retz. 732	N/Nd			S		2			

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	Poa sinaica Steud. JPM										
	Polypogon monspeliensis (L.) Desf. 202	N/ Nd			S					4	
	Saccharum ?barberi Jeswiet (sugar cane)	Nd				Cr			3	4	
	Saccharum griffithii Munro ex Boiss. 19, ?563	N	W						3	4	5
	(?syn Saccharum ravennae (L.) Murr.)	N	W								
	Schismus barbatus (L.) Thell. [JPM*]										
P	Setaria verticillata (L.) Beauv. 376, 797	N/ Nd			S				3	4	
	Setaria viridis (L.) P.Beauv. 526	N/ Nd			S				3		
P	?Sorghum sp. 794 (cultivated) ?halepense (L.) Pers.	Nd				Cr			3	4	
	Sporobolus airaeformis Chiov. [JPM]										
	Sporobolus arabicus Boiss. e. descr. 319	N	W								5
	Sporobolus arenarius (Gouan) Duval-Jouve [JRE 3301]									4	
	Sporobolus minutiflorus Link [JPM**]										
P	Sporobolus spicatus (Vahl) Kunth 196	N	?	R	S					4	
	Stipa sp. [JPM]										
	Stipagrostis ciliata (Desf.) de Winter [JPM]										
	Stipagrostis hirtiglumis (Steud.) de Winter [JRE 3506 ?3 or 4 JPM]										
	Stipagrostis obtusa (Del.) Nees [R-S] (Izki to Haima)										5
	Stipagrostis plumosa (L.) Munro ex. T. Anders. 251, 317	N	W								5
	Tetrapogon villosus Desf. 259,400	N	W					2	?		
	Trachynia distachya (L.) Link [JRE 3448 & JPM]									?*	
?P	Tragus berteronianus Schult. 616	N	W							4	
	Tragus racemosus (L.) All. [JPM]										
	Tricholaena teneriffae (L.f.) Link ?or Parl. 765	N/ Nd		R?					3		
	Tripogon purpurascens Duthie 245, 679	N	W					2			
RO	Triticum sp. (wheat) [RO & JPM**]	Nd				Cr			3		
	Gramineae indet. 275, 419, 617B(hirsute,small), 723(immature)										

84 JUNCACEAE

	Juncus sp. cf. leschenaultii Gay or J. monticola Steud. 914	N/ Nd	W					2			
	Juncus rigidus Desf.								3		
	Juncus socotranus (Buchenan) non comb. 71	N	W						3		
	(syn. J. maritimus var. socotranus Buchenan)										
	Juncus sp. 909	N/ Nd	W W					2			

85 LILIACEAE

RO	Agave sp.	Nd		?R		?Cr			3		
RO	Allium cepa L.	Nd				Cr			3	4	
RO	Allium sativum L.	Nd		R		Cr			3	4	
PO	Aloe vera (L.) Burm.f. var. vera	N/		R		?Cr	O		3	4	
	(syns. perfoliata var. vera L. and barbadensis Mill.)										
	Asphodelus fistulosus var. tenuifolius (Cav.) Baker 27, 111	N	W	R					3	4	
	(syn. A. tenuifolius Cav.)										
	Dipcadi erythraeum Webb & Berth. [JPM])										
	) [& JRE 3493]										
	?Dipcadi unicolor (Stocks) Baker [JPM])										

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

86	MUSACEAE								
PO	Musa spp.	Nd			Cr		3	4	
87	NAJACEAE								
	Najas graminea Del. [JRE 3334]						3		
	?Najas sp. [RPW 304]						3		
88	ORCHIDACEAE								
	Epipactis veratrifolia Boiss. [JPM]	N	W				3		
89	PALMAE								
	Chamaerops/Nannorhops ritchiana (Griff.) Wendl. (syn. N. arabica Burret) [JRE3402]	N	W				3		5
	Cocos nucifera	Nd			Cr			4	
	Phoenix dactylifera L.	Nd		R	Cr		3	4	5
90	POTAMOGETONACEAE								
	Potamogeton nodosus Poir. 915	N	W			2	?		
91	TYPHACEAE								
	Typha domingensis Pers. [JPM] [?JRE 3374]								
	GYMNOSPERMAE								
92	CUPRESSACEAE								
P	Juniperus excelsa M. Bieb. 249 (syns. Juniperus macropoda Boiss. and J. procera Endl.)	N	W			2	3		
93	GNETACEAE								
	Ephedra intermedia Schrenk & C.A. Mey 248, 267	N	W			2			
P	Ephedra sp. 601P	N	W				3		
	II PTERIDOPHYTA								
	ADIANTACEAE								
	Adiantum capillus-veneris L. 383, 587	N/ Nd	W	R		2	3		
	EQUISETACEAE								
	Equisetum ?ramosissimum Desf. 840, 910	N/ Nd	W	R		2			

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

	FAMILY?						
	Actiniopteris radiata (Sw.) Link [JPM]						
	OPHIOGLOSSACEAE						
	Ophioglossum polyphyllum A. Braun, apud. Seubert. 256	N	W		2		
	PARKERIACEAE						
	Ceratopteris thalictroides (L.) Brogn. s.l.						
	PTERIDACEAE						
	Pteris vittata L. [JPM]						
	SINOPTERIDACEAE						
	Cheilanthes catanensis (Cos.) Fuchs [JPM]						
	Cheilanthes coriacea Decne. [JPM]						
	Cheilanthes farinosa (Forssk.) Kaulf. Dhofar						
	Cheilanthes fragrans (L.f.) Schwartz ?425, 904	N	W		2	?	

III BRYOPHYTA

	Class MUSCI						
	Aloina sp. [JRE 3450a]						4*?
	Barbula sp. 272	N	W		2		
	Splachnobryum sp. [JRE 3275]					3	
	Timiella ?sp. nov 271	N	W		2		
	Bryophyta indet. 382, 847, 848, 912, 913 (502a, Dhofar)						

IV CHAROPHYTA

P	Chara cf. zeylanica Willd. 788P	N	W			3	
	Chara sp. 6	N	W			3	

V LICHENS

Unnumbered (except for one specimen - 680a). A few at Royal Botanic Gardens, Edinburgh - indet.

	VERRUCARIACEAE						
	Dermatocarpon ?t/lachneum (Ach.) ?O/A.L. Sm. [JPM & JRE 3450b]						?4*

CHECKLIST OF THE PLANTS OF NORTHERN OMAN cont. (key to symbols at beginning of Appendix III p. 435)

COLLEMATACEAE			
Collema sp.	¦	¦	¦
LECANORACEAE			
Candelariella sp. [JPM]	¦	¦	¦
Squamarina gypsacea (Sm.) Poelt. [JPM]	¦	¦	¦
LECIDEACEAE			
Lecidea decipiens (Hedw.) Ach.	¦	¦	¦
Toninia albomarginata Lesd.	¦	¦	¦
Lecideaceae sp.	¦	¦	¦
?WHICH FAMILY OF LICHENS			
Scytonema sp. [JRE 3276]	¦	¦	¦

REFERENCES

Adey, M.E. (1984) Bee behaviour in tripping some legume flowers. **Bee Wld** 65(2): 62-67.

Adams, R.J.; Smith M.V. (1981) Seasonal pollen analysis of nectar from the hive and of extracted honey. **J. apic. Res.** 20(4): 243-248.

Akratanakul, P. (1977) The natural history of the dwarf Honeybee (**Apis florea** F.) in Thailand. Ph.D. Thesis. Cornell University, Ithaca, New York, U.S.A.

Al-Asfour, T. (1978) The marine terraces of the Bay of Kuwait. **pp** 245-254 **from** "The environmental history of the Near and Middle East since the last ice age". **ed** W.C. Brice. Academic Press, London.

Allen, M.D. (1958) Drone brood in honeybee colonies. **J. econ. Ent.** 51(1): 46-48.

Allen, M.D. (1959) Respiration rates of worker honeybees of different ages and at different temperatures. **J. exp. Biol.** 36(1): 92-101.

Allen, M.D. (1963) Drone production in honeybee colonies (**Apis mellifera** L.). **Nature, Lond.** 199: 789-790.

Allen, M.D.; Jeffree, E.P. (1956) The influence of stored pollen and of colony size on the brood rearing of honeybees. **Ann. appl. Biol.** 44(4): 649-656.

Atwal, A.S.: Bain, S.S.; Singh, B. (1970) Bee flora for four species of **Apis** at Ludhiana. **Indian J. Ent.** 32(4): 330-334.

Atwal, A.S.; Goyal, N.P. (1974) **Apis mellifera** turns indifferent to shain (**Plectranthus rugosus**). **Everyday Sci.** 19(2): 25-26.

Augspurger, C.K. (1981) Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on **Hybanthus prunifolius** (Violaceae). **Ecology** 62(3): 775-788.

Avitabile, A. (1978) Brood rearing in honeybee colonies from late autumn to early spring. **J. apic. Res.** 17(2): 69-73.

Avitabile, A.; Stafstrom, D.; Donovan, K.J. (1978) Natural nest sites of honeybee colonies in trees in Connecticut, USA. **J. apic. Res.** 17(4): 222-226.

Baker, H.G.; Baker, I. (1975) Studies of nectar constitution and pollinator-plant coevolution. **pp** 100-140 **from** "Co-evolution of Animals and Plants". 1st ed. **eds** L.E. Gilbert and P.H. Raven. Univ. of Texas Press, Austin and London.

Baker, H.G.; Baker, I. (1983) Floral nectar sugar constituents in relation to pollinator type. **pp** 117-141 **from** "Handbook of experimental pollination biology", **eds** C.E. Jones and R.J. Little. Scientific and Academic Editions, New York.

Baker, H.G.; Hurd, P.D. (1968) Intrafloral ecology. **A. Rev. Ent.** 13: 385-414.

Bartholomew, J. and Son Ltd. (1977) World Travel Map. Arabian Gulf. John Bartholomew and Son, Edinburgh.

Batra, S.W.T. (1967) Crop pollination and the flower relationships of the wild bees of Ludhiana, India. (Hymenoptera: Apoidea). **J. Kans. ent. Soc.** 40(2): 164-177.

Batra, S.W.T. (1984) Solitary bees. **Scient. Am.** 250(2): 86-93.

Batschelet, E. (1965) Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. **Amer. Inst. Biol. Sciences** (Monograph). Washington, D.C.

* Bauer, M. (1982) Seasonal cycle of honey flows in pastures in Lautenback and Willenbach, 1982. Dissertation, Universitat Tubingen, German Federal Republic.

Bawa, K.S. (1983) Patterns of flowering in tropical plants **pp** 394-410 **from** "Handbook of experimental pollination biology", **eds** C.E. Jones and R.J. Little. Scientific and Academic Editions, New York.

Berkeley, A.G.M. (1979) Beekeeping in Dhofar. Unpublished report, Oman Ministry of Agriculture and Fisheries and Durham University, U.K.

Berthoud, T.; Cleuziou, S. (1980) Farming communities of the Oman peninsula and the copper of Makkan. **J. Oman Stud.** 6(2): 239-246.

Best, L.S.; Bierzychudek, P. (1982) Pollinator foraging on foxglove (**Digitalis purpurea**): a test of a new model. **Evolution** 36(1): 70-79.

Beutler, R. (1953) Nectar. **Bee Wld.** 34: 106-16, 128-36, 156-62.

Bhatnagar, S. (1975) Floral polymorphism in sympatric populations of **Calotropis procera** (Ait.) R.Br. **Acta bot. ind.** 3(1): 43-46.

Bisht, D.S. (1975) Pollen gathering activity of honeybees and **Halictus** sp. in roses. **Indian Bee J.** 37(14):1-3.

Blatter, E. (1919-1936) Flora Arabica. **Rec. Bot. Surv. India** 8: 1-

519. (Reprinted 1978, Bishen Singh Mahendra Pal Singh, India).

Boch, R. (1961) Honeybee activity on safflower (**Carthamus tinctorius** L.). **Canad. J. Pl. Sci.** 41: 559-562.

Bodenheimer, F.S. (1951) Insects as human food. Dr. W. Junk, The Hague.

Bodenheimer, F.S.; Ben-Nerya, A. (1937) One-year studies on the biology of the honey-bee in Palestine. **Ann. appl. Biol.** 24: 385-403.

Boissier, E. (1867-1888) Flora Orientalis, Vols. 1-5 and supplement. Genève.

Bolten, A.B.; Feinsinger, P. (1978) Why do hummingbird flowers secrete dilute nectar? **Biotropica** 10(4): 307-309.

Bonnefille, R.; Riollet, G. (1980) Pollens des savanes d'Afrique orientale. Centre National de la Recherche Scientifique, Paris.

Brian, A.D. (1957) Differences in the flowers visited by four species of bumble-bees and their causes. **J. Anim. Ecol.** 26: 71-98.

Brian, M.V. (1979) Caste differentiation and division of labour. **pp** 121-222 **from** "Social Insects", **ed.** H.R. Hermann. Academic Press, London, U.K.

Brice, W.C. (Ed) (1978) The environmental history of the Near and the Middle East since the last ice age. Academic Press, London.

Bridgnell, E. (1946) Beginner's success. **Indian Bee J.** 8: 134-135, 164.

Brown, B.; Hamer, I. (1983) An unusual recording of honeybees (**Apis florea**) in Abu Dhabi. **Bull. Emirates nat. Hist. Group** (Abu Dhabi) 19:28.

Burgett, D.M.; Morse, R.A. (1974) The time of natural swarming in honeybees. **Ann. ent. Soc. Am.** 67: 719-720.

Burrill, R.M.; Dietz, A. (1981) The response of honeybees to variations in solar radiation and temperature. **Apidologie** 12 (4): 319-328.

Butler, C.G. (1945) The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and nectar concentration and abundance. **J. exp. Biol.** 21: 5-12.

Butler, C.G. (1974) The world of the honeybee. Collins, London.

Butler, C.G.; Finney, D.J. (1942) The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and solar radiation. **J. exp Biol.** 18(3): 206-212.

Campbell, R.C. (1974) Statistics for biologists. 2nd edition. Cambridge University Press, London.

Chandler, M.T. (1976) The African honeybee - **Apis mellifera adansonii**; the biological basis of its management. **pp** 61-68 **from** "Apiculture in Tropical Climates" **ed.** E. Crane. International Bee Research Association, London.

Chappell, M.A. (1982) Temperature regulation of carpenter bees (**Xylocopa californica**) foraging in the Colorado desert of southern California. **Physiol. Zool.** 55(3): 267-280.

Chaubal, Pushpa D.; Kotmire, S.Y. (1980) Floral Calendar of Bee Forage Plants at Sangarmal (India). **Indian Bee J.** 42(3): 65-68.

Cherian, M.C.; Ramachandran, S.; Mahadevan, V.; (1974) Studies in bee behaviour. **Indian Bee J.** 9(7/8): 98-100 and 9(9/10): 116-124.

Choudhury, B.; Choomsai, M.L.A.; Menon, M.G.R.; (1973) Insect pollination in some vegetable crops. **Haryana J. hort. sci.** 2(1/2): 56-62.

Clements, F.A. (1981) Oman. World Bibliographical Series Vol. 29. Clio Press, Oxford.

Cope, T.A. (1980) Nomenclatural and taxonomic notes on **Lasiurus** (Gramineae). **Kew Bull.** 35(3) 451-452.

Corbet, S.A. (1978) Bee visits and the nectar of **Echium vulgare** L. and **Sinapis alba** L. **Ecol. Ent.** 3(1): 25-37.

Corbet, S.A.; Unwin, D.M.; Prys-Jones, O.E. (1979) Humidity, nectar and insect visits to flowers with special reference to **Crataegus, Tilia** and **Echium. Ecol. Ent.** 4(1): 9-22.

Cornuet, J.M.; Louveaux, J. (1981) Aspects of genetic variability in **Apis mellifera** L. **pp** 85-94 **from** "Biosystematics of Social Insects" **eds** P.E. Howse and J.L. Clement. Academic Press, London.

Crane, E. (1967) Bibliography on honeybees other than **Apis mellifera. Bee Wld** 48(1): 8-15, 18.

Crane, E. (1973) Honey sources of some tropical and subtropical countries. **Bee Wld** 54(4): 177-186.

Crane, E. (1975a) Honey: a comprehensive survey. Heinemann in cooperation with the International Bee Research Association, London.

Crane, E. (1975b) The flowers honey comes from. pp 1-76 **from** Honey: a comprehensive survey. ed E. Crane. Heinemann in cooperation with the International Bee Research Association, London.

Crane, E. (1978) Bibliography of tropical apiculture. International Bee Research Association, London, U.K. (Incl. No. 13, The little honeybee **Apis florea**).

Crane, E. (1980) The scope of tropical apiculture. **Bee Wld** 61(1): 19-28.

Crane, E. (1982) Introduction of non-native bees to new areas. **Bee Wld** 63(1): 50-53.

Crane, E. (1983a) The archaeology of beekeeping. Duckworth, London.

Crane, E. (1983b) Magnetism and bees. **Bee Wld** 64(4): 174-175.

Crane, E.; Walker, P.; Day, R. (1984) Directory of important world honey sources. International Bee Research Association, London.

Cruden, R.W.; Hermann, S.M.; Peterson, S. (1983) Patterns of nectar production and plant-pollinator coevolution. **pp** 80-125 **from** "The biology of nectaries" **eds** B. Bentley and T. Elias, Columbia University Press, New York.

Culliney, T.W. (1983) Origin and evolutionary history of the honeybees **Apis. Bee Wld** 64(1): 29-38.

Darchen, R. (1973) La thermoregulation et l'ecologie de quelques espèces d'abeilles sociales d'Afrique (Apidae, **Trigonini** et **Apis mellifica** var. **adansonii**). **Apidologie.** 4(4): 341-70.

Das, B. (1946) The Little Bee as it appears to a layman. **Indian Bee** J. 8: 62-65.

Davies, F.G. (1978) The identity of **Vernonia atriplicifolia (Compositae). Kew Bull.** 32(4): 775-778.

Davis, P.H. (1961) Hints for hard-pressed collectors. **Watsonia** 4(6): 283-289.

De Jong, D. (1982) Orientation of comb building by honeybees. **J. Comp. Physiol., A.** 147: 495-501.

Deodikar, G.B.; Ghatge, A.I.; Phadke, R.P.; Mahindre, D.B.; Kshirsagar, K.K.; Muvel, K.S.; Thakar, C.V. (1977) Nesting behaviour of Indian honeybees. Nesting behaviour of **Apis dorsata** Fab. **Indian Bee J.** 39(1-4):1-12.

Dhaliwal, J.S.; Atwal, A.S. (1976) Note on the effect of air temperature, relative humidity and wind velocity on bees visiting berseem at Ludhiana. **Indian J. agric. Sci.** 46(1): 50-51.

Diwan, V.V.; Salvi, S.R. (1965) Some interesting behavioural features of **Apis dorsata** Fab. **Indian Bee J.** 27(1): 52.

Douglas, J.C. (1886) The hive-bee indigenous to India and the introduction of the Italian bee. **J. Asiat. Soc. Beng. Pt. II Nat. Sci.** 55: 83-96.

Dover, C. (1929) Wasps and bees in the Raffles Museum, Singapore. **Bull. Raffles Museum, Singapore** 2: 43-70.

Dubois, L.; Collart, E. ; (1950) L'apiculture au Congo belge et au Ruanda-Urundi. (Beekeeping in the Belgian Congo and in Ruanda-Urundi). Brussels: Ministere des Colonies. Direction de l'Agriculture, de l'Elevage et de la Colonisation.

Durham University (1978- ?) Research and development surveys in northern Oman. Final Reports Vols. I-IX. Durham, U.K.

Düster, J.; Scholz, F. (1980) Bibliographie uber das Sultanat Oman: Stand Juli 1980. Deutsches Orient-Institut, Hamburg, W. Germany.

Dutton, R.W.; Free, J.B. (1979) The present status of beekeeping in Oman. **Bee Wld** 60(4): 176-185.

Dutton, R.W.; Letts, S.E. (1982) Agriculture. Research and Development Surveys in northern Oman Vol. IVA, **ed** H. Bowen-Jones and R.W. Dutton. Durham University, U.K.

Dutton, R.W.; Mjeni, A.M. ; Whitcombe, R.P. (Eds.); Ryrie, J.A. (Illustr.) (1982) Honeybees in Oman (In English and Arabic). Office of the Adviser for Conservation of the Environment, Muscat, and Durham University, U.K.

Dutton, R.W.; Ruttner, F.; Berkeley, A.; Manley, M.J.D. (1981) Observations on the morphology, relationships and ecology of **Apis mellifera** of Oman. **J. apic. Res.** 20(4): 201-214.

Dutton, R.W.; Simpson, J. (1977) Producing honey with **Apis florea** in Oman. **Bee Wld.** 58(2): 71-76.

Dyer, F.C.; Gould, J.L. (1981) Honeybee orientation: a backup system for cloudy days. **Science, N.Y.** 214(4524): 1041-1042.

Edmondson, J.R. (1980) Botanical collections from Oman, February-

March 1980. Unpublished report, Dept. of Botany, University of Edinburgh, UK.

Eisikowitch, D.; Masad, Y. (1980) Nectar-yielding plants during the dearth season in Israel. **Bee Wld** 61(1): 11-18.

Eisikowitch, D.; Masad, Y.; (1982) Preferences of honeybees for different ornamental nectar-yielding plants during the dearth period in Israel. **Bee Wld** 63(2): 77-82.

Erdtman, G. (1952) Pollen morphology and plant taxonomy. Angiosperms. Almqvist and Wiksell, Stockholm, Sweden.

Faegri, K.; Van der Pijl, L. (1979) The principles of pollination ecology. 3rd ed. Pergamon, Oxford.

Fell, R.D.; Ambrose, J.T.; Burgett, D.M.; DeJong, D.; Morse, R.A.; Seeley, T.D. (1977) The seasonal cycle of swarming in honeybees. **J. apic. Res.** 16: 170-173.

Fletcher, D.J.C. (1975 and 1976) New perspectives in the causes of absconding in the African bee (**Apis mellifera adansonii** L.). **S. Afr. Bee J.** 47(6): 11, 13-14; 48(1): 6-9.

Fletcher, D.J.C. (1978) The African bee, **Apis mellifera adansonii** in Africa. **A. Rev. Ent.** 23: 151-171.

Fletcher, D.J.C.; Crewe, R.M. (1981) Nest structure and thermoregulation in the stingless bee **Trigona (Plebeina) denoiti** Vachal (Hymenoptera: Apidae). **J. ent. Soc. sth. Afr.** 44(2): 183-196.

Fletcher, D.J.C.; Tribe, G.D. (1977) Swarming potential of the African bee, **Apis mellifera adansonii** L. **pp** 25-34 **from** "African bees: taxonomy, biology and economic use". **ed.** D.J.C. Fletcher. Apimondia, Pretoria, South Africa.

Frankie, G.W.; Baker, H.G.; Opler, P.A. (1974a) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. **J. Ecol.** 62: 881-919.

Frankie, G.W.; Baker, H.G.: Opler, P.A. (1974b) Tropical plant phenology: applications for studies in community ecology. **pp** 287-96 **from** Phenology and Seasonality Modeling **ed** H. Leith. Springer-Verlag, Berlin.

Frankie, G.W.; Haber, W.A. (1983) Why bees move among mass-flowering neotropical trees. **pp** 360-372 **from** "Handbook of experimental pollination biology" **eds** C.E. Jones and R.J. Little, 558pp. Scientific and Academic Editions, New York.

Franssen, C.J.H. (1932) Aanteekeningen over Micrapis florea F. (Notes on Micrapis florea). **Natuurk. Tijdschr. Ned. - Indië**

92: 55-63. (Dutch and IBRA Translation E1170).

Free, J.B. (1960) The distribution of bees in a honey-bee (**Apis mellifera**) colony. **Proc. R. ent. Soc. Lond. A.** 35: 141-144.

Free, J.B. (1967) The production of drone comb by honeybee colonies. **J. apic. Res.** 6(1): 29-36.

Free, J.B. (1968) Dandelion as a competitor to fruit trees for bee visits. **J. Appl. Ecol.** 5: 169-178.

Free, J.B. (1970) Insect pollination of crops. Academic Press.

Free, J.B. (1977) The social organization of honeybees. The Institute of Biology's Studies in Biology No. 81. Edward Arnold, London.

Free, J.B. (1981) Biology and behaviour of the honeybee **Apis florea**, and possibilities for beekeeping. **Bee Wld.** 62(2): 46-59.

Free, J.B. (1982) The biology and behaviour of the honeybee **Apis florea. pp** 181-187 **from** "Social insects in the tropics, Vol. I" **ed** P. Jaisson, Presses de l'Université Paris-Nord, Paris, France.

Free, J.B.; Ferguson, A.W.; Pickett, J.A. (1983) Effect of the components of the Nasonov pheromone on its release by honeybees at the hive entrance. **J. apic. Res.** 22(3): 155-157.

Free, J.B.; Ferguson, A.W.; Pickett, J.A.; Williams, I.H. (1982) Use of unpurified Nasonov pheromone components to attract clustering honeybees. **J. apic. Res.** 21(1): 26-29.

Free, J.B.; Pickett, J.A.; Ferguson, A.W.; Smith, M.C. (1981) Synthetic pheromones to attract honeybee (**Apis mellifera**) swarms. **J. agric. Sci., Camb.** 97: 427-431.

Free, J.B.; Spencer-Booth, Y. (1960) Chill-coma and cold death temperatures of **Apis mellifera. Entomologia exp. appl.** 3: 222-230.

Free, J.B.; Spencer-Booth, Y. (1961) Effect of temperature on **Apis indica** workers. **Nature, Lond.** 190(4779): 933.

Free, J.B.; Spencer-Booth, Y. (1962) The upper lethal temperatures of honeybees. **Entomologia exp. appl.** 5: 249-254.

Free, J.B.; Williams, I.H. (1972) The transport of pollen on the body hairs of honeybees (**Apis mellifera** L.) and bumblebees (**Bombus** spp. L.). **J. appl. Ecol.** 9: 609-615.

Free, J.B.; Williams, I.H. (1975) Factors determining the rearing and rejection of drones by the honeybee colony. **Anim.**

Behav. 23: 650-675.

Free, J.B.; Williams, I.H. (1977) The pollination of crops by bees. Bucharest, Romania: Apimondia and International Bee Research Association.

Free, J.B.; Williams, I.H. (1979) Communication by pheromones and other means in **Apis florea** colonies. **J. apic. Res.** 18(1): 16-25.

Frifelt, K. (1976) Evidence of a Third Millenium B.C. town in Omar. **J. Oman Stud.** 2: 57-73.

Friis, I. (1978) A reconsideration of the genera **Monotheca** and **Spiniluma (Sapotaceae). Kew. Bull.** 33: 91-98.

Frisch, K. Von. (1967) The dance language and orientation of bees. Harvard University Press, Cambridge, Mass., U.S.A.

Fry, C.H. (1983) Honeybee predation by bee-eaters, with economic considerations. **Bee Wld** 64(2): 65-78.

Gadbin, C. (1980) Bee plants of southern Chad. **Apidologie** 11(3): 217-254.

Gallagher, M.; Woodcock, M.W. (1980) The birds of Oman. Quartet, London.

Gamal-Eldin, E. (1984) Studies in the flora of Arabia VIII: A new **Publicaria** from Oman. **Notes R. Bot. Gdn. Edinb.** 41(3): 467-471.

Gary, N.E. (1967) Diurnal variations in the intensity of flight activity from honeybee colonies. **J. apic. Res.** 6(2): 65-68.

Gary, N.E. (1975) Activities and behaviour of honey bees. **pp** 185-264 **from** "The Hive and the Honey Bee" **ed.** Dadant and Sons. Dadant and Sons, Hamilton, Illinois, U.S.A.

Ghatge, A. (1949) Some research work on **Apis florea. Indian Bee J.** 11(1/2): 5-6, 9.

Gross, R.S.; Werner, P.A. (1983) Relationships among flowering phenology, insect visitors, and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (**Solidago:** Compositae). **Ecol. Monogr.** 53(1): 95-117.

Guest, E. **et al** (1966) Flora of Iraq, Vols 1-4, 9. Republic of Iraq Ministry of Agriculture, Baghdad.

Hadidi, M.N.el-.; Boulos, L. (1968) Street trees in Egypt. **Publ. Cairo. Univ. Herb.** No. 1, Cairo, Egypt.

Hambleton, J.I. (1925) The effect of weather upon the change in weight of a colony of bees during the honey flow. **Bull. U.S. Dep. Agric.** No. 1339: 1-52.

Hameed, S.F.; Adlakha, R.L. (1973) Preliminary comparative studies on the brood rearing activities of **Apis mellifera** L. and **Apis cerana indica** F. in Kulu valley. **Indian Bee J.** 35(1-4): 27-35.

Hastings, A.; Humphries, J.H.; Meadow, R.H. (1975) Oman in the Third Millenium BCE. **J. Oman. Stud.** 1: 9-55.

Hawley, D. (1977) Oman and its renaissance. Stacey International, London.

Hedge, I.C. (1982) Studies in the Flora of Arabia: II. Some new and interesting species of Labiatae. **Notes R. bot. Gdn. Edinb.** 40(1): 63-73.

Hedge, I.C.; King. R.A. (1983) The Cruciferae of the Arabian Peninsula: a check-list of species and a key to genera. (Studies in the flora of Arabia IV). **Arab Gulf. J. scient. Res.** 1(1): 41-66.

Hedge, I.C.; Lamond, J.M. (1978) Further notes on Umbelliferae-Echinophoreae. **Notes R. bot. Gdn Edinb.** 37: 61-66.

Heinrich, B. (1974) Thermoregulation in endothermic insects. **Science, N.Y.** 185: 747-756.

Heinrich, B. (1975a) The role of energetics in bumblebee-flower interrelationships. **pp** 141-156 **from** Co-evolution of animals and plants. Symposium V. First International Congress of Systematic and Evolutionary Biology. Boulder, Colorado. 1973. **ed** L.E. Gilbert and P.H. Raven. Univ. of Texas Press, Austin and London.

Heinrich, B. (1975b) Bee flowers: A hypothesis on flower variety and blooming times. **Evolution** 29: 325-334.

Heinrich, B. (1975c) Energetics of pollination. **Annu. Rev. Ecol. and Syst.** 6: 139-170.

Heinrich, B. (1975d) Thermoregulation and flight energetics of desert insects. **pp** 980-105 **from** "Environmental Physiology of Desert Organisms" **ed** N.S. Hadley. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pa.

Heinrich, B. (1976a) Resource partitioning among some eusocial insects: bumblebees. **Ecology** 57(5): 874-890.

Heinrich, B. (1976b) Flowering phenologies: bog, woodland, and disturbed habitats. **Ecology** 57(5): 890-899.

Heinrich, B. (1979a) Bumblebee Economics. Harvard University Press, Cambridge, Massachusetts, U.S.A.

Heinrich, B. (1979b) Thermoregulation of African and European honeybees during foraging, attack, and hive exits and returns. **J. exp. Biol.** 80: 217-229.

Heinrich, B. (1979c) Keeping a cool head: honeybee thermoregulation. **Science, N.Y.** 205: 1269-1271.

Heinrich, B. (1980a) Mechanisms of body-temperature regulation in honeybees, **Apis mellifera.** I. Regulation of head temperature. **J. exp. Biol.** 85: 61-72.

Heinrich, B. (1980b) Mechanisms of body-tremperature regulation in honeybee, **Apis mellifera.** II. Regulation of thoracic temperature at high air temperatures. **J. exp. Biol.** 85: 73-87.

Heinrich, B. (Ed) (1981a) Insect Thermoregulation. John Wiley and Sons, New York.

Heinrich, B. (1981b) The mechanisms and energetics of honeybee swarm temperature regulation. **J. exp. Biol.** 91: 25-55.

Heinrich, B. (1981c) The regulation of temperature in the honeybee swarm. **Scient. Am.** 244(6): 120-129.

Heinrich, B. (1981d) The energetics of pollination. **Ann. Mo. bot. Gdn.** 68(2): 370-378.

*Heithaus, E.R. (1974) The role of plant-pollingator interactions in determining community structure. **Ann. Mo. bot. Gdn.** 61: 675-691.

Heithaus, E.R. (1979a) Community structure of neotropical flower visiting bees and wasps: diversity and phenology. **Ecology** 60(1): 190-202.

Heithaus, E.R. (1979b) Flower-feeding specialization in wild bee and wasp communities in seasonal neotropical habitats. **Oecologia (Berl.)** 42: 179-194.

*Heithaus, E.R. (1979c) Flower visitation records and resource overlap of bees and wasps in northwest Costa Rica. **Brenesia** 16: 9-52.

Hillcoat, D.; Lewis, G.; Verdcourt, B. (1980) A new species of **Ceratonia** (Leguminosae-Caesalpinioideae) from Arabia and the Somali Republic. **Kew. Bull.** 35: 261-271.

Hillman, F. (1983) Fibre re-inforced cement irrigation channels: progress May-November 1983. **Khabura Development Project Preliminary Reports** Vol. 8A No. 3. Centre for Overseas

Research and Development, Durham University, U.K.

Hocking, B. (1968) Insect-flower associations in the high Arctic with special reference to nectar. **Oikos** 19: 359-387.

Hodges, D. (1978) A calendar of bee plants. **Bee Wld** 59 (3): 97-100.

Horn, P.M.; Nielsen, J.B.; Issa, A.M.; Salaam, S. (1977) Climate of Jebel Akhdar (Saiq). F.A.O. Project OMA 77/001, Field Document No. 2. Water Resources Dept., Ministry of Agriculture and Fisheries/F.A.O., Muscat, Sultanate of Oman.

Horn, P.M.; Nielsen, J.B. (1977a) Rainfall in Oman 1974-1976. F.A.O. Project OMA/73/009, Field Document No. 3. Water Resources Dept., Ministry of Agriculture and Fisheries/F.A.O., Muscat, Sultanate of Oman.

Horn, P.M.; Nielsen, J.B. (1977b) Climate of the Batinah. F.A.O Project OMA/77/001, Field Document No. 4. Water Resources Dept., Ministry of Agriculture, Fisheries, Petroleum and Minerals, F.A.O., Muscat, Sultanate of Oman.

Hou, D. (1969) Pollen of **Sarawakodendron** (Elastraceae) and some related genera, with notes on techniques. **Blumea** 17(1): 97-120.

Hunter, R.F. (1962) Hill sheep and their pasture: a study of sheep-grazing in south-east Scotland. **J. Ecol.** 50: 651-680.

Hunting Surveys Ltd. (1977) Sultanate of Oman, a new topographical map. Shell Markets (Middle East) Ltd., Muscat.

Hurd, P.D.; Linsley, E.A.; Whitaker, T.W. (1971) Squash and gourd bees (**Peponapis, Xenoglossa**) and the origin of the cultivated curcurbits. **Evolution** 25: 218-234.

Huxley, P.A.; Van Eck, W.A. (1974) Seasonal changes in growth and development of some woody perennials near Kampala, Uganda. **J. Ecol.** 62: 579-591.

Ibrahim, S.H. (1976) A list of pollen plants visited by honeybees in Egypt. **Agric. Res. Rev., Cairo** 54(1): 217-219.

Ifantidis, M.D. (1978) Comb orientation in the honeybee. **Apidologie** 9: 57-73.

Indian Bee Journal 1942 Editorial. The **A. dorsata** colony. **Indian Bee J.** 4:64.

Indian Standards Institution (1973) Code for conservation and maintenance of honeybees. Indian Standard No. IS:6695-1972.

Ingrams, W.H. (1936) A report on the social, economic and political condition of the Hadhramaut. Colonial Report No. 123, issued by the Colonial Office, Aden Protectorate. H.M.S.O., London.

Inouye, D.W. (1977) Resource partitioning in bumblebees. **Jl. N.Y. ent. Soc.** 85(4): 253-254.

Jadhav, L.D. (1981) Role of insects in the pollination of onion (**Allium cepa** L.) in the Maharashtra State, India. **Indian Bee J.** 43(3): 61-63.

Jain, K.L.; Kapil, R.P. (1980) Foraging rhythm of megachilid bees in relation to the flowering of **Medicago sativa** L. and **Parkinsonia aculeata** L. **Indian Bee J.** 42(2): 35-38

Janzen, D.H. (1967) Synchronization of sexual reproduction of trees within the dry season in central America. **Evolution** 21: 620-637.

Jaycox, E.R. (1983a) Starting a bee business in Yemen. **Speedy Bee** 12(5): 14,16.

Jaycox, E.R. (1983b) Beekeeping in the Yemen Arab Republic. **Glean. Bee Cult.** 111(7): 376,382.

Jeffree, E.P. (1955) Observations on the decline and growth of honeybee colonies. **J. econ. Ent.** 48: 723-726.

Jeffree, E.P. (1956) Winter brood and pollen in honeybee colonies. **Insectes Soc.** 3: 417-422.

Jhajj, H.S.; Goyal, N.P. (1979) Comparative behaviour of pollen foragers of **Apis cerana indica** and **Apis mellifera**. **J. apic. Res.** 18(4): 279-284.

Kapil, R.P. (1957) The length of life and the brood-rearing cycle of the Indian bee. **Bee Wld** 38(10): 258-263.

Kapil, R.P. (1960) Osservazioni sulla temperatura del glomere dell'ape indiana (Observations on the temperature of the cluster of **Apis indica**). **Apicoltore d'Ital.** 27(4/5): 79-83.

Kapp, R.O. (1969) How to know "Pollen and Spores". 249pp. W.C. Brown, Dubuque, Iowa, U.S.A.

Kapyla, M. (1974) Diurnal flight activity in a mixed population of **Aculeata** (Hym.) **Ann. Ent. Fenn.** 40: 61-69.

Karpowicz, J. (1980) Special report - **Apis florea** in Dhofar. Unpublished report 7th Dec. 1980, to Oman Ministry of Agriculture and Fisheries and Durham University.

Keeler, K.H.: Kaul, R.B. (1979) Morphology and distribution of petiolar nectaries in **Ipomoea** (Convolvulaceae). **American Journal of Botany** 66(8): 946-952.

Kefuss, J.A. (1978) Influence of photoperiod on the behaviour and brood-rearing activities of honeybees in a flight room. **J. apic. Res.** 17(3): 137-151.

Kefuss, J.A.; Nye, W.P. (1970) The influence of photoperiod on the flight activity of honeybees. **J. apic. Res.** 9(3): 133-139.

Kevan, P.G.; Baker, H.G. (1983) Insects as flower visitors and pollinators. **A. Rev. Ent.** 28: 407-453.

King, R.; Stevens, J.H. (1973) A bibliography of Oman 1900-1970. University of Durham Centre for Middle Eastern and Islamic Studies. Occasional Papers Series No. 2, 1973.

Kleinschmidt, G.J.; Kondos, A.C. (1977) The influence of crude protein levels on colony production. **S. Afr. Bee J.** 49(4): 16-19.

Klungness, L.M.; Peng Y.S. (1983) A scanning electron microscopic study of pollen loads collected and stored by honeybees. **J. apic. Res.** 22(4): 264-271.

Koeniger, N. (1976) The Asiatic honeybee **Apis cerana. pp** 47-49 **from** "Apiculture in Tropical Climates" **ed.** E. Crane. International Bee Research Association, London.

Koeniger, N. (1982) Interactions among the four species of the genus **Apis. pp** 59-64 **from** "The Biology of Social Insects", **eds** M.D. Breed, C.D. Michener, H.E. Evans. Westview Press, Boulder, Colorado.

Koeniger, N.; Koeniger, G. (1980) Observation and experiments on migration and dance communication of **Apis dorsata** in Sri Lanka. **J. apic. Res.** 19(1): 21-34.

Koeniger, N.; Koeniger, G.; Punchihewa, R.K.W.; Fabritius Mo.; Fabritius Mi. (1982) Observations and experiments on dance communication in **Apis florea** in Sri Lanka. **J. apic. Res.** 21(1): 45-52.

Koeniger, N.; Vorwohl, G. (1979) Competition for food among four sympatric species of Apini in Sri Lanka (**Apis dorsata, Apis cerana, Apis florea** and **Trigona iridipennis**). **J. apic. Res.** 18(2): 95-109.

Koller, D. (1969) The physiology of dormancy and survival of plants in desert environments. **pp** 449-469 **from** Dormancy and Survival **ed** H.W. Woolhouse, Symp. Soc. exp. Biol 23, Cambridge University Press, London.

Krebs, C.J. (1978) Ecology. The experimental analysis of distribution and abundance. Harper and Row, New York.

Kronenberg, F.; Heller, H.C. (1982) Colonial thermoregulation in honeybees (**Apis mellifera**). **J. Comp. Physiol., B.** 148: 65-76.

Kshirsagar, K.K.; Muvel, K.S.; Mittal, M.C.; Phadke, R.P.; (1980) Some observations on **Apis florea** F. **II. Int. Conf. Apic. trop. Clim.** (1980) Delhi.

Kuterback, D.A.; Walcott, B.; Reeder, R.J.; Frankel, R.B. (1982) Iron-containing cells in the honey bee (**Apis mellifera**). **Science, N.Y.** 218 (4573): 695-697.

Larsen, T.B. (1984) The zoogeographical composition and distribution of the Arabian butterflies (Lepidoptera; Rhopalocera). **J. Biogeogr.** 11(2): 119-158.

Latif, A.; Qayyum, A.; Manzoor-ul-Haq. (1958) A contribution to bee flora of Pakistan. **Pakist. J. sci. Res.** 10(2): 67-71.

Lensky, Y. (1958) Some factors affecting the temperature inside hives in hot climates. **Bee Wld** 39(8): 205-208.

Lensky, Y. (1964a) Comportement d'une colonie d'abeilles a des temperatures extremes. (Behaviour of a honeybee colony at extreme temperatures). **J. Insect. Physiol.** 10(1): 1-12 and IBRA translation E1495.

Lensky, Y. (1964b) Les regulations thermiques dans la ruche en ete. (Temperature control in the hive in summer). **Ann. Abeille** 7(1): 23-45.

Leonard, J. (1980) **Chrozophora sabulosa** Kar. et Kir. **Bolm Soc. broteriana**, ser. 2 53: 465-467.

Lewis, T.; Taylor, L.R. (1964) Diurnal periodicity of flight by insects. **Trans. R. ent. Soc. Lond.** 116: 393-476.

Lindauer, M. (1956) Uber die Verstandigung bei indischen Bienen. [Communication among the honeybees and stingless bees of India]. **Zeitschrift fur vergleichende Physiologie** 38: 521-557.

Lindauer, M. (1957) Communication among the honeybees and stingless bees of India. **Bee Wld** 38: 3-14, 34-39.

Linsley, E.G. (1958) The ecology of solitary bees. **Hilgardia** 27: 543-599.

Linsley, E.G.; MacSwain, J.W.; Smith, R.F. (1955) Observations on the nesting habits and flower relationships of some species of **Melandrena. Pan-Pacif. Ent.** 31: 173-185.

Lorimer, J.G. (1908) Gazetteer of the Persian Gulf, Oman and Central Arabia, Vol. IIA, pp 444. Gregg International, Furnborough, England and Irish Univ. Press, Shannon. (Reprinted in 1970 from an original published by the Superintendent Government Printing, Calcutta, India).

Louveaux, J. (1966) Les modalités de l'adaptation des abeilles (**Apis mellifica** L.) au milieu naturel. (The adaptation of honeybee colonies to their natural environment). **Ann. Abeille** 9(4): 323-350.

Louveaux, J. (1969) Le cycle biologique annuel de la colonie d'abeilles. **Proc. VI Congr. IUSSI, Bern 1969**: 159-162.

Louveaux, J. (1973) The acclimatization of bees to a heather region. **Bee Wld** 54: 105-111.

Louveaux, J. (1976) Recent developments on the physiology and ecology of the honey bee. **pp** 95-97 **from** "Orientations et moyens. Presentation de quelques themes de recherche" (English Edition). Department de Zoologie, I.N.R.A., Ministere de l'Agriculture, France.

Louveaux, J.; Maurizio, A.; Vorwohl, G. (1978) Methods of melissopalynology. **Bee Wld** 59(4): 139-157.

Lundberg, H. (1980) Effects of weather on the foraging flights of bumblebees (Hymenoptera, Apidae) in a subalpine/alpine area. **Holarct. Ecol.** 3: 104-110.

Lundie, A.E. (1925) The flight activities of the honeybee. **Bull. U.S. Dep. Agric.** No. 1328: 1-37.

Maa, T. (1953) An enquiry into the systematics of the tribus **Apidini** or honeybee (Hym.) **Treubia** 21(3): 525-640.

Mandaville, J.P.Jr. (1977) Plants. **Oman Flora and Fauna Survey 1975. J. Oman. Stud.** Spec. Rep. No. 1: 229-267.

Mandaville, J.P. Jr.; Bovey, D. (1978) Wild flowers of northern Oman. John Bartholomew and Son, Bromley, Great Britain.

Mandaville, Jon. (1981) Impressions from a writer's notebook - At work in Yemen. **Aramco World Magazine** 32(3): 10-19.

Manley, M.J.D. (1978) Beekeeping in northern Oman. **Al Mawared al Tabei'eiah** 4(9): 11-14.

Manley, M.J.D. (1980) Technical aspects of extension work in northern Oman with reference to importation and distribution of movable frame hives. **II. Int. Conf. Apic. trop. Clim.** (1980) Delhi:

Martin, P. (1963) Die Steuerung der Volksteilung beim Schwarmen der Bienen. Zugleich ein Beitrag zum Problem der Wanderschwarme. (The mechanism of colony division in honeybee swarming, and a study of the problem of absconding). **Insectes soc.** 10(1): 13-42 (+ IBRA Translation).

Martin, H.; Lindauer, M. (1981) The orientation of bees in the earth's magnetic field. **pp** 328-332 **from** Sense organs. **ed.** M.S. Laverack; D.J. Cosens. Blackie and Son, Glasgow, U.K.

Mattu, V.K.; Verma, L.R. (1983) Comparative morphometric studies on the Indian honeybee of the north-west Himalayas I. Tongue and antenna. **J. apic. Res.** 22(2): 79-85.

McGregor, S.E. (1976) Insect pollination of cultivated crop plants. Agriculture Handbook, United States Department of Agriculture No. 496.

Mehta, V.K. (1948) Apis florea. **Indian Bee J.** 10: 79,81.

Millen, T.W. (1943). Bee breeding. What bees can we keep on the plains of India? **Indian Bee J.** 5: 36-39.

Millen, T.W. (1944) **Apis florea. Indian Bee J.** 6: 106-108.

Miller, A.G. (1984) A revision of **Ochradenus. Notes R. bot. Gdn. Edinb.** 41(3): 491-504.

Miller, A.G.; Hedge, I.C.; King, R.A. (1982a) Studies in the Flora of Arabia: I. A botanical bibliography of the Arabian Peninsula. **Notes R. bot. gdn Edinb.** 40(1): 43-61.

Miller, A.G.; Short, M.; Sutton, D.A. (1982b) A revision of **Schweinfurthia. Notes R. bot. Gdn Edinb.** 40(1): 23-40.

Miller, A.G.; Whitcombe, R.P. (1983) Studies in the flora of Arabia: V. A new **Campanula** from Oman. **Notes R. bot. Gdn. Edinb.** 41(1): 109-113.

Mohana Rao, G.; Lazar, M.; Suryanarayana, M.C. (1981) Foraging behaviour of honeybees in sesame (Sesamum indicum L.). **Indian Bee J.** 43(4): 97-100.

Moldenke, A.R. (1976) California pollinator ecology and vegetation types. **Phytologia** 34(4): 304-361.

Monasterio, M.; Sarmiento, G. (1976) Phenological strategies of plant species in the tropical savanna and the semi-deciduous forest of the Venezuelan Llanos. **J. Biogeogr.** 3: 325-356.

Moore, P.D.; Webb, J.A. (1978) An illustrated guide to pollen analysis. Hodder and Stoughton, London.

Morse, D.H. (1977) Foraging of bumblebees: the effect of other individuals. **Jl. N.Y. ent. Soc.** 85(4): 240-248.

Morse, D.H. (1978) Size-related foraging differences of bumblebee workers. **Ecol. Entomol.** 3(3): 189-192.

Morse, R.A. (1970) Annotated bibliography on **Apis florea.** **Biblphy Bee Res. Ass. No. 10: pp** 16.

Morse, R.A. (1977) Swarm orientation in honeybees **pp** 195-201 **from** "African bees: taxonomy, biology and economic use". **ed** D.J.C. Fletcher. Apimondia International Symposium. Apimondia, Pretoria.

Morse, R.A. (ed) (1978) Honey bee pests, predators, and diseases. Cornell University Press, Ithaca (New York) and London.

Morse, R.A. (1983) Cell orientation and comb strength in honeybee colonies. **Glean. Bee Cult.** 111(1): 10,14,16,18-19.

Morse, R.A.; Laigo, F.M. (1969) **Apis dorsata** in the Philippines (including an annotated bibliography). **Monogr. Philipps. Ass. Ent., Inc.** No. 1: **pp** 96.

Mosquin, T. (1971) Competition for pollinators as a stimulus for the evolution of flowering time. **Oikos** 22: 398-402.

Mott, J.J. (1972) Germination studies on some annual species from an arid region of Western Australia. **J. Ecol.** 60: 293-304.

Mott, J.J. (1973) Temporal and spatial distribution of an annual flora in an arid region of Western Australia. **Trop. Grassl.** 7(1): 89-97.

Mott, J.J. (1974) Factors affecting seed germination in three annual species from an arid region of Western Australia. **J. Ecol.** 62: 699-709

Munton, P.N. (198?) The conservation of the Arabian Tahr **Hemitragus jayakari.** IUCN/WWF Joint Op., Project 1290. **J. Oman Stud.** (in press).

Murrell, D.C.; Nash, W.T. (1981) Nectar secretion by Toria (**Brassica campestris** L. v. **Toria**) and foraging behaviour of three **Apis** species on Toria in Bangladesh. **J. apic. Res.** 20(1): 34-38.

Muttoo, R.N. (1956) Facts about bee-keeping in India. **Bee Wld.** 37: 125-133, 154-157.

Nair, P.K.K.; Singh, K.N. (1974) A study of two honey plants, **Antigonon leptopus** Hook and **Moringa pterigosperma** Gaertn. **Indian J. Hort.** 31(4): 375-379.

Narayanan, E.S.; Sharma, P.L.; Phadke, K.G. (1960) Studies on biometry of the Indian bees. II **Indian Bee J.** 22 (10/12): 81-88.

Nash, W.T.; Murrell, D.C. (1981) Beekeeping in Bangladesh. **Am. Bee J.** 121(5): 352-356.

Nelson, E.V.; Jay, S.C. (1968) Flight activity of honeybees in a flight and rearing room. II The influence of constant and cycling temperatures. **J. apic. Res.** 7(2): 71-76.

Neukirch, A. (1982) Dependece of the life span of the honeybee (**Apis mellifica**) upon flight performance and energy consumption. **J. Comp. Physiol., B.** 146(1): 35-40.

Nolan, W.J. (1925) The brood-rearing cycles of the honeybee. **Bull. U.S. Dep. Agric.** No. 1349: 1-55.

Nunez, J. (1977) Nectar flow by melliferous flora and gathering flow by **Apis mellifera ligustica. J. Insect Physiol.** 23: 265-275.

Opler, P.A. (1983) Nectar production in a tropical ecosystem **pp** 30-79 **from** "The Biology of Nectaries" **eds** B. Bentley and T. Elias. Columbia University Press, New York.

Opler, P.A.; Frankie, G.W.; Baker, H.G. (1976) Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. **J. Biogeogr.** 3: 231-236.

Opler, P.A.; Frankie G.W.; Baker, H.G. (1980) Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. **J. Ecol.** 68: 167-188.

Otis, G.W. (1982) Population biology of the Africanized honeybee. **pp** 209-219 **from** "Social insects in the tropics" **ed** P. Jaisson. Université Paris-Nord, Paris.

Otis, G.W.; Taylor, O.R. (1979) Beekeeping in the Guianas. **pp** 145-154 **from** "Beekeeping in rural development: unexploited beekeeping potential in the tropics". Commonwealth Secretariat, London.

Otis, G.W.; Winston, M.L.; Taylor, O.R. (1981) Engorgement and dispersal of Africanized honeybee swarms. **J. apic. Res.** 20(1): 3-12.

Oustuani, A.M. (1976) Das mikroskopische Bild der Honige des ostlichen Mittelmeergebieles. (Microscopic analysis of the honeys of the Eastern Mediterranean region). Dissertation zur Erlangung des Grades eines Doktors der Naturwissenschaften, Universitat Hohenheim (LH), German Federal Republic.

Oxford University Press (1980) The Oxford map of the Sultanate of Oman. GEO Projects, Lebanon, in association with Oxford University Press, U.K.

Panchabhavi, K.S.; Devaiah, M.A. (1977) A note on the activities of insect pollinators on sunflower during winter and summer seasons at Bangalore. **Curr. Res.** 6: 88-89.

Pandey, R.S. (1974) Honey collection in relation to migration schedules of wild honey bees in U.P. (India). **Am. Bee J.** 114(10): 379.

Papadopoulo, P. (1973) Rhodesian cultivated fruit trees, ornamental trees, shrubs, crops and flowers. Salisbury, Rhodesia: Dept. of Conservation and Extension.

Paradine, C.G.; Rivett, B.H.P. (1960) Statistical methods for technologists. 2nd edition. English Universities Press, London.

Parrish, J.A.D.; Bazzas, F.A. (1978) Pollingation niche separation in a winter annual community. **Oecologia (Berl.)** 35(2): 133-140.

Pedgley, D.E. (1970) The climate of interior Oman. **Met. Mag., Lond.** 99(1171): 29-37.

Pemadasa, M.A.; Lovell, P.H. (1974) Factors controlling the flowering time of some dune annuals. **J. Ecol.** 62: 869-880.

Percival, M.S. (1955) The presentation of pollen in certain angiosperms and its collection by **Apis mellifera. New Phytol.** 54(3): 354-368.

Percival, M.S. (1961) Types of nectar in angiosperms. **New Phytol.** 60: 235-281.

Percival, M.S. (1965) Floral Biology. Pergamon Press, Oxford.

Percival, Mary. (1974) Floral ecology of coastal scrub in southeast Jamaica. **Biotropica** 6(2): 104-129.

Phadke, R.P. (1967) Studies on Indian honeys. 1 Proximate composition and physico-chemical characteristics of Indian multifloral apiary honeys from **Apis indica** bees. **Indian Bee J.** 29:14-26.

Pleasants, J.M. (1983) Structure of plant and pollinator communities **pp** 375-393 **from** "Handbook of experimental pollination biology", **eds** C.E. Jones and R.J. Little. Scientific and Academic Editions, New York.

Pleasants, J.M.; Zimmerman, M. (1979) Patchiness in the dispersion of nectar resources: evidence on hot and cold spots. **Oecologia (Berl.)** 41: 283-288.

Pliny the Elder 23-79 A.D. **Naturalis Historia** (Natural History).

from "The Loeb Classical Library" **eds** T.E. Page **et al.** Latin with an English translation by H. Rackham. 1942 edition Vol. II, Heineman, London.

Pourasghar, D. (1979) Investigations on morphological characteristics of Iranian native honeybees. **pp** 95-96 **from** "Apicultura em clima quente: symposio internacional, Florianopolis, SC, Brasil, 19-28/10/78". Apimonida, Bucharest, Romania.

Proctor, M.; Yeo, P. (1973) The Pollination of Flowers. Collins, London.

Pundir, R.S. (1971) Hiving **Apis florea. Indian Bee J.** 33 (3-4): 63.

Punnett, E.N.; Winston, M.L. (1983) Events following queen removal in colonies of european-derived honey bee races (**Apis mellifera**). **Insectes soc.** 30(4): 376-383.

Purseglove, J.W. (1968) Tropical Crops: Dicotyledons. Longman, London.

Purseglove, J.W. (1972) Tropical Crops: Monocotyledons. Longman, London.

Radcliffe-Smith, A. (1978) Lists of plants collected in Oman **pp** 195-196 **from** "Livestock Sector Review and Project Identification, Final Report Vol. 1, for Sultanate of Oman, Ministry of Agriculture and Fisheries". Hunting Technical Services Ltd., England.

Rahman, K.A. (1945) The Indian honeybee (**Apis indica** F.) (Hymenoptera) at Lyallpur. **Proc. R. Ent. Soc. Lond. (A)** 20: 33-42.

Rahman, K.A.; Singh, S. (1940) Beekeeping in India. **Indian Fmg.** 1: 10-17.

Raj, J.; ChannaBasavanna, G.P. (1980) Influence of brood on the attraction and mobility of worker honeybees (**Apis cerana** F.). **Mysore J. agric. Sci.** 14: 224-226.

Ranta, E. (1981) Structure of bumblebee communities in Northern Europe. Thesis (Abstract of 7 publications) presented to the Faculty of Science, University of Helsinki, Finland.

Ranta, E. (1983) Foraging differences in bumblebees. **Ann. Ent. Fenn.** 49: 17-22.

Ranta, E.; Lundberg, H. (1980) Resource partitioning in bumblebees: the significance of differences in proboscis length. **Oikos** 35: 298-302.

Ranta, E.; Lundberg, H. (1981a) Food niche analyses of bumblebees:

a comparison of three data collecting methods. **Oikos** 36: 12-16.

Ranta, E.; Lundberg, H. (1981b) Resource utilization by bumblebee queens, workers and males in a subarctic area. **Holarctic Ecology** 4: 145-154.

Ranta, E.; Teras, I; Lundberg, H. (1981) Phenological spread in flowering of bumblebee-pollinated plants. **Ann. Bot. Fenn.** 18: 229-236.

Ray, C. (1960) The application of Bergmann's and Allen's Rules to the poikilotherms. **J. Morph.** 106: 85-108.

Reddy, C.C. (1980) Observations on the annual cycle of foraging and brood rearing by **Apis cerana indica** colonies. **J. apic. Res.** 19(1): 17-20.

Renner, M. (1960) The contribution of the honeybee to the study of time-sense and astronomical orientation. **Cold Spring Harb. Symp. quant. Biol.** 25: 361-367.

Ricciardelli D'Albore, G. (1980) Preliminary studies on the Moroccan honey flora by microsopical analysis. **Riv. Agric. subtrop. trop.** 74: 57-72.

Ricciardelli D'Albore, G.; Vorwohl, G. (1980) Unifloral honeys of the Mediterranean countries, classified by microscopical analysis. **Riv. Agric. subtrop. trop.** 74: 89-118.

Rinderer, T.E.; Tucker, K.W.; Collins, A.M. (1982) Nest cavity selection by swarms of European and Africanized honeybees. **J. apic. Res.** 21(2): 98-103.

Ritter, W. (1982) Experimental study of thermoregulation by honeybee colonies. **Apidologie** 13(2): 169-195.

Robinson, F.A.; Oertel, E. (1975) Sources of nectar and pollen **pp** 283-302 **from** "The Hive and the Honey Bee" **ed** Dadant and Sons. Dadant and Sons, Hamilton, Illinois, U.S.A.

Robinson, E.G. (1982) A unique beekeeping experience in Colombia. **Bee Wld** 63(1): 43-46.

Roubik, D.W. (1978) Competitive interactions between neotropical pollinators and Africanised honeybees. **Science, N.Y.** 201: 1030-1032.

Roubik, D.W. (1982) Ecological impact of Africanised honeybees on native neotropical pollinators **pp** 233-247 **from** "Social insects in the tropics" **ed** P. Jaisson. Universite Paris-Nord, Paris.

Rust, R.W. (1977) Pollintaor service in sympatric species of jewelweed (**Impatiens**: Balsaminaceae). **Jl. N.Y. ent. Soc.** 85(4): 234-239.

Ruttner, F. (1975) African races of honeybees. **Proc. XXV . int. Beekeep. Congr.**:325-344.

Ruttner, F. (1981) On the taxonomy of honeybees of tropical Africa. **Proc. XXVIII int. Beekeep. Congr.**: 278-283.

Rutter, F.; Woyke, J.; Koeniger, N. (1972) Reproduction in **Apis cerana** 1. Mating behaviour. **J. apic. Res.** 11(3): 141-146.

Sakagami, S.F. (1959) Some interspecific relations between Japanese and European Honeybees. **J. Anim. Ecol.** 28: 51-68.

Sakagami, S.F.; Yoshikawa, K. (1973) Additional observation on the nest of the dwarf honeybee, **Apis florea** (Hymenoptera, Apidae). **Kontyu** 41(2): 217-219.

Sandhu, A.S.; Singh, S (1960) The biology and brood rearing activities of the little honeybee (**Apis florea** Fabricius). **Indian Bee J.** 22 (4/6): 27-34.

Saraf, S.K. (1972) Bee flora of Kashmir. **Indian Bee J.** 34(1/2):1-10.

Sawyer, R. (1981) Pollen identification for bee-keepers. University College Cardiff Press, Cardiff.

Schaffer, W.M.; Jensen, D.B.; Hobbs, P.E.; Gurevitch, J.; Todd, J.R.; Schaffer, M.V. (1979) Competition, foraging energetics, and the cost of sociality in three species of bees. **Ecology** 60(5): 976:987.

Schwabe, W.W. (1971) Physiology of vegetative reproduction and flowering **pp** 233-411 **from** Plant Physiology: A Treatise, VIA **ed** F.C. Steward. Academic Press, New York.

Schwartz, O. (1939) Flora des tropischen Arabien. **Mitt. Inst. Allg. Bot. Hamburg** 10: 1-393.

Seeley, T.D. (1978) Life history strategy of the honeybee, **Apis mellifera. Oecologia** 32: 109-118.

Seeley, T.D. (1982a) How honeybees find a home. **Scient. Am.** 247(4): 144-152.

Seeley, T.D. (1982b) Colony defense strategies of honeybees in Thailand **pp** 285-287 **from** "The Biology of Social Insects", **eds** M.D. Breed, C. D. Michener, H.E. Evans. Westview Press, Boulder, Colorado.

Seeley, T.D. (1983) The ecology of temperate and tropical honeybee societies. **American Scientist** 71(3): 264-272.

Seeley, T.D.; Heinrich, B. (1981) Regulation of temperature in the nests of social insects pp 159-234 **from** "Insect Thermoregulation", **ed** B. Heinrich, John Wiley and Sons, New York.

Seeley, T.D.; Morse, R.A. (1976) The nest of the honeybee (**Apis mellifera** L.). **Insectes soc.** 23(4): 495-512.

Seeley, T.D.; Morse, R.A. (1978) Nest site selection by the honey bee **Apis mellifera. Insectes soc.** 25: 323-337.

Seeley, T.D.; Morse, R.A.; Visscher, P.K. (1979) The natural history of the flight of honeybee swarms. **Psyche** 86: 103-113.

Seeley, T.D.; Seeley, R.H.; Akratanakul, P. (1982) Colony defence strategies of the honeybee in Thailand. **Ecol. monogr.** 52(1):43-63.

Seeley, T.D.; Visscher, P.K. (Unpubl.) Survival of honeybee colonies in cold temperate climates: the critical timing of brood rearing and colony reproduction.

Serjeant, R.B.; Doe, B. (1975) A fortified tower-house in Wadi Jirdan (Wahidi Sultanate) I. **Bulletin of the School of Oriental and African Studies** 38: 1-23.

Severson, D.W.; Parry, J.E. (1981) A chronology of pollen collection by honeybees. **J. apic. Res.** 20(2): 97-103.

Shahid, M.; Qayyum, A. (1977) Bee flora of the N.W.F.P. **Pak. J. For.** 27(1): 1-10.

Shannon, M.O. (1978) Oman and Southeastern Arabia: a bibliographic survey. G.K. Hall, Boston, Mass., U.S.A.

Sharma, M. (1972) Studies in the flower of **Datura stramonium** Linn. in relation to bee botany. **J. Palynol.** 8: 17-21.

Shepherd, A. (1961) Arabian Adventure. Collins, London.

Sidhu, A.S.; Singh, S. (1961) Studies on agents of cross pollination in cotton. **Indian Cott. Gr. Rev.** 15(6): 341-353.

Sidhu, A.S.; Singh, S. (1962) Role of honeybees in cotton production. **Indian Cott. Gr. Rev.** 16(1): 18-23.

Siegel, S. (1956) Nonparametric statistics for the behavioural sciences (International Student Edition). McGraw-Hill Kogakusha, Tokyo.

Simpson, J. (1958) The factors which cause colonies of **Apis mellifera** to swarm. **Insectes soc.** 5(1): 77-95.

Simpson, J. (1959) Variation in the incidence of swarming among colonies of **Apis mellifera** throughout the summer. **Insectes soc.** 6: 85-99.

Simpson, J. (1972) Recent research on swarming behaviour, including sound production. **Bee Wld** 53(2): 73-78, 86.

Sims, D. (1984) Changes in English farming practice and their implications for beekeeping. **Bee Wld** 65(1): 6-12.

Smith, F.G. (1956) Bee Botany in Tanganyika. University of Aberdeen: D.Sc. Thesis.

Smith, F.G. (1957) Bee Botany in East Africa. **E. Afr. agric. J.** 23(2): 119-126.

Smith, F.G. (1958) Communication and foraging range of African bees compared with that of European and Asian bees. **Bee Wld** 39(10): 249-252.

Smith, F.G. (1964) The hive environment in hot climates. **J. apic. Res.** 3(2): 117-122.

Sokall, R.R.; Rohlf, F.J. (1969) Biometry: the principles and practice of statistics in biological research. W.H. Freeman, San Franciso, U.S.A.

Stiles, E.W. (1977) Foraging behaviour of bumblebees on false foxglove. **Jl. N.Y. ent. Soc.** 85(4): 249-252.

Stitz, J.; Szebe, P. (1933) The evolution of the races of bees and their geographical distribution. **Bee Wld** 14(11): 128-130.

Stork, A. L.; Wüest, J. (1980) **Morettia** DC (Cruciferae): a morphological and taxonomical study. **Bolm. Soc. broteriana**, ser.2,53: 241-273.

Strabo. (?7 A.D. Poss 18/19 A.D.) The Geography of Strabo. Book 16 (iv): 2 **from** "Loeb Classical Library" **eds** Page, T.E.; Capps, E. and Rouse W.H.D. Greek with an English translation by Jones, H.L. 1930 edition Vol. VII: 308-311. Heinemann, London.

Swaminathan, R.; Bhardwaj, S.C. (1982) Bee pollinators of sunflower and their foraging behaviour. **Indian Bee J.** 44(2): 32-34.

Szabo, T.I. (1980) Effects of weather factors on honeybee flight activity and colony weight gain. **J. apic. Res.** 19(3): 164-171.

Täckholm, V. (1974) Students' Flora of Egypt. 2nd edition. Cairo University, Egypt.

Taniguchi, S. (1954) Biological studies on the Japanese Bees: 1.

Comparative study of glossa. **Scient. Rep. Hyogo Univ. Agric.** 1(2) Ser. Agric.: 81-89.

Taylor, L.R. (1963) Analysis of the effect of temperature on insects in flight. **J. Anim. Ecol.** 32: 99-117.

Taylor, O.R. (1977) The past and possible future spread of Africanized honeybees in the Americas. **Bee Wld** 58(1): 19-30.

Taylor, O.R.; Spivak, M. (1984) Climatic limits of tropical African honeybees in the Americas. **Bee Wld** 65(1): 38-47.

Tepedino, V.J.; Parker, F.D. (1982) Interspecific differences in the relative importance of pollen and nectar to bee species foraging on sunflowers. **Environ. Entomol.** 11(1): 246-250.

Tevis, L. (1958a) Germination and growth of ephemerals induced by sprinkling a sandy desert. **Ecology** 39: 681-688.

Tevis, L. (1958b) A population of desert ephemerals germinated by less than one inch of rain. **Ecology** 39: 688-695.

Thakar, C.V.; Diwan, V.V.; Salvi, S.R. (1962) Floral calendar of major and minor bee forage plants in Mahabaleshwar Hills (Western Ghats). **Indian Bee J.** 24 (4/6): 35-48.

Thakar, C.V.; Tonapi K.V. (1962) Nesting behaviour of Indian honeybees. II Nesting habits and comb cell differentiation in **Apis florea** Fab. **Indian Bee J.** 24 (No. 1-3): 27-31.

Thomas, J.K. (1983) The pollen loads of honeybees foraging in rural and urban environments (**Apis mellifera** L.). M.Sc. Thesis, University College, Cardiff, U.K.

Tirgari, S.; Polous, H.; Fouroughi, H.; Fakhrai, F.; Nabavi, M.A. (1969) [On the occurrence and biology of little bee (**Micrapis florea** F.) and the first account on their migration (Hymenoptera, Apidae)]. **II. Natn. Congr. Ent. Pest Control Iran:** 4pp Evine, Teheran. (In Persian).

Tirgari, S. (1971) On the biology and manipulation of **Apis (Micrapis) florea** F. in Iran. **Proc. XXIII Int. Beekeep. Congr.**: 330-332.

Tosi, M. (1975) Notes on the distribution and exploitation of natural resources in ancient Oman. **J. Oman Stud.** 1: 187-206.

Venkata Rau, P.N. (1946) My final report of the observations made on the **Apis dorsata** hive built in the Ramkrischna mission students' home in Mylapore, Madras. **Indian Bee J.** 8(?11/12): 160-163.

Verhagen, R. (1971) Observations apicole en Afghanistan (Beekeeping observations in Afghanistan). **Abeilles et Fleurs** 208: 4-5.

Verma, L.R. (1970) A comparative study of temperature regulation in **Apis mellifera** L. and **Apis indica** F. **Am. Bee J.** 110(10): 390-391.

Verma, L.R.; Edwards, D.K. (1971) Metabolic acclimatization to temperature, and temperature tolerance in **Apis mellifera** and **Apis cerana indica** kept in India. **J. apic. Res.** 10(3): 105-108.

Visscher, P.K.; Seeley, T.D. (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. **Ecology** 63(6): 1790-1801.

Viswanathan, H. (1950) Temperature reading on **Apis dorsata** combs. **Indian Bee J.** 12: 72.

Vorwohl, G. (1981) Pollen spectra of African honeys. In **Proceedings of the IVth International Palynological Conference, Lucknow, India, 1976-77**: 499-502.

Waddington, K.D.; Allen, T.; Heinrich, B. (1981) Floral preferences of bumblebees (**Bombus edwardsii**) in relation to intermittent versus continuous rewards. **Anim. Behav.** 29(3): 779-784.

Wareing, P.F.; Philips, I.D.J. (1970) The control of growth and differentiation in plants. Pergamon, Oxford, U.K.

Wagenitz, G. (1984) Studies in the flora of Arabia VII : **Centaurea** in the Arabian peninsula. **Notes R. bot. Gdn. Edinb.** 41(3): 457-466.

Watt, Sir G. (1966) The commercial products of India being an abridgement of "The dictionary of the economic products of India", **pp** 123-129. Today and Tomorrow's Printers and Publishers, New Delhi. (Reprint, First Edition 1885).

Wells, H.; Wells, P.H.; Smith, D.M. (1981) Honeybee responses to reward size and colour in an artificial flower patch. **J. apic. Res.** 20(3): 172-179.

West-Eberhard, M.J. (1982) The nature and evolution of swarming in tropical social wasps **pp** 97-128 **from** "Social insects in the tropics" **ed** P. Jaisson. Université Paris-Nord, Paris.

Whitcombe, R.P. (1980) Honeybees in the Sultanate of Oman. Illustrated booklet for Conference of Gulf Agriculture Ministers. (In Arabic). Ministry of Agriculture and Fisheries, Muscat, Sultanate of Oman.

Whitcombe, R.P. (1981) Notes on the Arabian plant collections of Joseph Fernandez. **Durham University Khabura Development**

Project, Preliminary Reports 2B(2): 6 + (ii) pp.

Whitcombe, R.P. (1982a) Experiments with a hive for Little Bees: some observations on manipulating colonies of **Apis florea** in Oman (Part I). **Indian Bee J.** 44(3): 57-63.

Whitcombe, R.P. (1982b) Experiments with a hive for Little Bees: some observations on manipulating colonies of **Apis florea** in Oman (Part II). **Indian Bee J.** (in press).

Whitcombe, R.P. (1982c) Ants (Formicidae), especially those associated with honeybees (**Apis** spp.), from the Sultanate of Oman: list of collections and records made by R.P. Whitcombe, Dec. 1977 to Aug. 1980; identifications by B. Bolton. **Durham University Khabura Development Project, Preliminary Reports** 2C(3): iii + 25pp.

Whitcombe, R.P. (1982d) Meteorological conditions in the Batina region of Oman. **Durham University Khabura Development Project, Preliminary Reports** 4(1): 24pp.

Whitcombe, R.P. (1984) The bedouin bee. **Aramco World Magazine** 35 (2): 34-41.

Wickens, G.E. (1982) Studies in the Flora of Arabia: III. A biographical index of plant collectors in the Arabian peninsula (including Socotra). **Notes R. bot. Gdn Edinb.** 40(2): 301-330.

Wilkinson, J.C. (1977) Water and tribal settlement in South-East Arabia: a study of the aflaj of Oman. Clarendon, Oxford.

Wilkinson, J.C. (1980) The origins of the aflaj of Oman. **J. Oman Stud.** 6(1): 177-194.

Williams, I.H. (1977) Behaviour of insects foraging on pigeon pea (**Cajanus cajan** (L.) Millsp.) in India. **Trop. Agric., Trin.** 54(4): 353-363.

Williams, I.H. (1979) Bee-keeping in the Sultanate of Oman. **Am. Bee J.** 510-511, 532-533, 535.

Williams, J.B.; Batzli, G.O. (1982) Pollination and dispersion of five species of lousewort (**Pedicularis**) near Atkasook, Alaska, U.S.A. **Arctic Alpine Res.** 14(1): 59-74.

Wilson, E.O. (1971) The Insect Societies. Harvard Univ. Press, U.S.A.

Winston, M.L. (1977) The establishment and spread of the Africanized honeybee in the Western Hemisphere. **J. agric. Soc. Trin.** 77: 306-313.

Winston, M.L. (1979a) Intra-colony demography and reproductive rate of the Africanized honeybee in South America. **Behav. Ecol. Sociobiol.** 4: 279-292.

Winston, M.L. (1979b) Events following queen removal in colonies of Africanized honeybees in South America. **Insectes soc.** 26: 373-381.

Winston, M.L. (1980a) Seasonal patterns of brood rearing and worker longevity in colonies of the Africanized honeybee (Hymenoptera: Apidae) in South America. **J. Kans. ent. Soc.** 53: 157-165.

Winston, M.L. (1980b) Swarming, afterswarming and reproductive rate of unmanaged honeybee colonies (**Apis mellifera**). **Insectes soc.** 27(4): 391-398.

Winston, M.L.; Dropkin, J.A.; Taylor, O.R. (1981) Demography and life history characteristics of two honeybee races (**Apis mellifera**). **Oecologia** 48: 407-413.

Winston, M.L.; Otis, G.W.; Taylor O.R. (1979) Absconding behvaiour of the Africanized honeybee in South America. **J. apic. Res.** 18 (2): 85-94.

Winston, M.L.; Taylor, O.R. (1980) Factors preceding queen rearing in the Africanized honeybee (**Apis mellifera**) in South America. **Insectes soc.** 27(4): 289-304.

Winston, M.L.; Taylor, O.R.; Otis, G.W. (1980) Swarming, colony growth patterns, and bee management. **Am. Bee J.** 120: 826-830.

Winston, M.L.; Taylor, O.R.; Otis, G.W. (1983) Some differences between Temperate European and Tropical African and South American honeybees. **Bee Wld** 64(1): 12-21.

Witherell, P.C. (1972) Flight activity and natural mortality of normal and mutant drone honeybees. **J. apic. Res.** 11(2): 65-75.

Woyke, J. (1976) Brood-rearing efficiency and absconding in Indian Honeybees. **J. apic. Res.** 15 (3/4): 133-143.

Woyke, J. (1977) Brood rearing and absconding of tropical honeybees. **pp** 96-102 **from** "African bees: taxonomy, biology and economic use" **ed** D.J.C. Fletcher. Apimondia, Pretoria, South Africa.

Wykes, G.R. (1952) An investigation of the sugars present in the nectar of flowers of various species. **New Phytol.** 51: 210-215.

Wykes, G.R. (1953a) The influence of variations in the supply of carbohydrate on the process of nectar secretion. **New**

Phytol. 51: 294-300.

Wykes, G.R. (1953b) The sugar content of nectars. **Biochem. J.** 53: 294-296.

Zimmerman, M. (1981a) Optimal foraging, plant density and the marginal value theorem. **Oecologia (Berl.)** 49: 148-53.

Zimmerman, M. (1981b) Patchiness in the dispersion of nectar resources: probable causes. **Oecologia (Berl.)** 49: 154-157.

*Not consulted in the original.