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ASPECTS OF THE ECOLOGY OF *COLEOPHORA ALTICOLELLA* ZELLER (LEPIDOPTERA) WITH PARTICULAR REFERENCE TO ALTITUDE

MARTIN G.M. RANDALL B.Sc. (Dunelm)

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..... being a thesis presented in candidature for the degree of Doctor of Philosophy in the University of Durham,

1980

"Yesterday afternoon set in misty and cold. I had half a mind to spend it by my study fire, instead of wading through heath and mud ....."

Emily Brontë 1847.

ABSTRACT

Aspects of the ecology of the moth *Coleophora alticolella* have been investigated at a low-altitude site on the Cumbrian coast (15m above sea-level) and along a transect from 215m to 610m on the western escarpment of the northern Pennines. The larvae of this moth feed on the seeds of the rush *Juncus squarrosus*. Seed production by the food-plant is reduced at higher altitudes, where the climate is severe. The oviposition period is delayed with increasing altitude and the eggs are laid singly, if there are sufficient oviposition sites on the developing inflorescences. Survival of the larvae, between hatching and establishment inside the food supply, is directly related to the proportion of *J. squarrosus* florets developing into seed capsules. Consequently, as a result of the progressive reduction in seed capsule production with increasing altitude, there is greater mortality during larval establishment at the higher sites. Larval case production and subsequent migration to overwinter in the leaf-litter are both retarded with increasing altitude, provided that the food supply is adequate. Both the number of species of parasitic Hymenoptera, attacking the larvae, and the percentage parasitization are reduced with increasing altitude. Hyperparasitoids were present at the lowest site. Starvation of the larvae, as a result of the reduced *J. squarrosus* seed production, was the most important mortality factor in the population dynamics of *Coleophora alticolella* at the highest altitudes. Parasitoids controlled the population at the lowest altitude. Between these two extremes, competition for food by the fourth instar larvae is most important. This acts as a density-dependent factor, reducing natality in the following spring. The larvae often eat all of the seeds produced by the food-plant in this middle region, but not at sites of higher or lower altitude.

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CHAPTER 1

INTRODUCTION

Animal populations fluctuate around a mean level of abundance. However, this mean level is not the same in all parts of the animal's range; it is generally lower towards the edge of the distribution (Klomp 1962). Despite this, insects, and other animals, are usually studied where they are most abundant and conditions are favourable (Wilson 1968). Huffaker (1958), among others, has stressed that insects should be considered in both salubrious and hazardous environments. Few studies have actually achieved this, a notable exception being that of Whittaker (1971).

This thesis describes the results of an investigation into the ecology of the moor rush moth *Coleophora alticolella* Zeller, over a large altitudinal range in northern England; from 15m to 610m above sea-level. Previous ecological studies of this species have mainly concentrated on the upper part of this range (Pearsall 1950; Jordan 1958, 1962; Reay 1964; Welch 1965). Coulson and Whittaker (1978) have suggested that a study of this species in the lower part of its altitudinal range may reveal regulation of the population density. This does not occur in the harsher conditions at higher altitudes; here, large fluctuations in numbers and frequent local extinctions are characteristic (Cragg 1961).

Insects are not affected by altitude *per se*, but by the whole gamut of associated climatological changes. These are primarily temperature, rainfall and windspeed, which act synergistically to produce more severe conditions at the higher altitudes (Manley 1952; Taylor 1976; Francis 1978). In addition, the use of an altitudinal gradient, to study

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the effects of different climatic regimes on insect populations eliminates the differential effects of photoperiod, which might otherwise complicate the problem if latitude were used.

Coleophora alticolella is one of the rush-feeding Coleophoridae and its larvae feed on the seeds of many species of Juncaceae (Richards and Clapham 1941; Jordan 1958). The heath rush, *Juncus squarrosus* L., is the most commonly utilized food-plant in the area used for this investigation, but the larvae have also been observed feeding on the seeds of *J. effusus* L. and *J. conglomeratus* L. Older larvae have been recorded feeding on the seeds of *Luzula* spp. (Jordan *loc. cit.*). However, it is the relationships between *Coleophora alticolella*, *Juncus squarrosus* and altitude which have been studied during the research reported here.

The climatic differences associated with altitudinal changes are expected to affect insects both directly, for example on their development rates, and indirectly, through their food supply. For this latter reason the responses of the larval food-plant to the climatic gradient have been investigated. These studies show that seed production is reduced under the strictures of the harsher climate at higher altitudes.

The distribution and abundance of the *Coleophora alticolella* eggs and larvae have been investigated in relation to the available food, and the changes along the transect are enumerated. Results of studies into the development of *C. alticolella* at different stages of the life-cycle show its response to the cooler conditions at higher altitudes.

Just as *C. alticolella* is affected by the climatic changes along its altitudinal distribution, so are the parasitic insects which attack its larvae. Some of the factors affecting these natural enemies in the different parts of the host range have been investigated, in order to explain the reduced rate of parasitization at higher altitudes.

The data collected on these various aspects of *C. alticolella* ecology have been incorporated into life-tables. These enable the author to show that the factors affecting the population dynamics of the insect vary in different parts of its range. The effect of *C. alticolella* on the survival of the *Juncus squarrosus* seeds has also been considered.

Finally, the results are discussed in relation to theories on the biological control of insect pests and weeds, and to current population models.

It is convenient, at this point, to give a brief introduction to *Coleophora alticolella*, with an outline of its life-cycle. *C. alticolella* is a small moth, with a wing-span of a little over ten millimetres. The identity of the adult moths was confirmed by comparing the genitalia with those of Zeller's type-specimens, prepared by Bradley (1955) and held in the British Museum (Natural History). The life-history of *C. alticolella* has been described in detail by Jordan (1958) and is as follows. The adults emerge at the end of May or in June, to coincide with the flowering of the food-plant. They are weak flyers and spend much of the adult life on the vegetation. The eggs are laid on the developing *Juncus squarrosus* inflorescences during June and early July. After hatching, the larva burrows through the pericarp of the developing seed capsule to feed on the seeds. The larva remains entirely within the seed capsule until August or September when, at the end of the third or beginning of the fourth instar, it spins a papery protective case. The larva then has an errant phase, moving about the inflorescence in search of further seed capsules. It is at this stage that *Coleophora alticolella* is most conspicuous, as the larval cases protrude from the seed capsules

like grains of rice (Plate I). In the late summer and autumn, the larvae leave the food-plant and move down into the leaf-litter where they spend the winter in diapause, as fourth instars. Pupation occurs during the following spring, also in the leaf-litter.

PLATE I

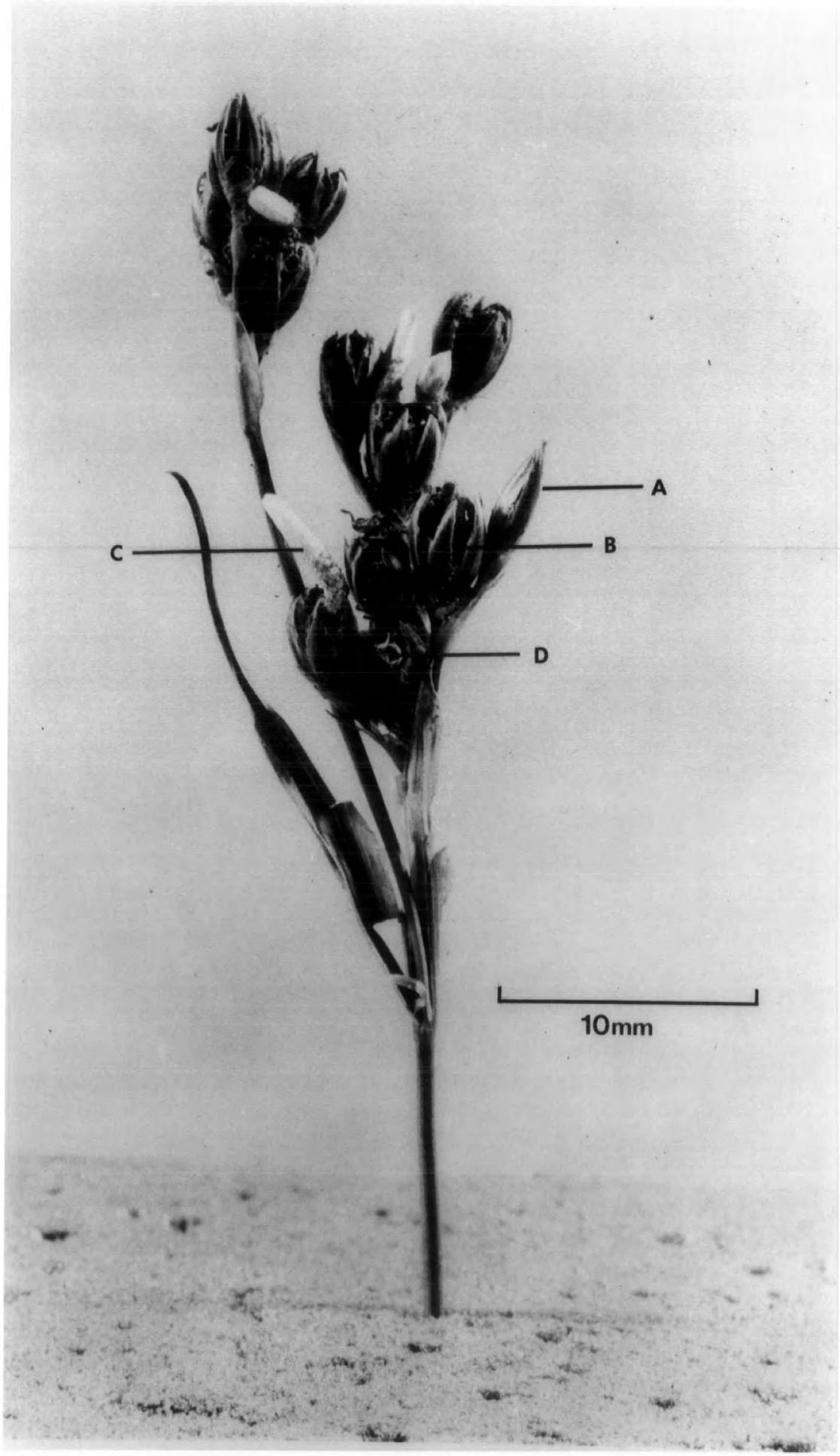
The head of a *Juncus squarrosus* inflorescence collected at Drigg in September 1978:

A A floret

B A floret which has produced a swollen seed capsule

C The case of a fourth instar *Coleophora alticolella* larva

D The characteristic hole in the pericarp of a seed capsule which has had its seeds eaten by *Coleophora alticolella*


A
B
C
D
10mm

CHAPTER 2

SAMPLE SITES AND GENERAL METHODS

2.1 Location of the sample areas

Two areas in northern England were used during this study; their locations are shown in Figure 2.1. The main area (A) was a transect of sample sites from 215 metres to 830 metres on the western escarpment of Little Dun Fell (Nat. Grid ref. NY 705330) in the northern Pennines. Much of this transect was within the boundary of the Moor House National Nature Reserve (N.R. 80); the sites below 335 metres were on adjacent farmland. Area B was a low altitude sample site, 15 metres above sea level, at Drigg on the Cumbrian coast (Nat. Grid ref. SD 049987).

2.2 Sample site descriptions

Extensive areas of *Juncus squarrosus*-dominated sward were chosen as the main sample sites. They were on near-level ground and, where possible, not in sheltered positions. However, it was not always possible to fulfil these criteria without restricting the number of sites available. The altitude of each sample site was measured, to the nearest 5m, using an aneroid barometer calibrated from Ordnance Survey data.

2.2a The Little Dun Fell transect

This was the same area as used by Jordan (1962) for his western transect; although the exact locations of his sample sites were not known, many of the sites used in this study are considered to be comparable. Figure 2.2 shows the extent of the transect with the main sample sites marked.

Figure 2.1: A map of northern England showing the location of the two sample areas

A Little Dun Fell

B Drigg

The thick contour is 244m, and the thin contour shows land over 488m.

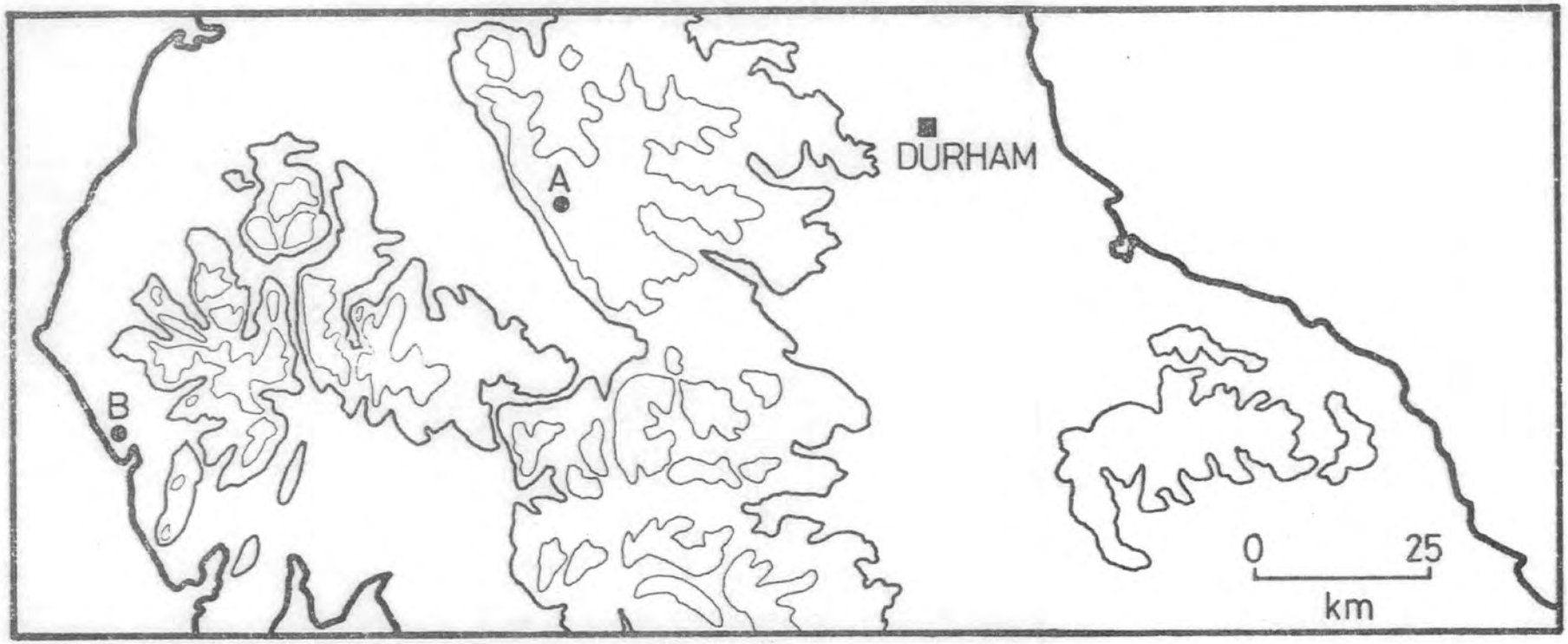
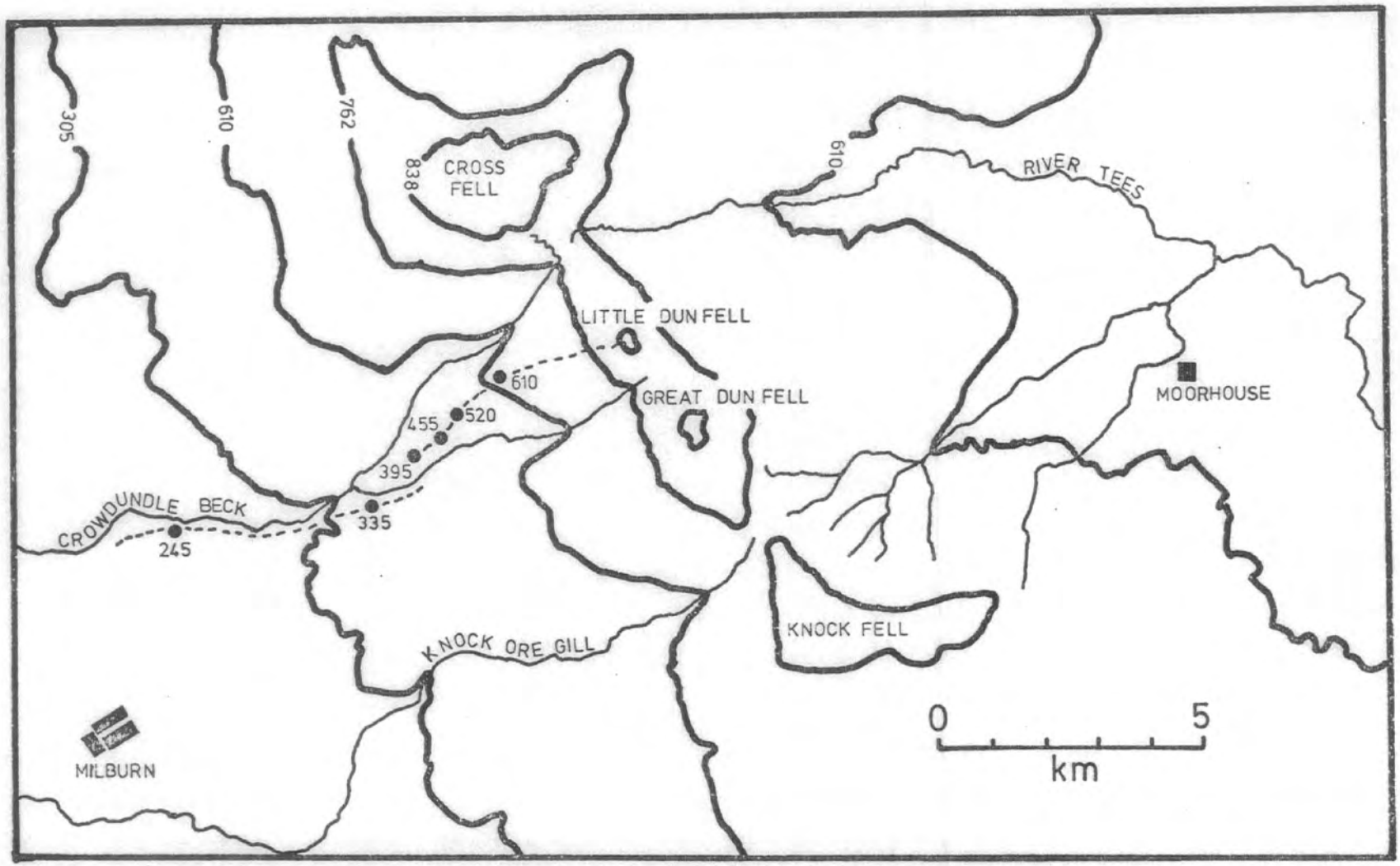

DURHAM
A
B
0
25
km

Figure 2.2: A map of the Cross Fell area of the Pennines, with the Little Dun Fell transect marked by the broken line. The six main sample sites are shown (○) with their respective altitudes.


305
610
762
838
CROSS FELL
610
RIVER TEES
LITTLE DUN FELL
610
GREAT DUN FELL
MOORHOUSE
455
520
395
CROWDUNDLE BECK
335
245
KNOCK FELL
KNOCK ORE GILL
MILBURN
0
5
km

Little Dun Fell (842m) lies between Great Dun Fell (847m) and Cross Fell (893m), the highest point in the Pennines. The two main streams in this study area are Crowdundle Beck and its tributary, Middle Tongue Beck, which flow into the River Eden. The area of land between these two becks is called Middle Tongue; it contained four of the six main sample sites.

The geology of the Moor House Reserve has been described by Johnson and Dunham (1963). On the western escarpment most of the underlying rock is sandstone and limestone of the Carboniferous Yoredale series. In places the limestone outcrops to form steep slopes. The soils at the sample sites are mainly shallow peaty gleys or peaty gleyed podzols. The vegetation of that part of the study area within the Reserve has been described by Eddy, Welch and Rawes (1969), and the phytosociology of similar communities containing *Juncus squarrosus* has been discussed by Welch (1967a). The communities at this series of sample sites correspond to the peaty gley or peaty podzol noda. The lower slopes are drier and here *Nardus stricta* L. is present, whereas at the higher, wetter sites this is replaced by *Eriophorum* spp.

The climate at the Moor House Reserve has been likened to that at sea level in southern Iceland, being oceanic and sub-arctic rather than temperate (Manley 1936). These climatological studies were mainly based on data from the weather stations at Moor House field station, on the east of the Pennine ridge, and at the summit of Great Dun Fell. The conditions on the western escarpment may well be different because of its exposure to the prevailing winds; however at the lower altitudes the climate is a great deal milder. The lapse rate for air temperature in this part of Britain is about $0.7^{o}C$ per 100 metre increase in altitude (Manley 1943). Thus the difference in mean temperature between the

lowest site (15 metres) and the highest of the main sample sites (610 metres) will amount to some 4.2°C.

Six main sample sites on the Little Dun Fell transect were used for intensive studies; other altitudes were used for collecting samples at critical times during the life-cycle of *Coleophora alticolella*. The main sample sites were at 245m, 335m, 395m, 455m, 520m and 610m.

The 245m sample site was on agricultural land and had been drained by a series of deep parallel ditches. It was in an area accessible to cattle and sheep which grazed the *Juncus squarrosus* and damaged the inflorescences by trampling. The 335m site was at the lowest part of the reserve. From here *J. squarrosus* stretches almost continuously for much of the rest of this part of the fell (see the vegetation map in Eddy, Welch and Rawes 1969). The sites at 395m and 455m were similar to this, with *Nardus stricta* present in species-rich *Juncetum squarrosi sub-alpinum* communities (*sensu* Welch 1967a).

Above 500m there was more *Eriophorum* spp.present in the communities. At 520m there were areas of free-standing water, and much of the site was in a slight hollow caused by the erosion of the underlaying limestone. The highest of the main sample sites was at 610m, and was similar to the 520m site with hummocks and swallow holes. Samples of inflorescences were taken from the more exposed parts of this site to avoid the effects of shelter.

The supplementary sample sites on this transect can be divided into the following four groups:

1. The sites outside the reserve boundary. These were at 215m, 260m, 275m, 290m and 305m. All except the 305m site had been drained to some extent. The 215m site compares with Jordan's

(1962) lowest site of 198m (650 feet). Here, the *Juncus squarrosus* plants were in widely spaced clumps, often separated by several metres. Very few inflorescences were collected from this site because it could not support a full sample programme.

ii. The 350m and 365m sample sites lay on the same side of Middle Tongue Beck as the 335m sample site, but slightly higher up the slope.

iii. Two sample sites lay between 520m and 610m; they were at 550m and 580m.

iv. The final group of sites was those above 610 metres. They were sampled infrequently because they were above the upper limit of distribution of the *Coleophora alticolella* larvae. These sites were at 685m, 760m and 830m. The 830m sample site was just below the summit of Little Dun Fell and had a westerly aspect.

2.2b The Drigg sample site

This low altitude sample site was at 15 metres above sea level. It was easily accessible from the Drigg shore road and was near to the Ravenglass Gullery Local Nature Reserve, an area described by Ranwell and Ratcliffe (1977). It was not exactly the same as the sites on the Little Dun Fell transect, but was suitable for studying *Coleophora alticolella* in much less rigorous climatic conditions.

The site had a dune heath vegetation with *Erica cinerea* L. and *E. tetralix* L. in large patches. Although on sandy soil, it did have some parts that were badly drained, and here there were areas of *Juncus squarrosus*. The line of dunes sheltered this site from the prevailing westerly winds from the sea.

2.3 General methods

2.3a Fieldwork

The field seasons lasted from late May until early November each year. Samples of *Juncus squarrosus* inflorescences were taken every week in the early part of the season, but less frequently in the later part of each year. Samples were only taken on one occasion at each site in 1979.

The density of the inflorescences was measured with a 50cm x 50cm quadrat frame.

The presence of *Coleophora alticolella* larval cases in late summer makes some of the inflorescences very conspicuous, and there can be a tendency to select them in preference to those without cases. In order to avoid this bias, and to ensure that there was no overt selection of unrepresentative inflorescences at other times during the year, the inflorescence that lay nearest to a marked corner of the quadrat square was taken on each throw. As a result, samples were taken from the sub-areas used during the measurement of the inflorescence density. The inflorescences from each site were sealed into polythene bags and preserved in a deep-freeze at -20^{o}C for later examination.

For certain experiments it was necessary to follow events on the same set of inflorescences. To facilitate this, permanent quadrats were staked out at the sample sites. These quadrats could be relocated on each visit to the area.

It was possible to test if the samples of *Juncus squarrosus* inflorescences collected were representative of the sample site as a whole, by using the larval cases as markers. The mean number of cases per inflorescence in the samples was compared with the mean number per inflorescence in the quadrats. Table 2.1 gives the results from the

335m and 395m sample sites, and shows that there was no significant difference between the two measurements at either sample site. Thus the samples were representative of the population, or at least of the areas within the quadrats.

Table 2.1 : *The mean number of* Coleophora alticolella *larval cases per inflorescence of* Juncus squarrosus *on 3 September 1977 at 335m, and 2 September 1977 at 395m. The values are calculated from the samples and from the quadrats. The t-tests show that there is no significant difference between the two methods.*

	335 metres		395 metres	
	Sample	Quadrat	Sample	Quadrat
Larval cases	28	299	14	176
Inflorescences	30	304	30	346
Cases per inflorescence	0.93	0.98	0.47	0.51
Standard error	0.20	0.06	0.12	0.05
t	0.239		0.308	
	Not Significant		Not Significant	

Adult insects, both *Coleophora alticolella* and parasitic Hymenoptera, were collected by sweep netting. This was not possible during wet weather, which was frequent at the higher altitudes.

2.3b Laboratory work

Much of the processing of the *Juncus squarrosus* samples in the laboratory was done under the low power magnification of a dissecting microscope. The number of florets, seed capsules and damaged seed capsules was recorded (examples of these are shown in Plate I); seeds were also counted. The *Coleophora alticolella* larvae were dissected from the seed capsules of the samples that had been frozen, and examined for evidence of parasitism. Some of the larvae were identified as 'dead prior to collection' because they were either dry and shrivelled or flaccid and discoloured. The cause of death is not known. The remaining 'live' larvae were assigned to instars by measuring the width of their head capsules. The number of *C. alticolella* eggs present on each inflorescence was also recorded.

Some of the samples were not frozen; these were collected for rearing the parasitic Hymenoptera which attack the larvae. The parasitized larvae were removed from these samples and placed into gelatin capsules; these were then retained in the laboratory until the adult parasites emerged.

2.3c Data analyses

The statistical analyses used in this thesis have been based on methods given by Bailey (1959) or Snedecor and Cochran (1967). A list of the symbols and abbreviations used is given in Appendix 1.

Two prepared computer packages were also used. They were 'Statistical Package for the Social Sciences' (Nie *et al.* 1975), and 'Biomedical Data Programmes' (Dixon 1975), developed at the Health Services Computing Facility, University of California, Los Angeles.

The latter was used for least squares curvilinear regression analysis, to fit logistic equations to sigmoid relationships.

2.4 The logistic equation

The logistic equation is a convenient way of describing a sigmoid relationship. It was developed by Verhulst (1838) and Pearl and Reed (1920) for describing the cumulative growth of populations.

The rate of increase of a population N growing with unlimited resources could be exponential, with

$$\frac{dN}{dt} = bN \qquad (2.1)$$

where t is time and b a constant defining the rate of increase. When a population is growing with limited resources, food or space for example, each additional individual reduces the rate of increase by a constant amount until a stable upper limit (K) is reached. The value of K can be regarded as the carrying capacity. In this case

$$\frac{dN}{dt} = bN\left(\frac{K-N}{N}\right) \qquad (2.2)$$

The integrated form of equation 2.2 may be written as

$$N = \frac{K}{1 + e^{(a-bt)}} \qquad (2.3)$$

a and b are constants and e is the base of natural logarithms. This defines a logistic curve which is measured from a lower asymptote at zero.

It is not necessary to apply these biological assumptions in conjunction with this equation when it is being used purely for data description, as in this thesis. Davidson (1942, 1944) used the logistic

curve as an empirical representation of temperature-dependent development rates for insects.

Bliss (1970) has pointed out that the logistic curve resembles the cumulative normal distribution over most of its range, and can therefore be used to estimate the mean and standard deviation of a normal distribution.

The curve has a point of inflexion at the coordinates

$$t = {}^{a}/_{b} \ , \quad N = {}^{K}/_{2} \ .$$

This, in fact, measures the median, but in a normal distribution is equal to the mean. This value is often called the L.D. 50 in other fields of research, such as pharmacology, where it may be used to represent the lethal dose of a drug which results in 50% mortality of a group of animals. Andrewartha and Birch (1954) use this measurement in discussing the effects of temperatures on the mortality of insects.

The standard deviation can be calculated knowing that 68.3% of a normally distributed population lies within one standard deviation on either side of the mean (Snedecor and Cochran 1967).

CHAPTER 3

STUDIES ON *JUNCUS SQUARROSUS*, THE LARVAL FOOD-PLANT

3.1 Introduction

The ecology of *Juncus squarrosus* has been discussed in detail by Welch (1966a, 1966b, 1967a, 1967b). Much of his work was carried out on the Moor House National Nature Reserve, on sites of a similar phytosociological nature to those used in this research. In addition to the work by Welch, there had been earlier studies by Pearsall (1950), which highlighted the relationship between *Coleophora alticolella* and this species of rush.

Juncus squarrosus is a widespread plant in the British Isles, occurring from sea-level to over 1000 metres, although it is commoner in the north and west (Welch 1966a). It is restricted to uncultivated land, being confined to moist or wet habitats and usually on acidic soils or peat. It can tolerate waterlogged soil but is absent or dwarfed in dry soil conditions. Studies on this species of rush have been restricted to areas of high altitude, where it is abundant and often a dominant member of the floral community. In the region studied in this research it was absent from agricultural land below 200 metres, occurring again at a much lower altitude, near sea-level, on the Cumbrian coast.

Juncus squarrosus is a perennial plant, which reproduces by seed production as well as by vegetative growth from an underground rhizome. Because of the vegetative spread, it is difficult to count the numbers of plants in areas of *J. squarrosus*-dominated sward. A similar problem occurs in many plant communities of this type (Grieg-Smith 1957). In high-level *J. squarrosus* communities in Wales, Kershaw and Tallis (1958)

have demonstrated that even if the vegetation is visually uniform over considerable areas, within these areas the community consists of a mosaic of patches. Between these patches the vigour of the *J. squarrosus* depends upon such factors as soil-depth and water-retaining capabilities.

The plant consists of a group of leafy rosettes which produce inflorescences in late May at low altitudes and early June in the higher parts of their range. Each inflorescence bears florets which, if fertilized, may produce seeds in a swollen capsule; each floret producing one seed capsule (Plate I).

Several studies give information about the seed production of *J. squarrosus* (Jordan 1962; Reay 1964; Welch 1966b). However, none of these studies has considered seed production by this plant at low altitudes. Welch (1966b) only considered seed production between 351 metres and 829 metres. Jordan (1962), in his studies, used sample sites between 198 metres and 838 metres on the western escarpment of Little Dun Fell, and between 465 metres and 608 metres on the eastern side of the Pennines. Reay (1964) also gives data for *J. squarrosus* seed production between the same limits on these eastern slopes.

As the ecology of *J. squarrosus* has been so extensively studied by previous workers, only those aspects which could have a direct bearing on *Coleophora alticolella* were considered for this research. These aspects are mainly concerned with seed production, and how this is affected by the prevailing environmental conditions at different altitudes. Seed production was measured, on an area basis, using four parameters: the density of inflorescences, the number of florets per inflorescence, the proportion of these florets that develop into seed-bearing capsules and the number of seeds per capsule. In addition, information on the flowering phenology and effect of grazing animals was also collected.

3.2 The density of *Juncus squarrosus* inflorescences

The density of the *Juncus squarrosus* inflorescences was measured by using a 50cm x 50cm quadrat frame on the areas from where samples of inflorescences were taken for more detailed analysis. Most of the sample sites were on common grazing land and in some areas the inflorescences are grazed by sheep; they nip off the tops of the seed heads, leaving the stalks as evidence.

Counts of the inflorescences were taken on several occasions during 1977 and 1978, but only the inflorescences which had not had their seed capsules removed were recorded. Sampling was only done on one occasion in 1979 (28 August at Drigg and 29 August on Little Dun Fell), when two measurements of density were made. Firstly, the number of inflorescences which still had their florets and seed capsules was recorded, and then the grazed stems were counted. The sum of these two values gave the number produced in each quadrat.

Data on the changes in the density of inflorescences at some sites, throughout 1977, were obtained by counting the inflorescences in sixteen permanently marked $^{1}/_{4}m^{2}$ quadrats. Mean values for the densities of inflorescences over the whole period of this study are given in Appendix 2.

3.2a Changes in the density of inflorescences during the year

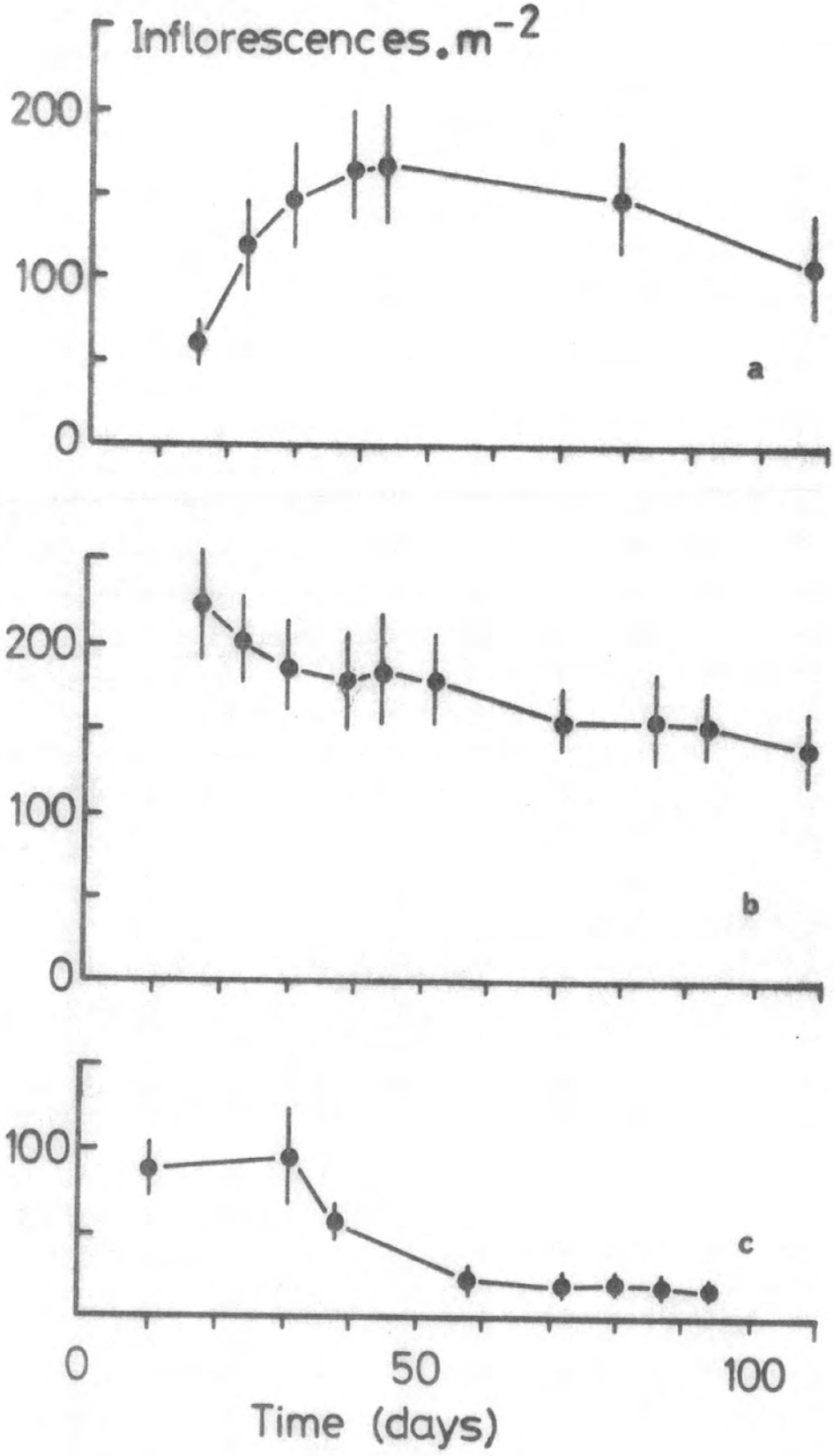
Figure 3.1 shows the density of *Juncus squarrosus* inflorescences in the permanent quadrats at three altitudes during 1977. At the highest site (610 metres) there was a significant ($P < 0.001$) increase in the density of inflorescences after the first sample date, 16 June. After mid-July there was a gradual decline in density to the final sample date, 16 September.

Figure 3.1: The density of *Juncus squarrosus* inflorescences in permanent quadrats at three sites during 1977. The values are expressed as the number per square metre with 95% confidence limits calculated from the t distribution. Time is in days with 1 = 1 June 1977.

3.1a 610 metres

3.1b 455 metres

3.1c 245 metres


Inflorescences.m^{-2}
200
100
0
a
200
100
0
b
100
c
0
50
100
Time (days)

Data for two other sample sites, 455 metres (Figure 3.1b) and 245 metres (Figure 3.1c), do not show an initial increase in the density of inflorescences, as the appearance of the new flower heads had ceased by the first sample date at these sites. The initial increase in density at 610 metres is only detected because the development of the plant is retarded at the higher altitude. However, all of these sites show a significant ($P < 0.01$) reduction in the density of inflorescences towards the latter part of the season.

3.2b The variation in the density of inflorescences between years

Figure 3.2 shows the density of inflorescences produced on *Juncus squarrosus*-dominated sward at each of seven altitudes in the three years of the study. As the development rate of the plants is slower at higher altitudes, these data are for different sample dates. (The values used in this figure are indicated in Appendix 2.) These data show that there is remarkably little variation in the density of inflorescences between sites in any one year, especially in 1979. There are, however, consistent differences between years. An analysis of variance was performed on these mean values; the sample sizes were equal throughout ($n = 16$). Table 3.1 gives the results of this analysis and indicates that there is significant variation in the mean density of *J. squarrosus* inflorescences produced between years ($P < 0.001$), but that there is no significant variation in the density produced between different altitudes in any one year.

Figure 3.2 : The number of *Juncus squarrosus* inflorescences produced per square metre at different altitudes in the three years of the study.

○ 1977

□ 1978

○ 1979

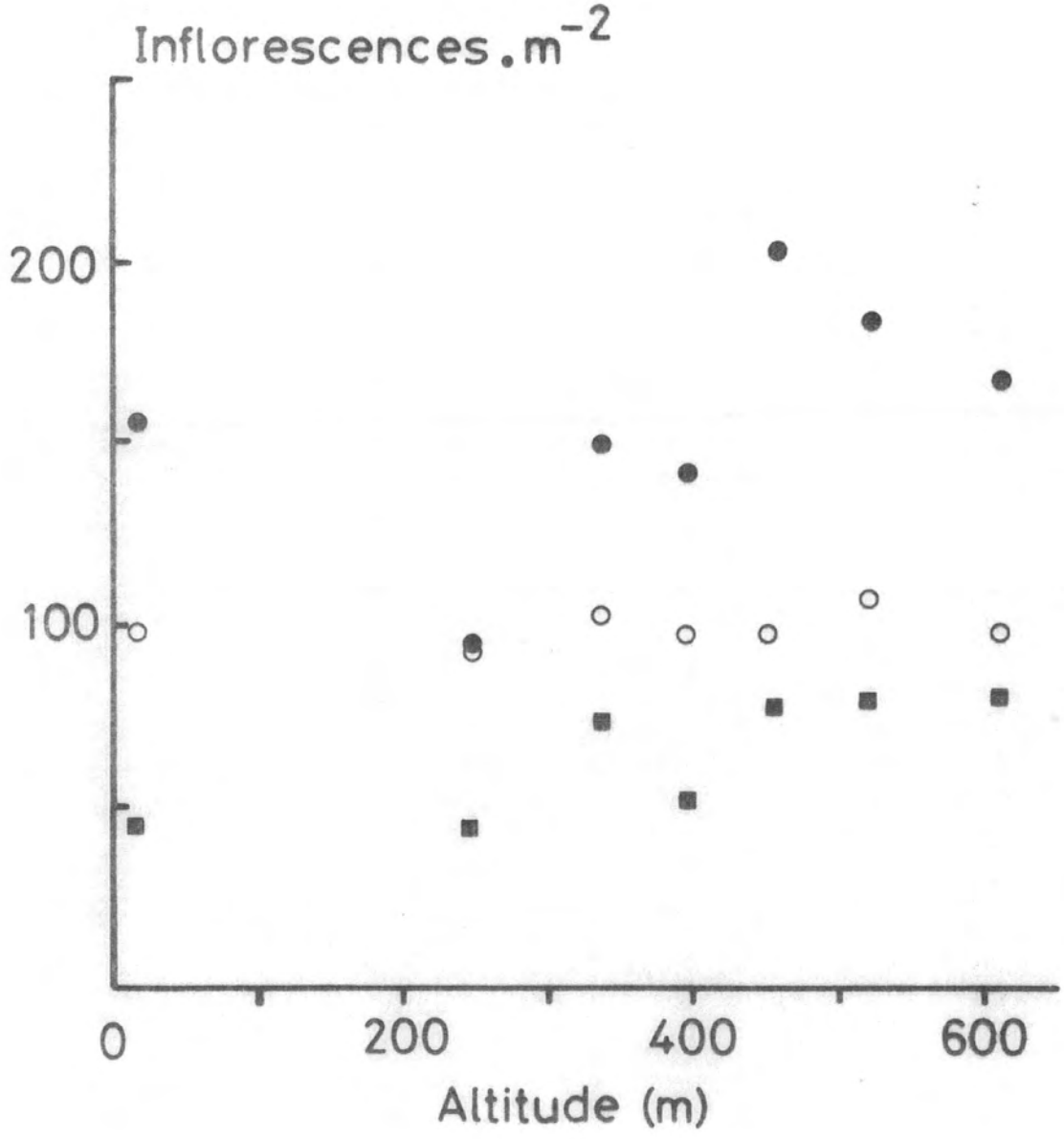

Inflorescences . m^{-2}
200
100
0
200
400
600
Altitude (m)

Table 3.1 *The results of an analysis of variance test on the mean density of* Juncus squarrosus *inflorescences produced at seven sample sites in 1977, 1978 and 1979, as shown in Figure 3.2.*

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Squares	Variance Ratio	*P*
Years	29906.30	2	14953.15	46.755	< 0.001
Sites	4984.69	6	830.78	2.598	> 0.075
Residual	3837.80	12	319.82		
Total	38728.79	20			

A *Juncus squarrosus* rosette is composed of shoots of different ages. The youngest, or front shoot, of a rhizome produces an inflorescence in the spring following the year of its development, but no inflorescence develops if the shoot is weak or in unfavourable conditions (Welch 1964). Welch (1966b) suggests that the density of inflorescence production is reduced in years with low spring rainfall. (Unfortunately he included June rainfall in his analysis; this cannot affect *J. squarrosus* inflorescence density, since most inflorescences are produced by this month.)

Data for the rainfall during April and May were obtained from the Meteorological Office for two of their weather stations. One being at Sellafield (Nat. Grid ref. NY 027032), 13m above sea-level on the Cumbrian coast, 4.8km north of the site at Drigg. The other, at Blencarn, 170m above sea-level (Nat. Grid ref. NY 637312), a small village at the foot of Cross Fell, 4km from the 335m sample site. Table 3.2 gives values

for the total rainfall during the two month period, as well as the density of inflorescences produced at Drigg and 335m, from 1977 to 1979. The 335m site was chosen from the range on the Little Dun Fell transect because it was the nearest site to Blencarn which had not been modified by drainage.

Table 3.2 : *The rainfall recorded at Sellafield and Blencarn weather stations for April and May of 1977, 1978 and 1979, and the density of* Juncus squarrosus *inflorescences produced at Drigg and 335m over the same period*

	1977	1978	1979	Location
April + May rainfall (mm)	88.0	29.0	161.9	Sellafield
Inflorescence density (No. per m^2)	156.8	45.6	98.8	Drigg
April + May rainfall (mm)	71.4	40.1	131.6	Blencarn
Inflorescence density (No. per m^2)	149.6	73.6	103.2	335m Little Dun Fell

These data support the observation by Welch (1966b), in that 1978, the year with the lowest density of inflorescences, was also the year with the least rainfall in April and May. However, the year with the highest rainfall during this period, 1979, did not have the highest density of inflorescences. As the buds are formed in the year previous to their growth into inflorescence shoots, it is possible that rainfall may not only affect the density of inflorescences produced in that year, but also the following year. In addition, other factors such as

sunshine and temperature during the growing season may contribute to the development of the buds for the following year's growth.

3.3 Floret production

In this section, the total number of florets on the inflorescences is used; this includes the florets which had developed into capsules as well as those which failed to produce seed. Figure 3.3 shows the mean number of florets per inflorescence at different altitudes in 1978. Values from the August and November samples were used for the construction of these two graphs because samples were taken over the whole range of altitudes on these dates. Data for these and other sampling occasions are given in Appendix 3.

In general, there is a reduction in the number of florets per inflorescence with an increase in altitude. The mean numbers of florets per inflorescence, calculated from all of the samples taken during 1978 at 15 metres and 455 metres, are given in Table 3.3. Between these two altitudes, there was a reduction of 1.99 florets per inflorescence per 100 metre increase in altitude. However, as shown by Figure 3.3, there was considerable deviation from the overall trend between 200 metres and 350 metres.

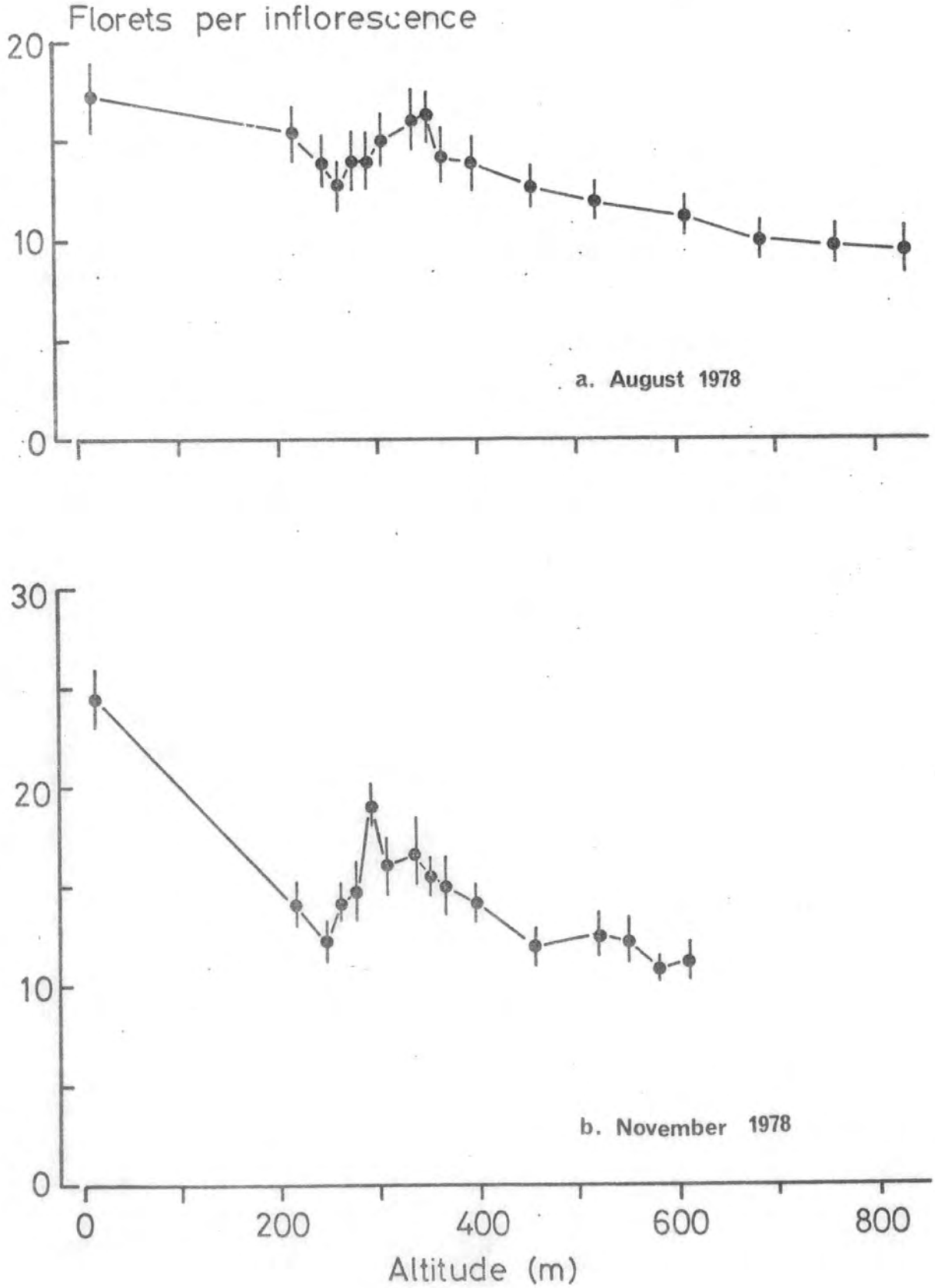
Table 3.3 : *The mean number of florets per inflorescence calculated from all of the samples taken during 1978 at 15 metres and 455 metres*

Altitude (m)	Florets per inflorescence		
	$\bar{x}$	s	n
15	21.25	5.26	420
455	12.50	3.39	420

Figure 3.3 : The mean number of florets per inflorescence of *Juncus squarrosus*, with 95% confidence limits, at different altitudes in 1978

a August 1978

b November 1978


Florets per inflorescence
20
10
0
a. August 1978
30
20
10
0
b. November 1978
0
200
400
600
800
Altitude (m)

In 1979,samples of inflorescences were taken from a very wet area by a *Sphagnum* flush at 275 metres, as well as from a more typical area nearby. The mean number of florets per inflorescence at these two sites is compared in Table 3.4. These data show that there were significantly ($P < 0.001$) more florets per inflorescence at the wetter of the two sites. This, of course, is not proof of a causal relationship between water availability and floret number; many unmeasured factors such as nutrient availability may also influence floret production. It does, however, provide circumstantial evidence in support of Welch's (1966b) claim that floret number is affected by water availability as well as altitude. This could be an explanation for the low number of florets found at the drained sites on the lower part of Little Dun Fell.

Table 3.4 : *A comparison of the mean number of florets per inflorescence at a wet site and at a drier site more typical of the area at 275 metres in 1979*

Site	Florets per inflorescence			t	P
	$\bar{x}$	S.E.	n		
Wet	25.35	1.31	20		
				4.962	<0.001
Typical	16.70	1.15	20		

3.4 The effect of altitude on flowering phenology

The production of *Juncus squarrosus* inflorescences was retarded at high altitudes. The effect of altitude on the development of *J. squarrosus* can also be demonstrated by examining the opening of the individual florets.

As the inflorescence grows the flower head emerges from a protective sheath and while the florets grow they increase in size and separate from each other. Finally, the perianth opens to allow fertilization. The great majority of florets open at all altitudes, although not all of them develop into seed-bearing capsules. The florets that have opened by any particular date can be distinguished because the perianth segments are not as tightly packed around the ovary as in the younger florets. Also the three brush-like stigmas protrude from the apex of the florets that have been open, but remain coiled around the ovary of the unopened ones.

Figure 3.4 shows the percentage of florets that had opened in samples taken at different altitudes on either 28 or 29 June 1978. This figure shows the delayed development of the florets at the higher altitudes; over 70% of the florets had opened below 500m, but significantly ($P < 0.001$) fewer had opened above this altitude. Over 90% of the florets had opened at all of the altitudes by the beginning of August.

3.5 Seed capsule production

3.5a Changes in relation to altitude

There is a far more marked reduction in the number of seed capsules per inflorescence, with increasing altitude, than in the number of florets per inflorescence (Figure 3.5). The mean numbers of seed capsules per inflorescence, calculated from all of the samples taken at 15 metres and 455 metres after the completion of seed development, are given in Table 3.5. The reduction in the number of capsules per inflorescence between these two sites was 3.7 per 100 metre increase in altitude.

Figure 3.4 : The percentage of *Juncus squarrosus* florets that had opened in samples taken from different altitudes on 28 June (□) or 29 June (○) with 95% confidence limits calculated from the arcsin transformation

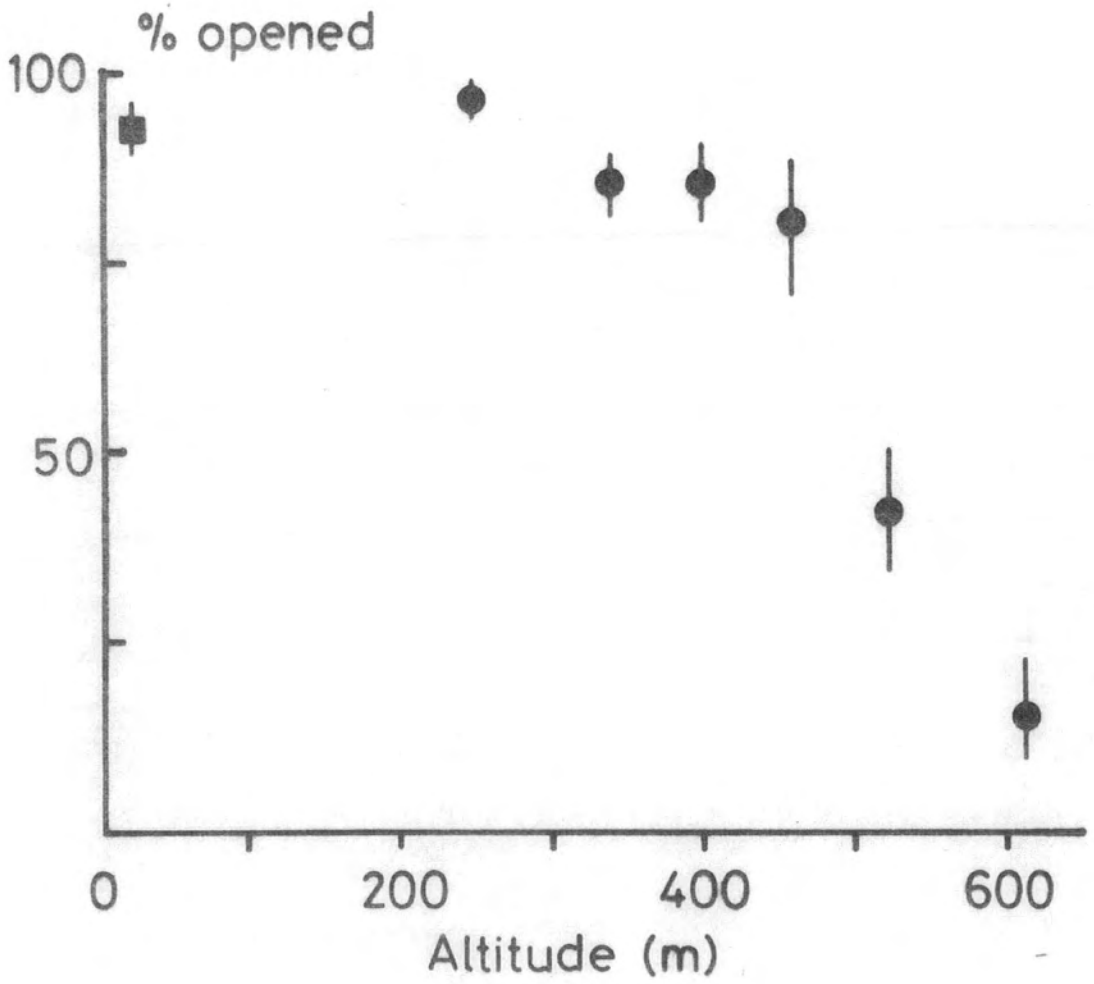

% opened
100
50
0
200
400
600
Altitude (m)

Figure 3.5 : The mean number of seed capsules per inflorescence of *Juncus squarrosus*, with 95% confidence limits, at different altitudes in 1978.

a August 1978

b November 1978

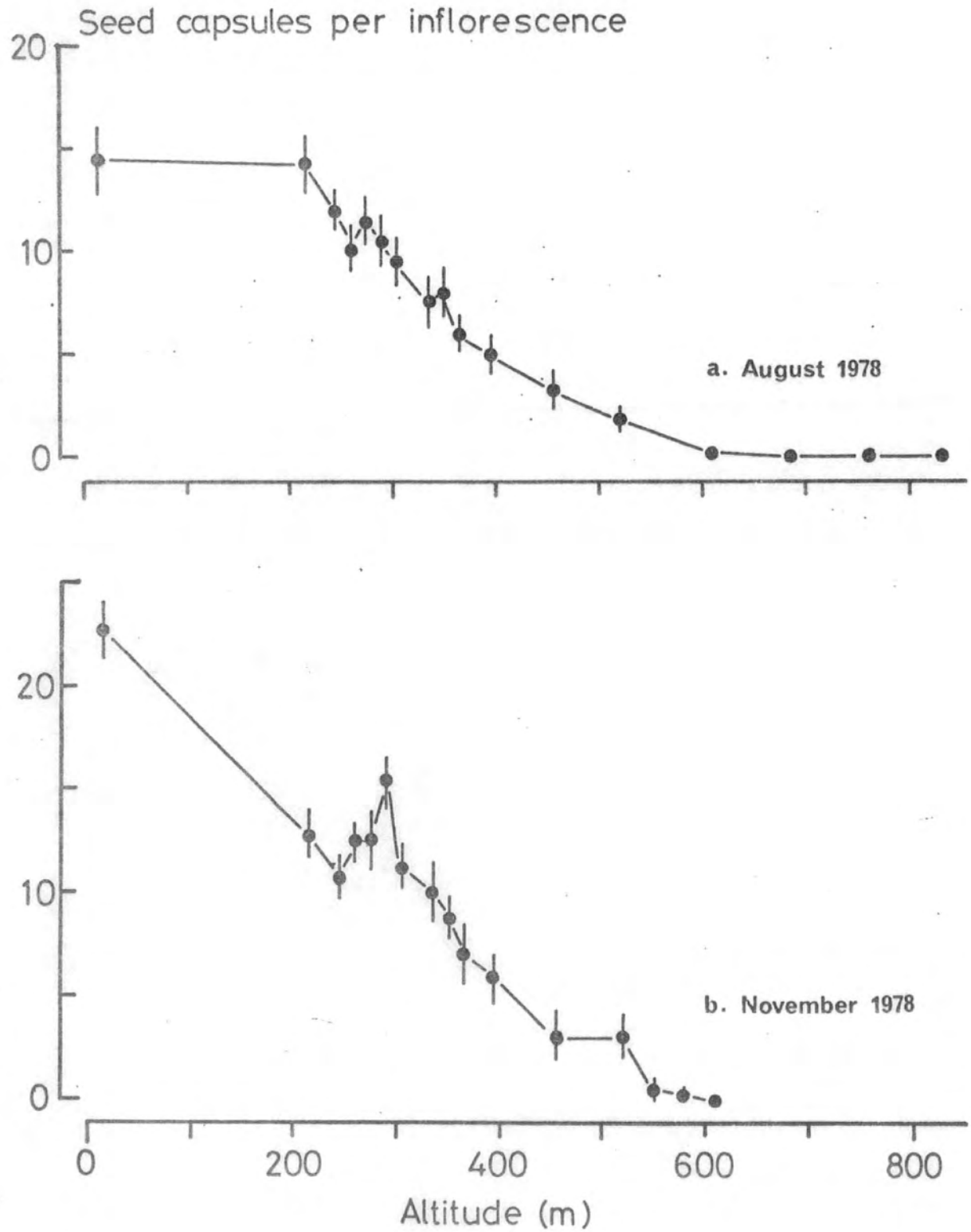

Seed capsules per inflorescence
20
10
0
a. August 1978
20
10
0
b. November 1978
0
200
400
600
800
Altitude (m)

Table 3.5 : *The mean number of seed capsules per inflorescence calculated from all of the samples taken after the completion of seed development in 1978, at 15 metres and 455 metres*

Altitude (m)	Seed capsules per inflorescence		
	$\bar{x}$	s	n
15	18.94	5.16	300
455	2.66	2.42	240

The greater reduction in the number of seed capsules per inflorescence, than in the number of florets per inflorescence, with increasing altitude, is more obvious when the number of seed capsules is expressed as a percentage of the florets. In this case 89.1% of the florets developed into seed capsules at 15 metres, but only 21.3% at 455 metres.

3.5b Variation between years

The proportion of florets developing into seed capsules can be used to compare the extent of ripening between years, as well as to compare the ripening in different samples in the same year.

Table 3.6 gives the proportion of florets producing seed capsules at each altitude sampled for November 1977, August 1978, November 1978 and August 1979. These data show a general fall-off in the value for the proportion developing into seed capsules with increasing altitude. Inverse non-linear relationships between altitude and this proportion are evident for each of these sample dates. Logistic curves were fitted to these data using the method of least squares. The equations have the formula:

Table 3.6 *The proportion of* Juncus squarrosus *florets developing into seed capsules at a series of altitudes on four sampling occasions.* * *The value for the 520m sample site in November 1978 was found to be discordant with the rest of the data for that group of samples and was omitted from the regression analysis (see text)*

Altitude (m)	November 1977	August 1978	November 1978	August 1979
15	0.9344	0.8356	0.9258	0.8375
215	-	0.9179	0.9096	0.9306
245	0.8309	0.8590	0.8804	0.9507
260	-	0.7886	0.8778	-
275	0.8822	0.8294	0.8475	0.8713
290	-	0.7605	0.8063	-
305	0.7672	0.6341	0.6992	0.8415
335	0.6464	0.4741	0.5936	0.8584
350	-	0.4917	0.5621	-
365	0.5000	0.4246	0.4644	0.6834
395	0.5817	0.3554	0.4145	0.7893
455	0.3995	0.2602	0.2583	0.4385
520	-	0.1504	(0.2586)*	0.2596
550	-	-	0.0378	0.0680
580	-	-	0.0247	0.0485
610	-	0.0088	0.0030	0.0233

$$Y = \frac{k}{1 + \exp\ (a - bX)} \qquad (3.1)$$

where Y is the proportion ripe at each altitude X, in metres; k is the upper asymptote, b is the rate of decrease in the proportion ripe with an increase in altitude and a is the constant of integration that defines the position of the curve with respect to the origin.

Preliminary analysis of all of the data for the November 1978 samples showed the value for the proportion ripening at the 520m sample site to be discordant with the rest of the data. Anscombe and Tukey (1963) suggest that points can be tested as outliers from the rest of the data by examining the residuals from the regression (the difference between the observed and expected values) together with the respective standard deviations (s) of the expected values of the dependent variables. They suggest that a possible rule to use in this situation is:

> "reject that observation whose residual is greatest in magnitude, provided the magnitude exceeds $C.s$, where C is a given constant. If this observation is rejected recompute all the residuals and s and apply the rule again, and so on until there are no more rejections."

For the purpose of these analyses, C was chosen as 3.9 because in a normal distribution the probability of a value lying between ± 3.9 standard deviations from the mean is 1.0000, to four decimal places (Snedecor and Cochran 1967). For the 520m sample site in November 1978 the residual was $5.841s$, so this point was rejected and the regression recomputed. On recomputation without the 520m value, no residual was more than $3s$. For the other sample dates no residuals were more than $3.9s$, so no more rejections were needed.

The difference at the 520m site in November 1978 is possibly due to samples being taken from a somewhat sheltered position, in a slight hollow. These plants would be subjected to much less rigorous conditions than would otherwise be expected for this altitude. It has been demonstrated by Jordan (1962) and Welch (1966b) that a greater proportion of the florets develop into seed capsules in such sheltered conditions.

The values for the constants for the regression analyses on the data in Table 3.6 are given in Table 3.7, as well as the sample sizes (n). The results of F tests comparing the variation due to the regressions with that due to the residuals are also given in this table. The equation for November 1977, where the sample size was small, explains over 82% of the variation in the proportion ripening, whilst the equations for the other occasions explain between 95% and 99% of the variation. The maximum possible value of k is 1, which represents total ripening. This is never achieved, either in the observed results or as predicted by the equations. However, only the data for the August 1979 sample give a value of k significantly ($P < 0.01$) less than unity.

The curves described by the equations are shown in Figure 3.6. They are all of the same appearance but their positions with respect to the origin differ. The curve for August 1979 is shifted to the right of those for 1978; the curve for 1977 lies between the other two years.

Table 3.8 gives the values for the points of inflexion ($^{a}/_{b}$) for each of the four equations. This value is used as a comparison of the proportion of the florets developing into seed capsules over the whole range of altitudes on the different sample dates. It is the altitude at which half of the maximum achieved on each sample date is realized(i.e. the value of X when Y = $^{k}/_{2}$). These values are also marked on Figure 3.6.

Table 3.7 : *The results of least squares regression analyses to fit the data for the proportion of florets developing into seed capsules at different altitudes on four sample dates (as given in Table 3.6) to the logistic equation (see text)*

Sample date	*N*	*k*	Standard deviation of *k*	*a*	*b*	*F*	d.f.	*P*	R^2
Nov 1977	8	0.9673	0.0787	-4.6122	-0.01116	23.16	2, 5	< 0.01	0.825
Aug 1978	14	0.9377	0.0599	-5.6776	-0.01559	115.64	2,11	< 0.001	0.946
Nov 1978	15	0.9718	0.0300	-6.1637	-0.01656	612.76	2,12	< 0.001	0.989
Aug 1979	13	0.8963	0.0299	-9.6657	-0.02105	223.41	2,10	< 0.001	0.974

Figure 3.6 : The proportion of *Juncus squarrosus* florets developing into seed capsules in relation to altitude on four sampling occasions during the study. The curves are the lines described by the equations in Table 3.7; the points of inflexion are also shown. The observed values are shown with 95% confidence limits calculated from the arcsin transformation.

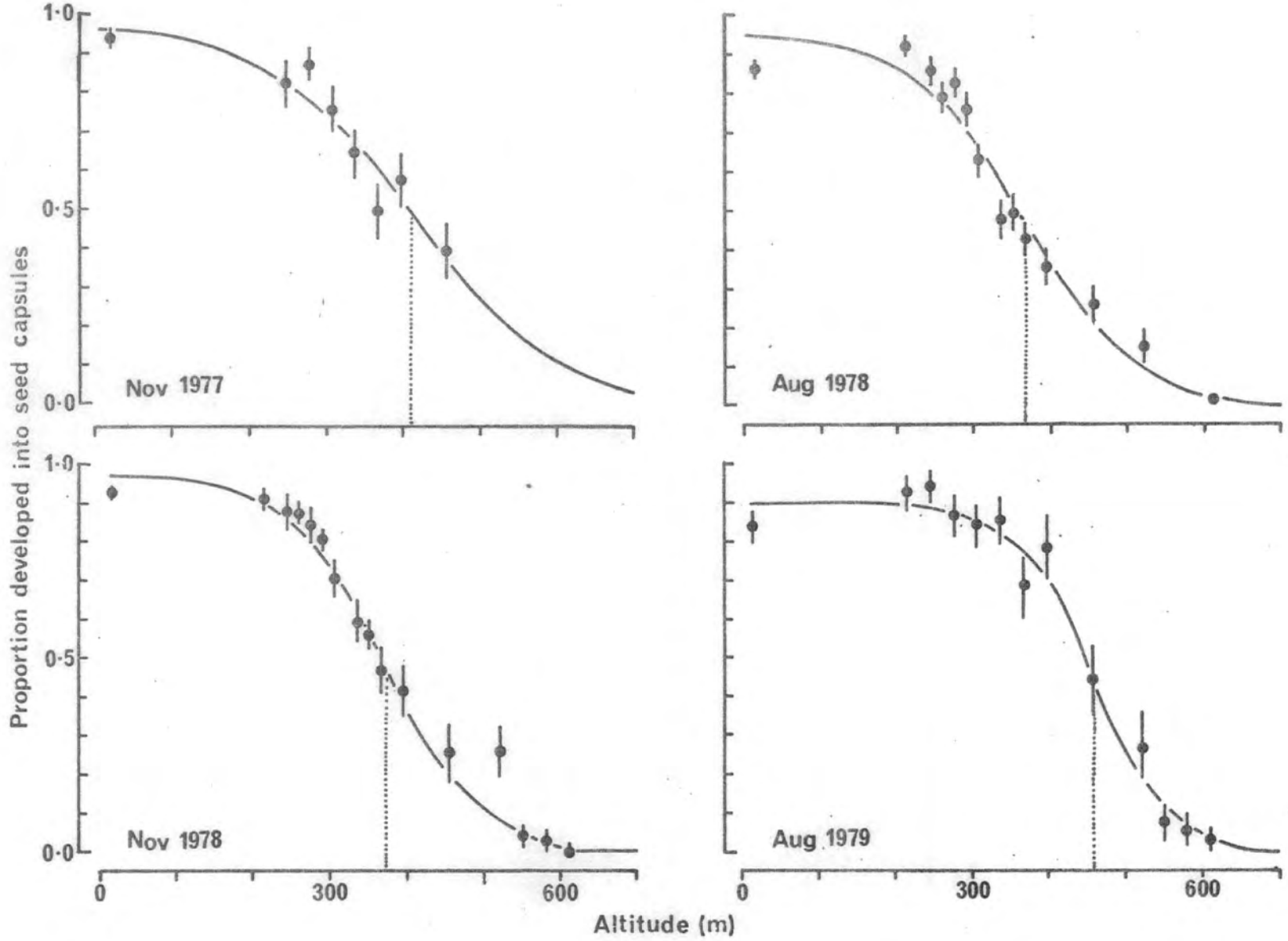

1·0
0·5
0·0
Nov 1977
Aug 1978
Nov 1978
Aug 1979
Proportion developed into seed capsules
0
300
600
Altitude (m)

Table 3.8 : *The points of inflexion (as altitude in metres) of each of the curves describing the change in the proportion of florets developing into seed capsules in relation to altitude*

Sample	November 1977	August 1978	November 1978	August 1979
a/b (metres)	413.7	364.3	372.2	459.1

There is little difference between the values of a/b for the samples taken in August and November 1978. By the time that the samples were taken in August, all of the florets that were going to produce seed had developed into seed capsules.

The point of inflexion of the curve in August 1978 was 94.8 metres lower than in August 1979.

The point of inflexion for the 1977 samples lay at an altitude between those for the other two years.

As the proportion of florets developing into seed capsules is reduced with increasing altitude, this process could be determined by temperature, as suggested by Pearsall (1950) and Welch (1966a). If this were the case, one would expect the curve for the proportion of florets developing into seed capsules to be shifted to the left, with respect to the origin, in years with cooler temperatures during the fertilization and development period. This would also result in an altitudinal lowering of the point of inflexion. Meteorological data are available from the weather station at Moor House. Although this is some distance from the sample areas, these data give a guide to the

relative level of mean temperatures in the region each year. Table 3.9 gives the mean daily temperature in June and July during the three years, and the average value for this period of seed capsule development.

Table 3.9 : *The mean daily temperature in June and July recorded at Moor House in 1977, 1978 and 1979. The average temperature for this two month period is also given*

Year	Month	Mean daily temperature ½ (max + min) °C	Average temperature during the two months. °C
1977	June	8.3	9.80
	July	11.3	
1978	June	9.1	9.55
	July	10.0	
1979	June	10.8	10.95
	July	11.1	

The data in Table 3.9 show that the average temperatures in June and July were 1.4°C higher in 1979 than in 1978. The temperature for the same period in 1977 lay between the values for the other two years. A comparison between these data and the values for the points of inflexion of the seed capsule production curves reveals that the year with the highest point of inflexion was the warmest. 1978 was the year with the lowest point of inflexion and also with the coolest average temperatures during June and July.

Data from many years would be needed to show the extent to which this measurement of seed capsule production is dependent on the level of the temperature during the period of fertilization and seed development. Unfortunately, this type of data is not available from the work of previous authors.

3.6 The number of seeds per capsule

The number of seeds in the seed capsules was recorded from some of the samples taken in August 1977 and 1979, by which time all of the seeds were full-sized but the capsules had not opened to distribute them. There were high densities of *Coleophora alticolella* larvae in 1978, resulting in very few undamaged seed capsules, so this measurement was not made in that year. The number of seeds from 20 capsules, one from each inflorescence, was recorded; these were chosen as the first capsules examined, which did not contain larvae, thus avoiding under-estimates due to seed predation.

Values for the mean number of seeds per capsule, with their standard deviations, are given in Table 3.10. There is no trend between these values and altitude for either 1977 or 1979. In 1979 the seed capsules at the 15 metre site contained fewer seeds than at the other altitudes, but the mean value had a comparatively large standard deviation. The smaller values for the standard deviations from the other sites indicate that there was usually very little variation between the number of seeds in each capsule. Overall, the mean number of seeds per capsule (with 95% confidence limits) is 80.5 ± 2.1.

Table 3.10 *The mean number of seeds per capsule of* Juncus squarrosus, *with their respective standard deviations, at different altitudes in August 1977 and 1979*

Altitude (m)	1977 Seeds per capsule $\bar{x}$	s	n	1979 Seeds per capsule $\bar{x}$	s	n
15	87.8	16.6	20	68.4	29.8	20
245	87.5	12.2	20	85.8	17.6	20
335	81.2	10.3	20	74.4	12.2	20
395	83.8	12.2	20	77.0	17.0	20
455	73.2	16.3	20	80.6	16.2	20
520	83.7	9.7	20	83.0	15.6	20
610	78.9	7.6	20	-	-	-

3.7 Grazing of inflorescences

It was suggested in a previous section that much of the reduction in the density of inflorescences, at any one site during the year, is caused by grazing animals. The fells are used as common grazing land by many of the local farmers and the shepherd's guide for the area lists 39 different sheep flocks which could be grazed on the reserve. Six main flocks were seen on the eastern slopes of Little Dun Fell in 1976 (Randall 1976), although sheep from other flocks were occasionally observed on the higher parts of the fell. Rawes and Welch (1969) recorded 3.2 sheep per hectare on these slopes; Randall (1976) found 3.4 per hectare on the same area. Casual observations during the period of the present research revealed a similar situation.

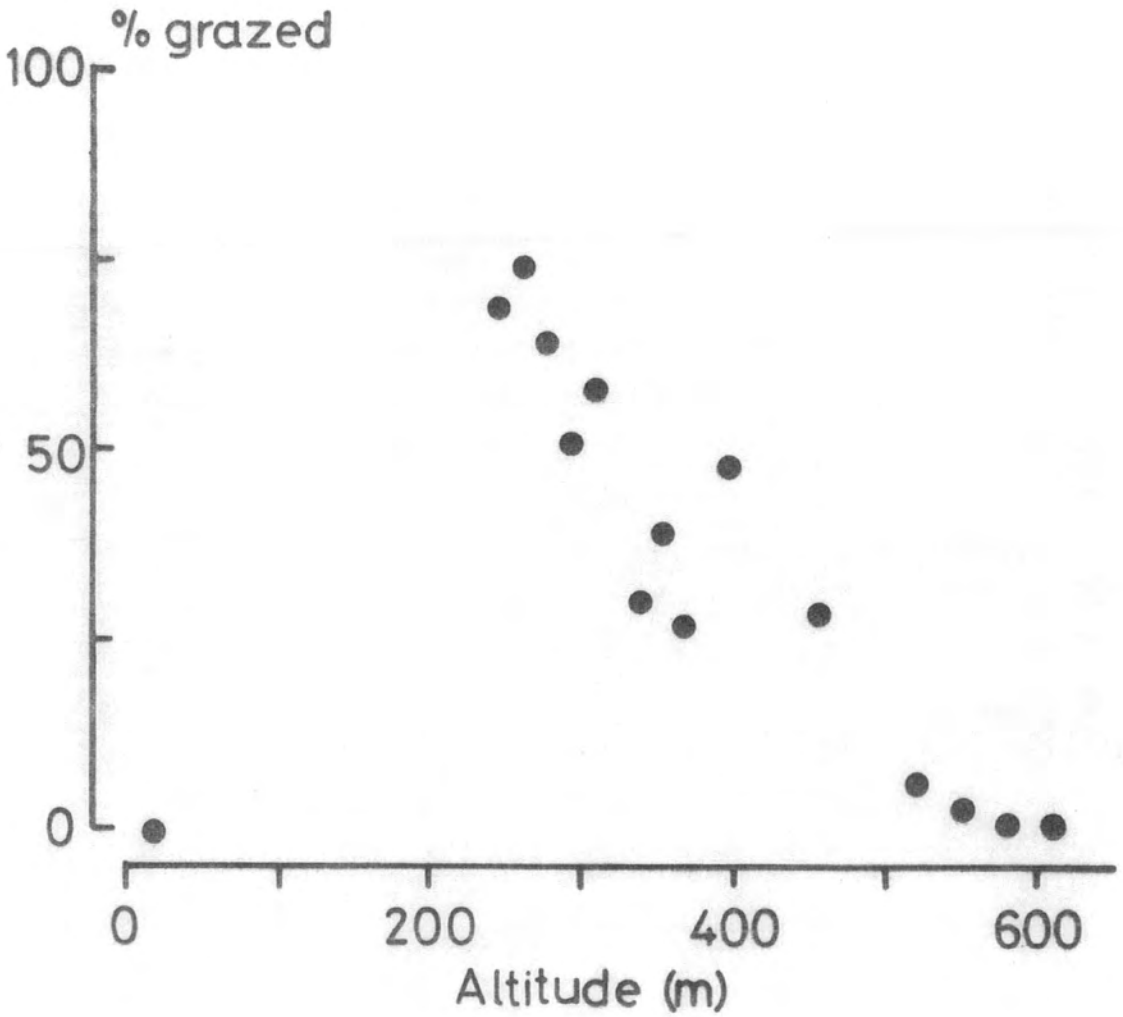
Cattle graze on the lower, enclosed slopes, and one farmer keeps fell ponies in this area; up to 24 have been seen at any one time (M. Rawes, pers. comm.). It is possible that rabbits (*Oryctolagus cuniculus* (L.)) and hares (*Lepus capensis* L.), which have been seen in the area, could feed on the *Juncus squarrosus*. Red Grouse (*Lagopus lagopus scoticus* Lath.) have been recorded feeding on the seed capsules of this rush in autumn (Lipscombe 1886; Wilson and Leslie 1911), as have snow buntings (*Plectrophenax nivialis* L.) (Henty 1979). Both of these species occur at Moor House (Parkin 1977).

Despite these other animals, sheep are the commonest grazers in the area and it is assumed that they are responsible for most of the reduction in the density of *Juncus squarrosus* inflorescences.

Figure 3.7 shows the effect of grazing on the *J. squarrosus* inflorescences in 1979. The reduction in the density of inflorescences up to the end of August is shown as a percentage of the total number of inflorescences produced at each site. There was an inverse relationship between the percentage of inflorescences grazed and altitude on Little Dun Fell, with over 50% grazed below 325 metres. There was very little grazing at the 15 metre site; there were few sheep here, cattle and rabbits being the major grazers.

Sheep eat *J. squarrosus* mainly in the spring, when the shoots are still tender, but they prefer the more succulent grasses. They do most of the damage to the *J. squarrosus* when the stocking rates are high; this often occurs at low altitudes, before they have been put back on to the fell. As there is now little shepherding, there is also a tendency for the sheep to wander back to the lower slopes during the year (Rawes and Welch 1964). Snow lay on the fell until very late in the year in 1979; there were deep drifts left at 425 metres on 8 June. This would have prevented the early return of the sheep to the upper slopes and could account for the very heavy grazing pressure at the lower altitudes.

Figure 3.7 : The percentage of *Juncus squarrosus* inflorescences produced at different altitudes that had been grazed on or before 24 August 1979 (23 August at 15m)


% grazed
100
50
0
0
200
400
600
Altitude (m)

Similar patterns of grazing were found in the two preceding years. Figure 3.8 shows the percentage of the initial density of inflorescences which were grazed at the seven main sites. Again, the heaviest grazing pressures in the first part of the season (up to mid-August) were at the low altitudes on Little Dun Fell. These graphs also show the percentage grazing over the whole of the year, and demonstrate that the greater part of the total grazing at the higher sites occurs during the second period (after mid-August).

3.8 The density of seeds produced

Seed production, on a unit area basis, by *Juncus squarrosus* is determined by four parameters: inflorescence density, florets per inflorescence, the proportion of florets developing into seed capsules and seeds per capsule. The density of seeds produced at different altitudes during the three years of this study has been calculated from data given in this chapter and the results are given in Table 3.11. The values for the proportion of florets developing into seed capsules have been taken from equations given in Table 3.7 and the overall mean value of 80.5 ± 2.1 seeds per capsule has been used for the 1978 data.

Table 3.11 shows that there is considerable variation in the density of seeds produced at each site in different years, as well as the marked reduction in the density with increasing altitude. These variations in density are mainly due to two factors. Variation between years at each site is due to differences in the density of inflorescences produced (as shown in Figure 3.2). The reduction in the density of seeds with increasing altitude is mainly due to the lower proportion of florets developing into seed capsules in the cooler conditions at the higher sites.

Figure 3.8 : The percentage of *Juncus squarrosus* inflorescences produced at different altitudes that had been grazed by mid-August (○) and during the whole sampling period (○) in 1977 and 1978

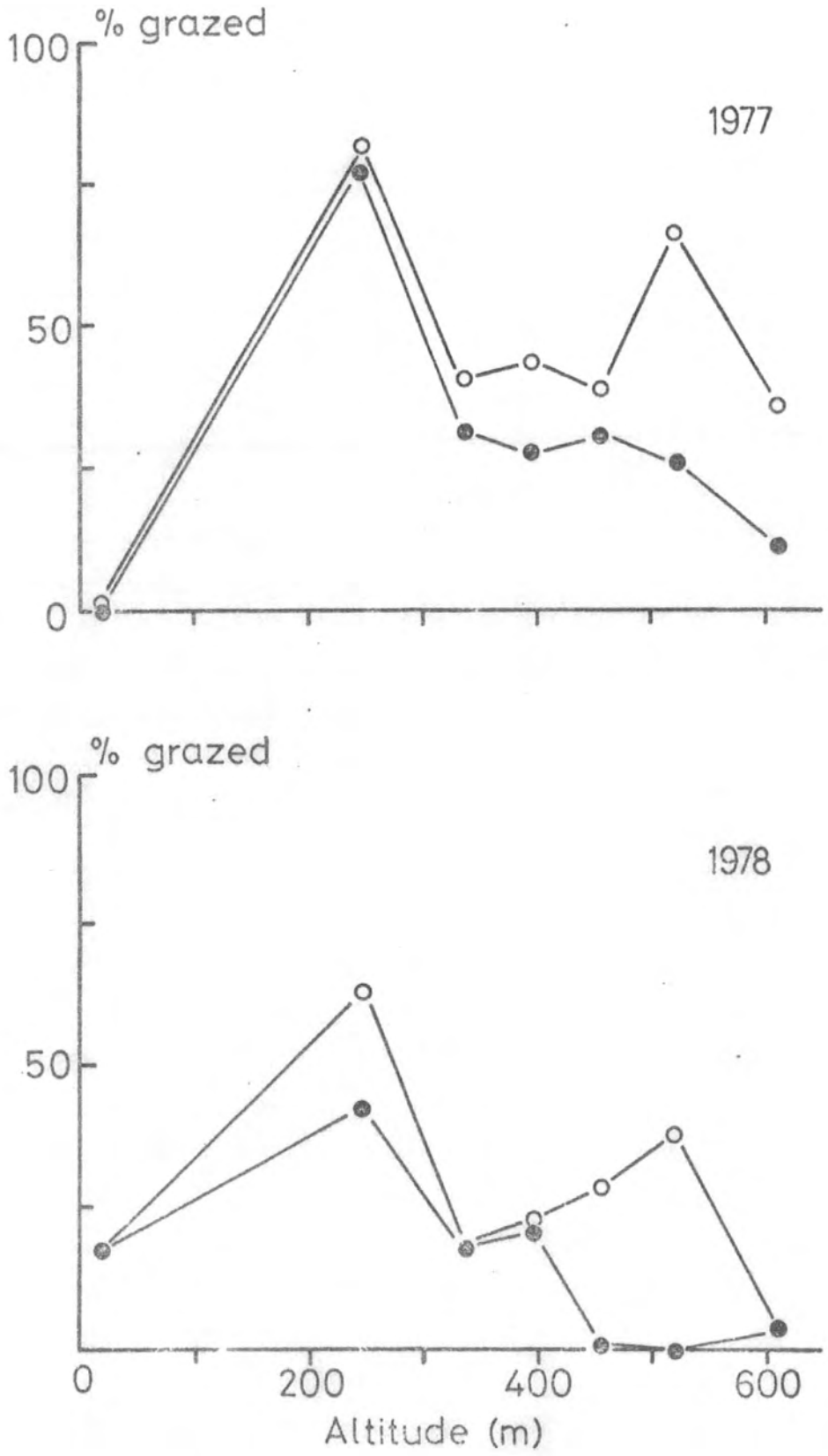

% grazed
100
50
0
1977
% grazed
100
50
1978
0
200
400
600
Altitude (m)

Table 3.11 : *The density of* Juncus squarrosus *seeds (number x* 10^{-3}*) produced per square metre at the seven major sample sites in the three years of the study. The values are given with their 95% confidence limits*

Altitude (m)	The number of *Juncus squarrosus* seeds x 10^{-3} produced per square metre. 1977	1978	1979
15	339.1 ± 89.7	87.3 ± 36.9	175.1 ± 46.2
245	81.3 ± 25.1	42.1 ± 11.5	108.2 ± 27.8
335	118.0 ± 26.7	62.5 ± 17.5	102.3 ± 22.0
395	88.0 ± 24.7	23.7 ± 5.7	83.9 ± 20.8
455	73.0 ± 25.6	14.4 ± 4.4	58.5 ± 14.8
520	41.0 ± 19.5	6.3 ± 2.6	29.7 ± 12.2
610	15.8 ± 7.5	1.4 ± 1.0	4.3 ± 3.9

3.9 Discussion

It is largely accepted among agronomists that the 'growing season' of a plant can be defined as the length of time for which the average daily mean temperature is above a certain threshold value (Francis 1978). For example, this value is around 6°C for grasses in Britain (Taylor 1967). Consequently, the onset of the growing season will be progressively retarded, and its length reduced, with increasing altitude. This has been demonstrated by the later production of inflorescences and florets of *Juncus squarrosus* at the higher sites.

The effects of altitude on temperature not only cause a retardation of the onset of growth, but also affect the seed production. There is a reduced proportion of the florets developing into seed capsules at the

higher altitudes, although this relationship may be modified by the topography of each site (Jordan 1962; Welch 1966b). There was, however, no relationship between the mean number of seeds maturing in the seed capsules and altitude. Welch (1966b) found a similar situation, and Reay (1964) showed that there was no difference in the dry weight of seeds per capsule in relation to altitude.

Floret production by the inflorescences is reduced with increasing altitude, but the overall trend can be disturbed where plants are growing on drier soil, causing lower production than would be expected.

The density of inflorescences produced on a *Juncus squarrosus*-dominated sward is variable between years. It is probably dependent on climatic and site conditions while the inflorescences are growing and the buds are forming for the following year. The density of inflorescences is later reduced by the grazing of sheep, especially at the low altitudes.

Welch (1966b) gave measurements of the reproductive capacity of *J. squarrosus* at many high altitude sites in northern England. Using the data from his lowest site, 472m, it is found that *J. squarrosus* produced 25.6×10^{3} seeds m^{-2} in 1963. This is of the same order as the density of seeds produced around the 455m and 520m sites during the present study.

Welch (1966b) carried out experiments on the germination of the *J. squarrosus* seeds from his sample sites. He found that the viability of seeds from plants at the higher altitude was reduced and that the viability was also variable between years. He calculated that 54% of the seeds were viable from the 472m site in 1963, and also estimated that approximately 25% of the seeds would be lost during dispersal. From these values he estimated that the number of viable

seeds dispersed by *Juncus squarrosus* was in the region of $10^{4}.m^{-2}$ at 472m. None of these calculations include the effects of the seed predator *Coleophora alticolella* which attacks the seeds after they have been produced but before they are dispersed. The larvae eat virtually all of the seeds in each capsule that they attack. Welch (*loc. cit.*) suggests that this predation would do no more than balance the increase in seed production expected above the value for his 472m site because of the greater floret number and capsule maturation below this altitude.

In the following chapters the ecology of *C. alticolella* is discussed in the light of the information on the seed production by *Juncus squarrosus* at different altitudes.

CHAPTER 4

STUDIES ON THE EGGS AND OVIPOSITION BEHAVIOUR OF *COLEOPHORA ALTICOLELLA*

4.1 Introduction

Coleophora alticolella lays most of its eggs between the florets of the developing inflorescences of its food plant, *Juncus squarrosus*. The eggs are often laid before the florets have opened and usually before the seed capsules have started to develop. Jordan (1958) found *C. alticolella* eggs in samples of *J. squarrosus* within one or two days of the first imagos being seen at each of his sample sites. On dissection of newly emerged females he found that their ovaries contained ten to twenty eggs of full size ready for laying. He concluded, from observations made in the field, that there was little, if any, difference between the dates of emergence of adults at various altitudes.

Jordan (1962) recorded the percentage infestation of *J. squarrosus* seed capsules by eggs and larvae in July 1953 and 1954, and Reay (1964) the number of eggs during June and July in 1956 and 1957. In this chapter I examine the changes in the density of eggs during the oviposition period over the whole altitudinal transect. The rate of egg-laying and the timing of the oviposition periods at each site are also discussed in relation to altitude.

In two previous studies on *C. alticolella* in this region (Jordan 1958, Reay 1964), the oviposition behaviour of the female moths was examined in relation to the *J. squarrosus* florets. Oviposition behaviour is discussed in greater detail in this chapter, and the effects of differences in the density and distribution of the inflorescences on egg-laying are also investigated.

4.2 The size of the eggs

Some of the eggs were measured using a microscope with a graticule eyepiece capable of resolving 0.013mm. The eggs are oval and the mean and standard deviation of two axes, based on samples of 30, are 0.398 ± 0.0.24mm and 0.200 ± 0.016mm. These dimensions are similar to those of the eggs of *Coleophora serratella* (L.) which Coshan (1974) recorded as 0.40mm long and 0.25mm broad.

4.3 The colour of the eggs

The eggs of *Coleophora alticolella* change colour during their development. Newly laid eggs are white, they then turn yellow and later orange. Finally, just before hatching, the head capsule of the developing larva is visible through the chorion. These different colours can be used to divide populations of eggs into age-classes, although these classes are not of the same duration.

4.4 Oviposition sites

An oviposition site is defined as any position on an inflorescence where an egg or group of eggs is present. The potential sites on an inflorescence cannot be quantified because the criteria that an ovipositing female moth applies in searching for, and accepting, oviposition sites are not known.

There is a direct relationship between the number of eggs and the number of florets per inflorescence. Figure 4.1a shows an example of this relationship for the 335m sample site on 29 June 1978. High densities of eggs were present in this sample and it is assumed that many of the potential oviposition sites would be occupied. The regression analysis shows that 43% of the variation in the number of eggs is explained by the number of florets per inflorescence.

Figure 4.1a : The relationship between the number of eggs of *Coleophora alticolella (y)* and the number of florets per inflorescence of *Juncus squarrosus (x)*. Data taken from the sample at 335m on 29 June 1978. The line is fitted by least squares regression and has the formula:

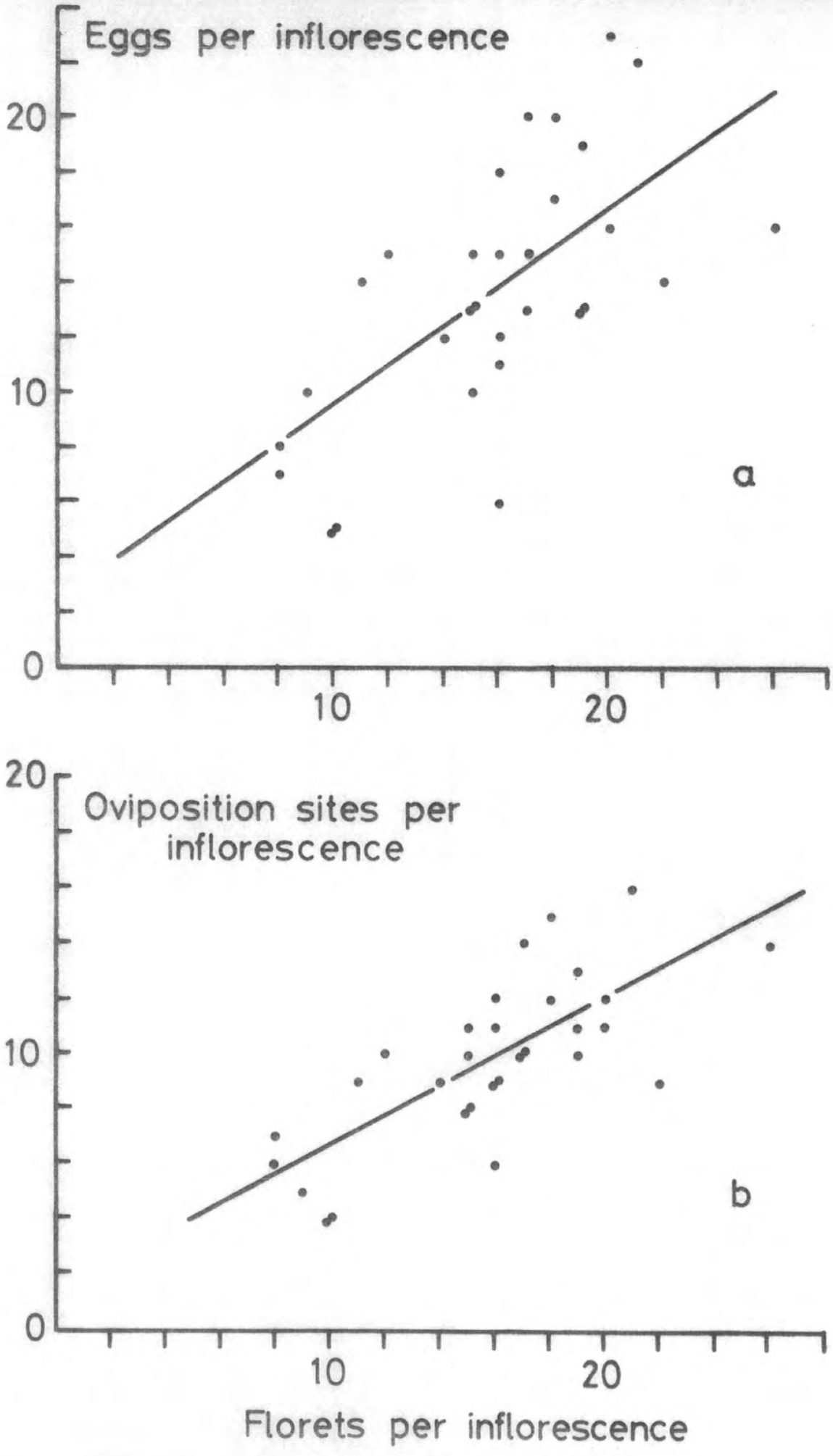
$$y = 0.720x + 2.265$$

$n = 30$ $r = 0.654$ $P < 0.001$ S.E. of slope = 0.157

Figure 4.1b : The relationship between the number of florets per inflorescence of *Juncus squarrosus (x)* and the number of oviposition sites (*y*). Data taken from the 335m sample site on 29 June 1978. The line is fitted by least squares regression and has the formula

$$y = 0.527x + 1.495$$

$n = 30$ $r = 0.739$ $P < 0.001$ S.E. of slope = 0.091


Eggs per inflorescence
20
10
0
10
20
a
20
Oviposition sites per inflorescence
10
0
10
20
b
Florets per inflorescence

There is no relationship between the number of eggs per floret and the number of florets per inflorescence (i.e. the size of each inflorescence); the intercept of the equation given for Figure 4.1a is not significantly different from zero ($x = 0$, $y = 2.265 \pm 3.115$).

Eggs were found in groups at some of the oviposition sites. The distribution of the eggs in different group sizes in the sample from 335m on 29 June is shown in Table 4.1. In most cases the eggs in a group were touching each other; if not, there was less than an egg's breadth between them. The largest group found during the study was of five eggs.

Table 4.1 *The frequency of different sized groups of* Coleophora alticolella *eggs in a sample of 30 inflorescences from 335m on 29 June 1978*

Eggs per oviposition site	1	2	3	4	5
Frequency	210	66	12	7	1

The number of oviposition sites is not the same as the number of eggs present, because not all of the eggs are laid singly. The variation around the regression line is reduced if the number of oviposition sites is plotted against the number of florets for each inflorescence, instead of the number of eggs against florets. Figure 4.1b shows this relationship for the data from the same sample as in Figure 4.1a. In this case, 55% of the variation in the number of oviposition sites is explained by the variation in the number of florets.

Thus the number of florets on an inflorescence can determine the number of oviposition sites but, because an oviposition site can contain more than one egg, the relationship between eggs and florets is more variable. Data on the number of eggs per oviposition site are discussed later, in relation to oviposition behaviour.

4.5 The density of eggs in relation to the *Juncus squarrosus* florets

The data for the density of *Coleophora alticolella* eggs presented in this section are expressed as the number per floret of *Juncus squarrosus*. This is not only because the number of florets determines the number of oviposition sites, but also because it shows the relationship between *Coleophora alticolella* and its potential food supply. Complete data for the samples taken during this part of the investigation are available in Appendix 4, but are also summarized in Table 4.2.

Towards the end of the oviposition period, some of the larvae hatch before egg-laying has stopped. This occurred at the lower altitudes in 1978. The density of the individuals present on the final sample dates at these low altitudes is expressed as the number of eggs plus larvae per floret, if this value is greater than the density on the previous sample date. Table 4.3 shows the number of larvae present as a percentage of the total eggs plus larvae on the final sample date at each site, and also the percentage of the eggs that had larval head capsules visible.

Some of the values of density given in Table 4.2 will be slight underestimates of the true density because there is some mortality of newly hatched larvae whilst they search for food. This will not apply to the sample sites above 335m. It is not known if

Table 4.2 : *The number of eggs (or eggs plus larvae) per floret of* Juncus squarrosus *at six sample sites during the 1978 oviposition period. Data are given up to, and including, the sample date with the maximum density of individuals.* ☆ *denotes larvae present in the sample.*

Date	15m	Date	245m	335m	395m	455m	520m
30 May	0.015						
6 June	0.155	7 June	0.084	0.109	-	-	-
		9 June	-	0.111	0.085	0.086	0.000
14 June	0.249	15 June	0.287	0.277	0.227	0.136	0.000
		18 June	0.373	0.452	0.335	0.181	-
21 June	☆0.262	22 June	0.395	0.678	0.531	0.365	0.014
28 June	☆0.287	29 June	☆0.735	0.865	0.709	0.540	0.040
		6 July	-	☆1.120	0.899	0.794	0.102

Table 4.3 : *The number of* Coleophora alticolella *larvae, expressed as a percentage of the total number of eggs and larvae present, and the percentage of eggs present with head capsules visible; in samples taken on the date with the maximum density at six altitudes during the 1978 oviposition period*

Altitude (m)	15	245	335	395	455	520
Sample Date for Maximum Density of eggs laid	28 June	29 June	6 July	6 July	6 July	6 July
Total number of eggs plus larvae in the sample	123	263	477	258	201	43
% present as larvae	10.6	4.6	2.1	0.0	0.0	0.0
% of eggs with head capsules visible	29.1	9.6	6.6	1.6	0.5	0.0

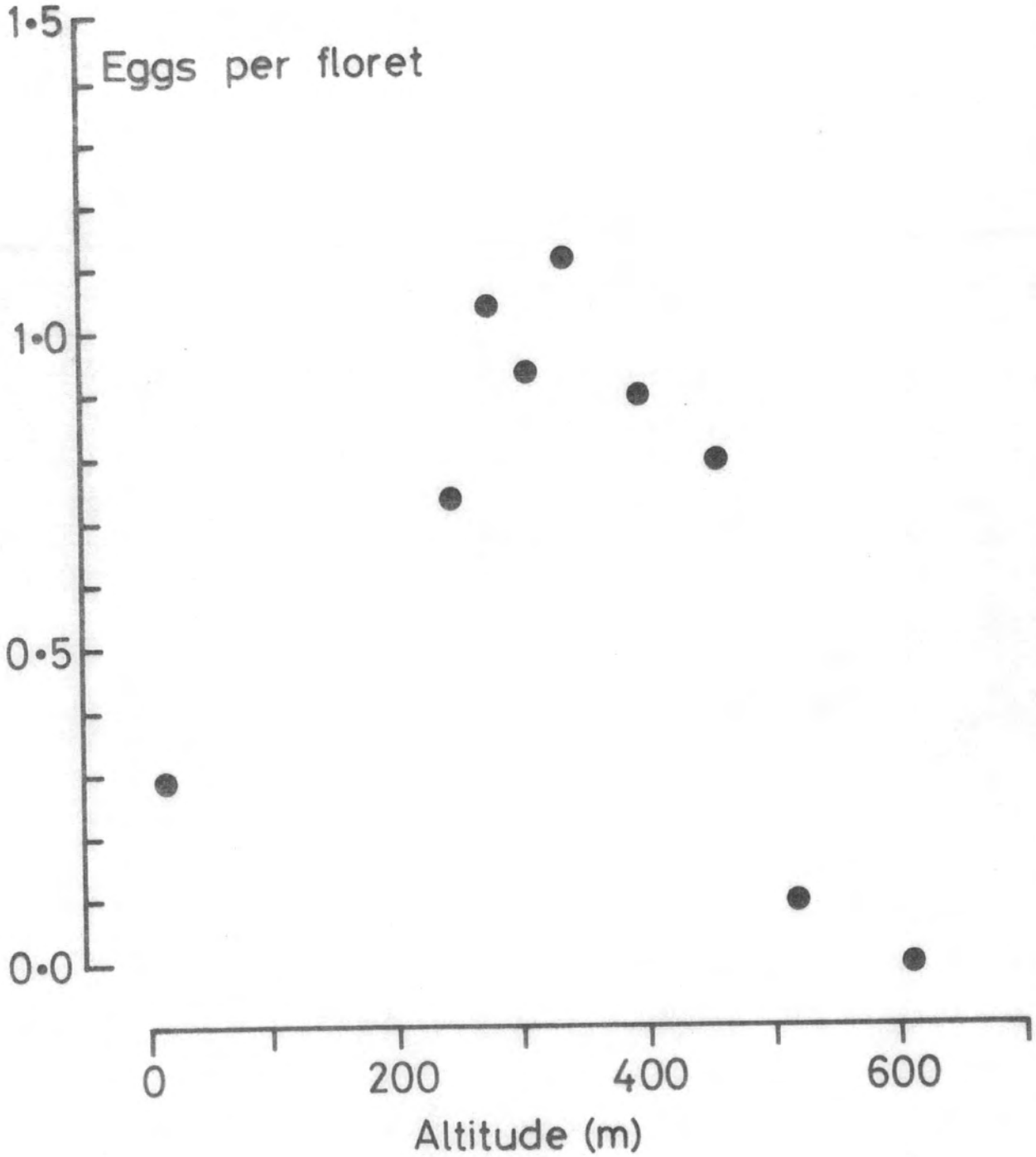
eggs were lost due to predation or to the actions of wind and rain, but as they were in such protected positions, loss due to these latter causes would be slight.

There is an increase in the number of eggs per floret during the oviposition period, with a maximum density attained some two weeks earlier at 15m than at some of the higher altitudes. The oviposition period also starts earlier at the lower sites. The length of the oviposition period cannot be measured accurately from these data because sampling was not frequent enough to detect small differences.

The later start of the oviposition period, and the cooler temperatures at higher altitudes results in the eggs being at an earlier stage of their development. The later embryonic development at these sites can be assessed by examining the percentage of eggs with head capsules visible. Table 4.3 shows that this value decreases with increasing altitude. Head capsules were not present in any of the eggs in samples taken above 245m on 29 June. Only one was found in this final stage of development at 455m on 6 July and none at 520m.

Samples were also taken at 275m and 305m on 29 June 1978 (Appendix 4). The number of eggs, or eggs plus larvae, per floret at these two altitudes, and the maximum densities at the other six sites, are shown in Figure 4.2. There is a peak in the density at 335m, with 1.120 eggs per floret. Very few eggs were found at 520m. The density of eggs laid below 335m falls to 0.735 per floret at 245m and 0.287 per floret at 15m. The density of eggs at 275m was almost as high as that at 335m, with more than one per floret. This could indicate very heavy pressure on the food supply, especially as not all of the florets develop into seed capsules.

Figure 4.2 : The maximum density of eggs, or eggs plus larvae, of *Coleophora alticolella* at different altitudes in 1978, expressed as the number per floret of *Juncus squarrosus*


1·5
Eggs per floret
1·0
0·5
0·0
0
200
400
600
Altitude (m)

4.6 The rate of egg-laying

Although it is not possible to measure the length of the oviposition period from the data, with the accuracy desired, it is possible to estimate the rate of egg-laying at each altitude. This rate has been calculated assuming that the change in the density of eggs, as seen in Table 4.2, is linear with respect to time. In reality, a sigmoidal relationship would be expected, with fewer eggs being laid at the beginning and end, than in the middle, of the oviposition period. The data for the 15m site are more suggestive of this type of relationship.

The rate of egg-laying is the slope of the relationship between eggs per floret and time. For the purpose of the calculation of the regression coefficients, time is measured in days with 1 = 1 June 1978. The results of the linear regression analyses are given in Table 4.4. All of the data given in Table 4.2 were used in these calculations, except for the 520m site where four sample dates were used; the three with eggs present, and also 18 June when it is assumed that there were no eggs present.

The regression coefficients with their standard errors, given in Table 4.4, are measurements of the increase in the number of eggs per floret per day at each altitude. The highest rate was found at 335m, but this was also the site with the highest total density of eggs. The distribution of these rates with respect to altitude would have a similar pattern to that seen in Figure 4.2, for the maximum density of eggs at each site. This may be due to differences in the density of ovipositing adults, resulting in variations in the total daily egg production between sites. No measurements of the densities of ovipositing adults were made during this study. It is possible to make

Table 4.4 : *The results of least squares regression analysis to describe the relationship between the number of eggs per floret and time by the equation $y = bx + a$; y is the density of eggs per floret on each sample date x, measured in days with 1 = 1 June 1978*

Altitude (m)	*n*	*b* (eggs.floret^{-1}.day^{-1})	S.E. of *b*	*a*	*r*	*P*
15	5	0.0090	0.0021	+0.0718	0.926	<0.05
245	5	0.0281	0.0037	-0.1372	0.974	<0.01
335	7	0.0368	0.0020	-0.1988	0.993	<0.001
395	6	0.0312	0.0015	-0.2069	0.995	<0.001
455	6	0.0275	0.0014	-0.2419	0.980	<0.001
520	4	0.0055	0.0009	-0.1063	0.973	<0.05

some comparisons between sites by calculating the percentage of the total number of eggs laid per day, using the formula:

$$\% \text{ of total eggs laid per day} = \frac{b \times 100}{\text{maximum eggs per floret}}$$

These values are shown in Table 4.5.

Table 4.5 : *The rate of oviposition of* Coleophora alticolella *as a percentage of the total eggs laid at different altitudes each day*

Altitude (m)	% of total eggs laid per day
15	3.14
245	3.82
335	3.29
395	3.47
455	3.46
520	5.43

After correcting the oviposition rates to allow for the difference in the total density of eggs laid at each altitude, it can be seen that there is little difference in the percentage of the total eggs laid each day. Between 3% and 4% of the total were laid each day below 500m. These values imply that the oviposition period was about 25 to 33 days long at these sites. There was a slightly higher percentage rate at 520m and therefore a shorter oviposition period.

4.7 The median date of the oviposition period in relation to altitude

The mid-point, or median date, of the oviposition period at each altitude can be calculated by substituting y = ½max. density into the formulae in Table 4.4. These values are given in Table 4.6 and are measured in days after 31 May 1978; their equivalent calendar dates are also shown. These values will approximate to the mean date of oviposition at each altitude, if egg-laying is distributed normally with respect to time.

Table 4.6 : *The mid-point of the oviposition period at different altitudes calculated as the value of x when y = ½max. density, in the equations in Table 4.4. The equivalent calendar dates are also given*

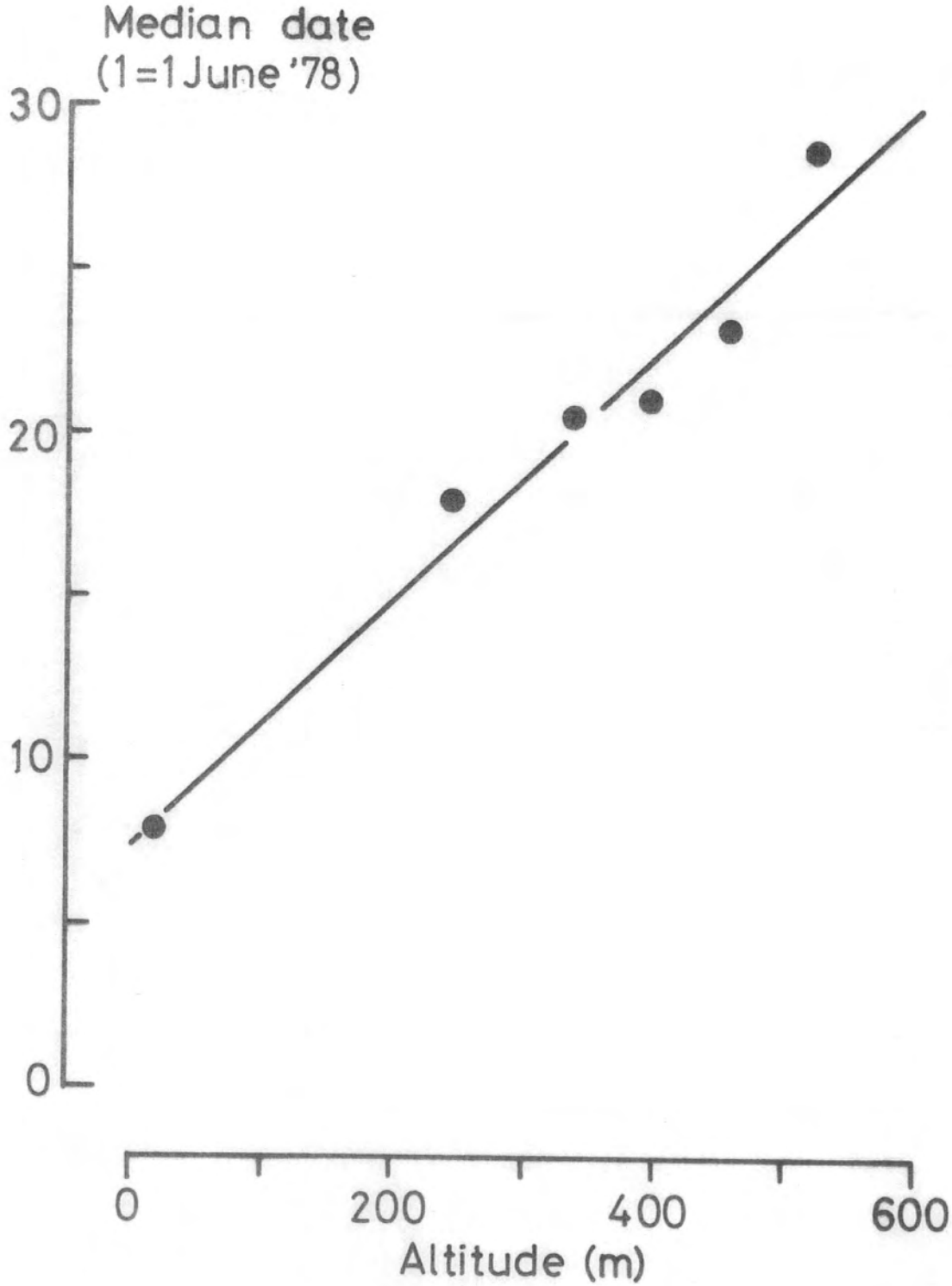
Altitude (m)	Mid-point of the oviposition period (1 = 1 June 1978)	Equivalent calendar date
15	8.0	8 June
245	18.0	18 June
335	20.6	21 June
395	21.0	21 June
455	23.2	23 June
520	28.6	29 June

Figure 4.3 shows the mid-points of the oviposition periods plotted against their corresponding altitudes. The trend shows that the oviposition period is delayed by 3.7 (± 0.3, S.E.) days for every 100 metre rise in altitude. This was equivalent to a delay of almost three weeks between 15m and 520m.

Figure 4.3 : The median date of the oviposition periods at different altitudes in 1978, measured in days with 1 = 1 June 1978. The regression line has been fitted by the method of least squares and has the formula

$$y = 0.037x + 7.697$$

$n = 6$, $r = 0.983$, $P<0.001$, S.E. of slope = 0.003


Median date
(1=1 June '78)
30
20
10
0
0
200
400
600
Altitude (m)

4.8 Oviposition behaviour in relation to food-plant development

Wood (1891) observed *Coleophora alticolella* females laying eggs on the inner surface of the perianth segments of *Juncus squarrosus* florets. This was confirmed by Jordan (1958), who added that eggs are also laid between adjacent florets. In another study on this species, Reay (1964) found that over 90% of the eggs were laid between adjacent florets. He commented that when oviposition sites were in excess it was rare to find more than one egg at a site, although he gave no data for this. Jordan (*loc. cit.*) suggests that the position where eggs are laid depends, to some extent, on the developmental stage of the floret at the time of oviposition. This aspect of oviposition behaviour is investigated by examining the change in the mean number of eggs per oviposition site in relation to the number of eggs per floret, and the development of the florets during the oviposition period.

4.8a The number of eggs per oviposition site

Despite Reay's comment, eggs are not infrequently laid in groups at oviposition sites (Table 4.1). The number of eggs at each site was recorded for the samples taken at 335m, 395m and 455m during the whole of the oviposition period. With the exception of the sample from 335m on 6 July, none contained newly hatched larvae, thus avoiding complications caused by dispersal from groups. The values for the mean number of eggs per oviposition site from all of the samples are given in Table 4.7.

If a female lays eggs randomly with respect to the oviposition sites, and with no regard to whether the site is already occupied, then the mean number of eggs per site will increase with the increase in the density of eggs laid. In addition, as eggs would be laid at sites

Table 4.7 : *The mean number of* Coleophora alticolella *eggs per oviposition site, with standard errors and sample sizes, at three altitudes on different dates during the oviposition period in 1978. The percentage of oviposition sites with more than one egg is also given*

Altitude (m)	Date	Number of eggs per oviposition site		Number of oviposition sites	% oviposition sites with more than one egg
		$\bar{x}$	S.E.	*(n)*	
335	7 June	1.200	0.088	45	13.3
	9 June	1.182	0.067	44	15.9
	15 June	1.286	0.039	91	26.4
	18 June	1.365	0.045	167	31.7
	22 June	1.414	0.046	203	33.0
	29 June	1.389	0.041	296	29.1
	6 July	1.310	0.033	364	23.6
395	9 June	1.125	0.039	32	12.5
	15 June	1.215	0.047	79	21.5
	18 June	1.327	0.051	113	29.2
	22 June	1.291	0.042	175	24.6
	29 June	1.258	0.040	209	19.1
	6 July	1.316	0.045	196	24.0
455	9 June	1.067	0.046	30	6.7
	15 June	1.133	0.051	45	13.3
	18 June	1.184	0.063	49	16.3
	22 June	1.316	0.060	95	25.3
	29 June	1.206	0.046	107	17.8
	6 July	1.297	0.048	155	23.9

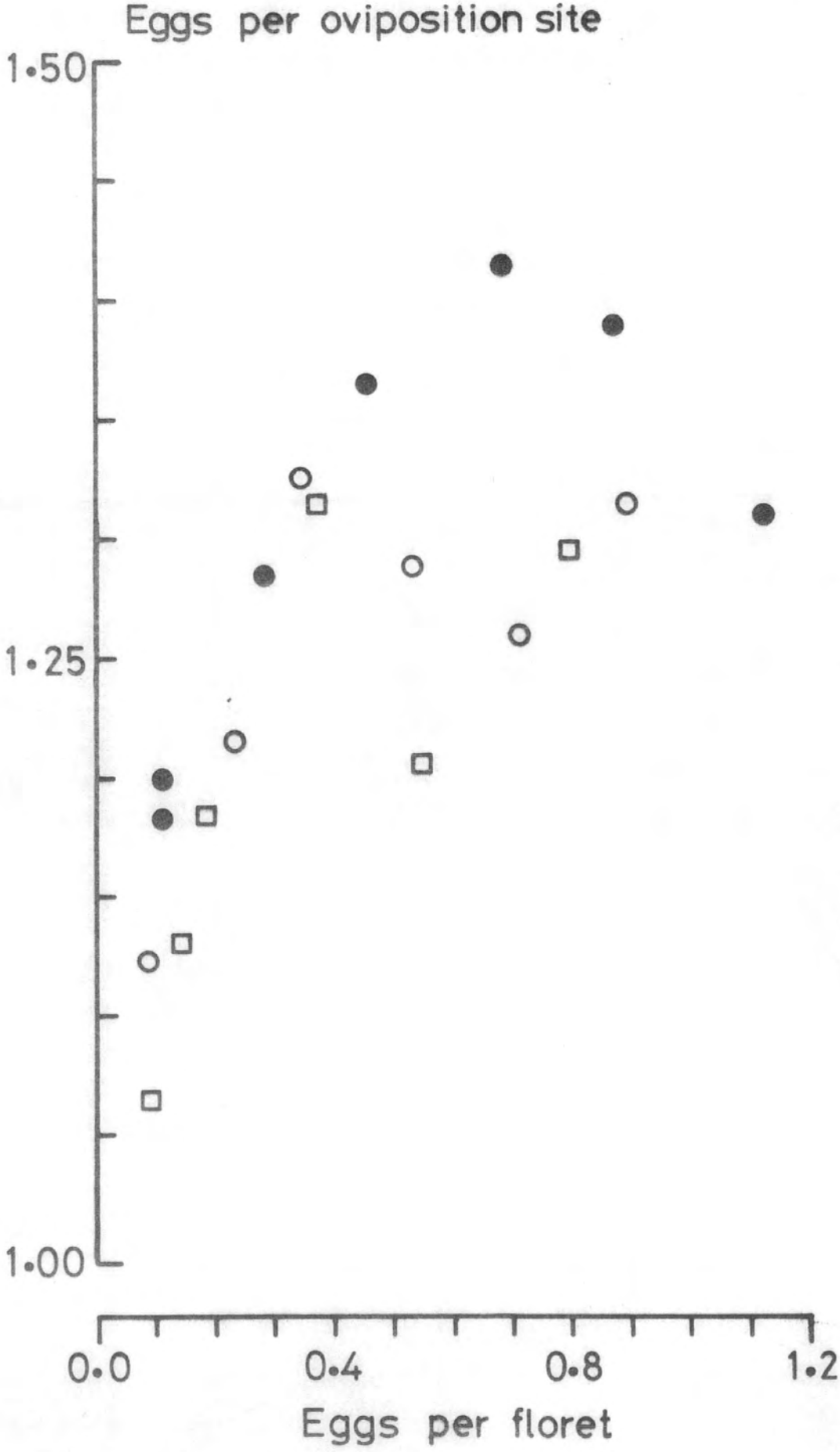
already occupied, the groups would contain eggs of different ages. If the females avoid sites where eggs are already present, then the mean number of eggs per site need not be related to the total density of eggs. However, the eggs in groups will all have been laid at the same time by the same female and will, therefore, be all of the same age.

The relationship between the mean number of eggs per oviposition site and the density of eggs per floret is shown on Figure 4.4. At the beginning of the oviposition period, when there are low egg densities, the mean number of eggs per oviposition site increases with the increasing density of eggs per floret. This increase is significant($P < 0.05$) at the three altitudes. The values from all three altitudes lie around a similar curve for this period, until they reach maxima on either 18 or 22 June. After these dates there is a tendency for a reduction in the mean number at each altitude. The majority of the values then remain between 1.25 and 1.4 eggs per site, despite the continued increase in the number of eggs per floret later in the season. Table 4.7 shows that the percentage of oviposition sites with more than one egg follows the same pattern, with an increase up to 18 or 22 June, followed by a decline.

4.8b The age of eggs in groups

All of the age-classes of eggs were present at the three altitudes on the last two sample dates during the oviposition period. The colour and position of all of the eggs in these samples was recorded. For the purpose of these analyses the 'orange-egg' age-class includes the few eggs with head capsules visible, when they occurred. Table 4.8 shows that when eggs were found in groups, they rarely contained more than one

Figure 4.4 : The mean number of eggs per oviposition site plotted against the number of eggs per floret in samples taken on different dates during the oviposition period at (○) 335m, (○) 395m and (□) 455m


Eggs per oviposition site
1·50
1·25
1·00
0·0
0·4
0·8
1·2
Eggs per floret

age-class. Some samples contained no mixed groups at all. The five mixed groups that were found each contained two eggs.

Table 4.8 : *The number of groups of eggs (i.e. oviposition sites with more than one egg present) and the percentage of groups containing more than one age-class, on the sample dates at three altitudes in 1978*

	Sample site					
	335m		395m		455m	
Date	No. of groups	% mixed	No. of groups	% mixed	No. of groups	% mixed
29 June	83	3.6	40	2.5	19	0.0
6 July	86	0.0	47	2.1	37	0.0

The detection of the mixed groups will depend on the duration of the different age-classes. If the first two age-classes are very short, then mostly orange eggs will be present; a site may then contain different-aged orange eggs which would be indistinguishable. Table 4.9 gives the number of eggs of each age class in the six samples and the number of florets present. This table shows that there were similar numbers of yellow and orange eggs in each sample, but fewer white ones. These data can be used to estimate the age of orange eggs.

By calculating the number of orange eggs per floret in each sample and substituting this measurement of density into the appropriate equations in Table 4.4, an approximation can be made to the date when the last orange egg was laid. By subtracting these values from the sample dates, the time taken for the eggs to turn orange is obtained.

Table 4.9 : *The number of each age-class of eggs and the number of florets in samples of* Juncus squarrosus *taken on two dates at three altitudes during the oviposition period in 1978. (The orange class at 335m on 6 July includes 10 newly hatched larvae)*

Altitude (m)	Date	White	Yellow	Orange	Florets
335	29 June	65	153	193	475
	6 July	22	189	266	426
395	29 June	59	107	97	371
	6 July	6	144	108	287
455	29 June	15	68	46	239
	6 July	6	98	97	253

All of these values are given in Table 4.10, which shows that it takes approximately two weeks for an egg to turn orange after it has been laid.

Any eggs laid in the two weeks after the last orange eggs would still be either yellow or white. This includes the period when the mean number of eggs per floret is still increasing, as this phase did not end until 18 or 22 June. If this rising phase was caused by females laying at sites that were already occupied, then mixed groups could have been detected and would occur more frequently than observed.

Table 4.10 : *The time taken (in days) for eggs to turn orange, calculated from two samples at each of three altitudes (see text for methods)*

Altitude (m)	Sample date	Laying date of the last orange egg in each sample (1 = 1 June)	Time taken for eggs to turn orange (days)
335	29 June	16.4	12.6
	6 July	22.4	13.6
395	29 June	15.0	14.0
	6 July	18.7	17.3
455	29 June	15.8	13.2
	6 July	22.7	13.3

Table 4.11 gives an example of the distribution of the different-aged eggs in oviposition sites, based on the data from the 335m site on 6 July. This table shows that most of the groups of eggs were of the oldest age-class. 36% of the oviposition sites with orange eggs contained more than one egg, whereas none of the sites with white eggs had more than one. All of the orange eggs present in this sample had been laid on or before 22 June, which was the sample date with the maximum number of eggs per oviposition site at this altitude. The reduction in the mean number of eggs per oviposition site after this date was caused by the later eggs being laid in smaller groups until, at the end of the oviposition period they were laid singly. The distribution of the different-aged eggs at the other sites followed the same pattern.

Table 4.11 : *The frequency of different-sized groups of eggs at oviposition sites, separated for each age-class. The data are from 335m on 6 July 1978*

Eggs per oviposition site	1	2	3	4	5	% of sites with more than one egg
White	22					0.0
Yellow	142	19	3			13.4
Orange	114	46	13	4	1	36.0

The mean number of eggs per oviposition site was calculated for each age-class separately, for the three altitudes on 6 July. The results of these calculations are given in Table 4.12; the few mixed groups have been omitted from the calculations. This table shows that the mean number of eggs per oviposition site increases with increasing age of eggs, all of the white eggs having been laid singly. The difference between the means for orange and white eggs was significant ($P < 0.001$) at all altitudes.

Competition between newly-hatched larvae for a food supply could be avoided if an ovipositing moth lays eggs singly at an oviposition site, and avoids sites that are already occupied. *Coleophora alticolella* does lay most of its eggs singly at oviposition sites. When they are in groups, they are very close together and usually of the same age, indicating that they had been laid at the same time and probably by the same female. It was mostly the older eggs which had been laid in groups, with an increase in the mean number of eggs per site only up until the middle of the oviposition period. This was followed by a period when the change in the mean number of eggs per site was not related to the total density

of eggs present. This change in the number of eggs laid at a site may be caused by the inability of females to control the number of eggs laid on each oviposition attempt.

Table 4.12 : *The mean number of different-aged eggs per oviposition site on the last sample date during the oviposition period at three altitudes in 1978. The orange eggs are the oldest and the white are the youngest; n is the number of sites with each age-class of eggs*

Altitude (m)		Age-class White	Yellow	Orange	Difference between orange and white t	P
335	$\bar{x}$	1.000	1.152	1.494		
	S.E.	0.000	0.032	0.058	8.517	<0.001
	n	22	164	178		
395	$\bar{x}$	1.000	1.233	1.466		
	S.E.	0.000	0.051	0.073	6.384	<0.001
	n	6	116	73		
455	$\bar{x}$	1.000	1.210	1.426		
	S.E.	0.000	0.049	0.090	4.733	<0.001
	n	6	81	68		

The females of some *Coleophora* species lay most of their eggs in the first few days after fertilization. Quednau (1967) found that *C. laricella* (Hbn.) layed 57% of their eggs within three days after copulation. Coshan (1974) found that *C. serratella* had a similar pattern

of egg-laying, with the highest daily rate on the second day after copulation. This resulted in the oviposition period corresponding closely with the adult emergence period. If this also applies to *Coleophora alticolella*, then it could be suggested that the occasional site with a group of eggs is the result of a female producing eggs in this period at a faster rate than she is able to search for suitable unoccupied sites, and so having to lay several eggs at once. The tail-off in the mean number of eggs laid at oviposition sites later in the season could then be due to more searching time being available between the production of each egg later in adult life. The increase in the mean number laid per site would be related to the overall density of eggs at each altitude since fewer suitable sites would be available at the high egg densities. It would be expected that when suitable sites are in excess, such as at the beginning of the egg-laying period, females could find sufficient to enable them to lay all of their eggs singly.

So far it has been assumed that the number of potential sites on an inflorescence is constant throughout the oviposition period and, as the density of eggs increases, so they are used up. If, however, the number of suitable sites is not constant, but increases during the egg-laying period, then competition would decrease. A change in the structure of the inflorescence during its growth and development could result in an increase in the number of sites where eggs could be laid. The degree of coincidence between the oviposition period and the flowering of the food-plant could then be responsible for the changes in the distribution pattern of the eggs.

4.8c The development of *Juncus squarrosus* during the oviposition period

During the oviposition period the *Juncus squarrosus* florets are developing and opening to allow fertilization (see Section 3.4). The percentage of the florets that has been open by each sample date at the three altitudes is shown in Figure 4.5. There is an increase in the percentage opening during the oviposition period, with the 50% level reached around 20 June. These values are a guide to the increase in the spatial complexity of the inflorescences. As the florets develop and open, more oviposition sites become available.

At the end of the oviposition period, when most of the florets had opened, some of the eggs were found to have been laid inside the perianth, next to the ovary. This is an oviposition site that is unavailable earlier in the season. Eggs in this position were always laid singly. Up to 50% of the white eggs in the last two samples were laid inside the florets (Table 4.13). The increase in the percentage of yellow eggs inside the florets on the second of the two sample dates in this table is due to ageing of these white eggs.

4.8d Conclusions

Although the number of oviposition sites is related to the number of florets on an inflorescence, the developmental stage of the florets determines the availability of the sites. In the first part of the egg-laying period, the florets were small and closely packed together. As the density of the eggs increased, the suitable sites were used up and some of the eggs were laid in groups. After the date when about 50% of the florets had opened, the mean number of eggs per oviposition site no longer increased with increasing egg density. Eventually, when most of

Figure 4.5 : The percentage of *Juncus squarrosus* florets that had been open in samples taken on different dates during the oviposition period at

a. 335m

b. 395m

c. 455m

Time is in days with 1 = 1 June 1978

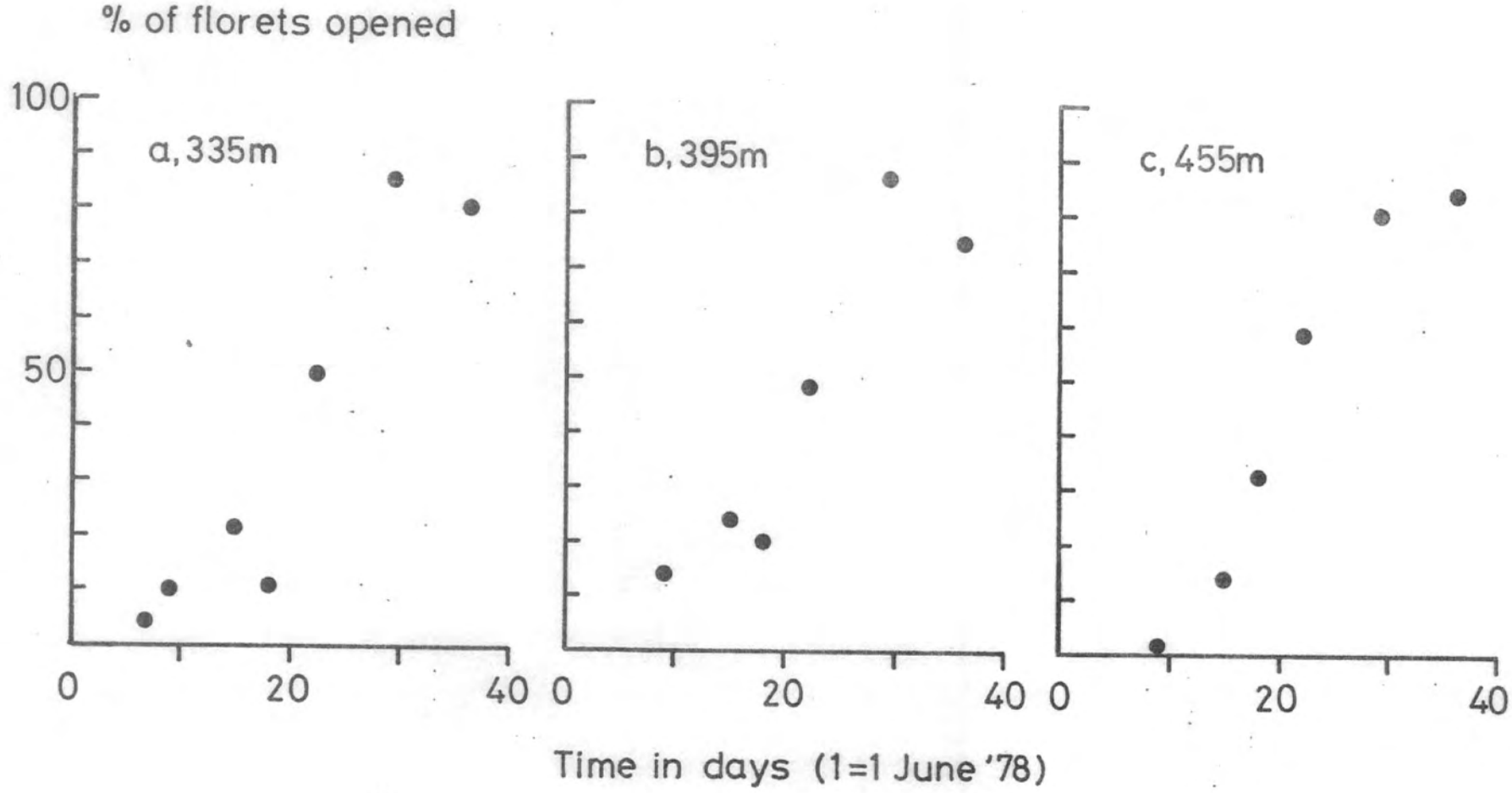

% of florets opened
100
50
a, 335m
b, 395m
c, 455m
0
20
40
0
20
40
0
20
40
Time in days (1=1 June '78)

Table 4.13 : *The percentage of each age-class of eggs found inside the* Juncus squarrosus *florets. Data from samples collected on two dates at 335m and 455m, and once at 395m. The total number of eggs in each age-class is also shown (n)*

Sample Site	Date	White		Yellow		Orange	
		n	%	*n*	%	*n*	%
335m	29 June	65	24.6	153	5.2	193	0.0
	6 July	22	50.0	189	7.9	266	0.0
395m	29 June	-	-	-	-	-	-
	6 July	6	50.0	144	13.9	108	0.0
355m	29 June	15	33.3	68	5.9	46	0.0
	6 July	6	33.3	98	7.2	97	0.0

the florets had opened, there was an excess of oviposition sites and all of the eggs could, once again, be laid singly at each site.

The extent to which the emergence of adults is synchronized with the development of the food-plant will determine the amount of competition for suitable oviposition sites, particularly at high densities of ovipositing adults. If suitable sites become available at a faster rate than they are used up, then all of the eggs could be laid singly. It is also possible that the rate of maturation of eggs by individual females could contribute to the increase in the mean number of eggs per site, if the places where eggs can be laid are in short supply during the first few days after copulation. However, there are, at present, insufficient data to test this hypothesis.

4.9 The effect of inflorescence density on oviposition behaviour

The distribution of *Juncus squarrosus* plants in a sward is not uniform, but is composed of a series of distinct patches (Kershaw and Tallis, 1958; Welch 1966a). Between each of these patches the density of the inflorescences may vary, resulting in a heterogeneous stand. The effects of this heterogeneity in the density of inflorescences, on the oviposition behaviour of *Coleophora alticolella* were investigated. This was done by setting up experimental plots, with different densities of inflorescences, at two of the sample sites.

4.9a Methods

At the beginning of June 1978, three permanent quadrats were staked out at both the 335m and 455m sample sites. These quadrats measured 2m by 2m, and were widely separated from each other. Within these areas, the density of the *Juncus squarrosus* inflorescences was modified. This was done by cutting away inflorescences to leave known densities of $20m^{-2}$, $40m^{-2}$ and $80m^{-2}$; the inflorescences that were left were distributed over the whole of each quadrat. The $80m^{-2}$ quadrat was situated in an area with a slightly higher density of inflorescences than the mean for the whole sample site, to ensure that there were sufficient for the experiment. This was an increase of 7 inflorescences per m^2 at 335m and 2 per m^2 at 455m. Both of these differences were within the 95% confidence limits for the overall densities.

In addition to these quadrats, at 455m two clumps each containing 20 inflorescences were isolated in separate $1m^2$ quadrats, with all other inflorescences removed. These two small quadrats were separated both from each other, and the three larger experimental plots. Although these two small quadrats had the same overall density as the

low-density plot described above, the distribution of the inflorescences within the quadrats was different. The $20m^{-2}$ plot had inflorescences widely distributed over the whole of each square metre, but the clumped plots had the same number of inflorescences in a much smaller area, resulting in a very high within-clump density. The circumference of each clump was measured, thus enabling the calculation of the density of the inflorescences contained, assuming that both clumps were circular. These measurements are given in Table 4.14. Inflorescences were harvested from all of the experimental plots on 29 June, near the end of the oviposition period.

Table 4.14 : *The circumference and area of two clumps of* Juncus squarrosus, *each containing 20 inflorescences, at the 455m sample site; the density of inflorescences within each clump is also given*

Clump	Circumference (m)	Area (m^2)	Density of inflorescence within each clump (m^{-2})
A	1.4	0.1560	128.2
B	1.2	0.1146	174.5

4.9b Results

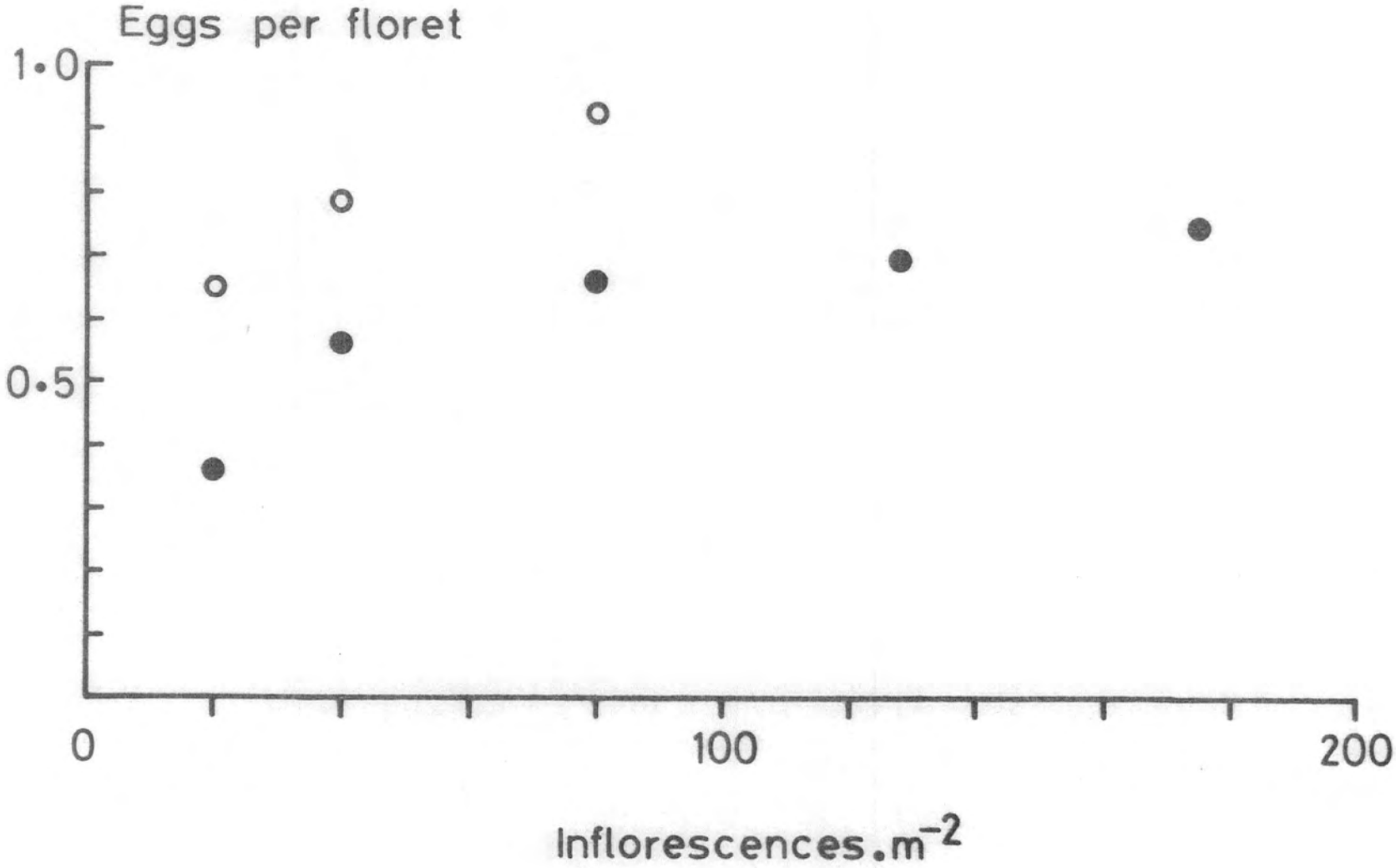
It can be seen from the data presented in Table 4.15 that there is an increase in the density of eggs per floret with increasing density of inflorescences at both altitudes. The values for the 335m site are higher than those at 455m for corresponding densities. This is expected because the final densities of eggs in the random samples was greater at the lower of the two altitudes (Table 4.2).

Table 4.15 : *The number of* Coleophora alticolella *eggs per floret of* Juncus squarrosus *in samples taken from plots of different densities of inflorescences on 29 June 1978. The values for the background densities have been calculated from the random samples taken on the same date, and are shown with 95% confidence limits*

Altitude	Inflorescence density (No_s per m^2)	Number of inflorescences examined	Eggs per floret
335	20	20	0.650
	40	20	0.786
	80	20	0.925
Background -	73.6 ± 20.5	30	0.865
455	20	30	0.362
	40	30	0.559
	80	30	0.665
Clump A -	128.2	20	0.699
Clump B -	174.5	20	0.749
Background -	78.0 ± 15.3	20	0.540

The relationship between eggs per floret and inflorescence density is not linear, but there is an increase in the density of eggs up to an asymptote (Figure 4.6). This feature is more apparent for the samples taken at 455m, where there was a greater range of densities, and the asymptote is lower. The values given in Table 4.15 for the background densities at both of the sample sites, calculated from the random samples on the same date, do not fit into this pattern because of this non-linear relationship.

Figure 4.6 : The density of *Coleophora alticolella* eggs per floret of *Juncus squarrosus* at different densities of inflorescences. Data are from samples collected on 29 June 1978 at 335m (O) and 455m (O)


Eggs per floret
1·0
0·5
0
100
200
Inflorescences.m^{-2}

If each inflorescence is considered as a patch of prey (oviposition sites or florets), and if the ovipositing females travel between inflorescences at the same speed, then in areas with a high inflorescence density less time will be spent in transit from one to another. Consequently, in the areas with higher densities more time will be available for searching and ovipositing within an inflorescence. It is possible to calculate the expected mean distance between an inflorescence and its nearest neighbour in a random distribution, if the density of inflorescence in an area is known, by using the formula of Clarke and Evans (1954).

$$E(\bar{r}) = \frac{1}{2\rho^{\frac{1}{2}}}$$

where $E(\bar{r})$ is the expected mean distance to nearest neighbours and ρ the mean density per unit area. The values for $E(\bar{r})$, in metres, for the densities under consideration are given in Table 4.16.

Table 4.16 : *The expected mean distance between nearest neighbours calculated from the density of inflorescences in the different experimental plots*

Inflorescences per m^2	$E(\bar{r})$ in metres
20	0.1118
40	0.0791
80	0.0559
128.2	0.0442
174.5	0.0378

Figure 4.7 shows the number of eggs per floret plotted against the calculated mean nearest neighbour distances for the different density quadrats. There is no significant difference between the regression coefficients for the two altitudes ($t = 0.345$ with 4 degrees of freedom). The regression coefficient for the 335m sample site is not significantly different from zero at the 5% probability level, but as only three data points were available to calculate this regression and 99% of the variation is explained, the relationship is considered to be representative of the real situation.

These graphs show that the number of eggs laid per floret is inversely proportional to the distance between neighbouring inflorescences. The greater the distance between inflorescences, the more time must be spent travelling, and searching for them. The fact that the slopes of the lines are so similar suggests that the travelling and searching behaviour of the female moths, with respect to the distribution of inflorescences, is the same at both altitudes.

The intercept on the y axis represents the upper asymptote when the data is expressed as in Figure 4.6. This would occur when the transit time between inflorescences is zero, that is, at an infinitely high inflorescence density. The intercept on the y axis for the 335m site is the higher of the two because of the higher densities of eggs in the samples from this altitude.

4.10 Discussion

The rate of egg-laying at any site is related to the total density of eggs laid, and hence the density of ovipositing adults. When a correction for this factor was made, no relationship was found between the oviposition rate and altitude. Although the length of the

Figure 4.7 : The density of *Coleophora alticolella* eggs per floret of *Juncus squarrosus*, in relation to the expected mean distance between individual inflorescences in the different density plots. Data are taken from samples collected on 29 June 1978 at 335m (O) and 455m (○). The straight lines were fitted by the least squares linear regression method, with x as the distance between inflorescences and y the density of eggs.

335m

$$y = 1.1876 - 4.8696x$$

$n = 3 \quad r = -0.9946 \quad 0.05 < P < 0.10$

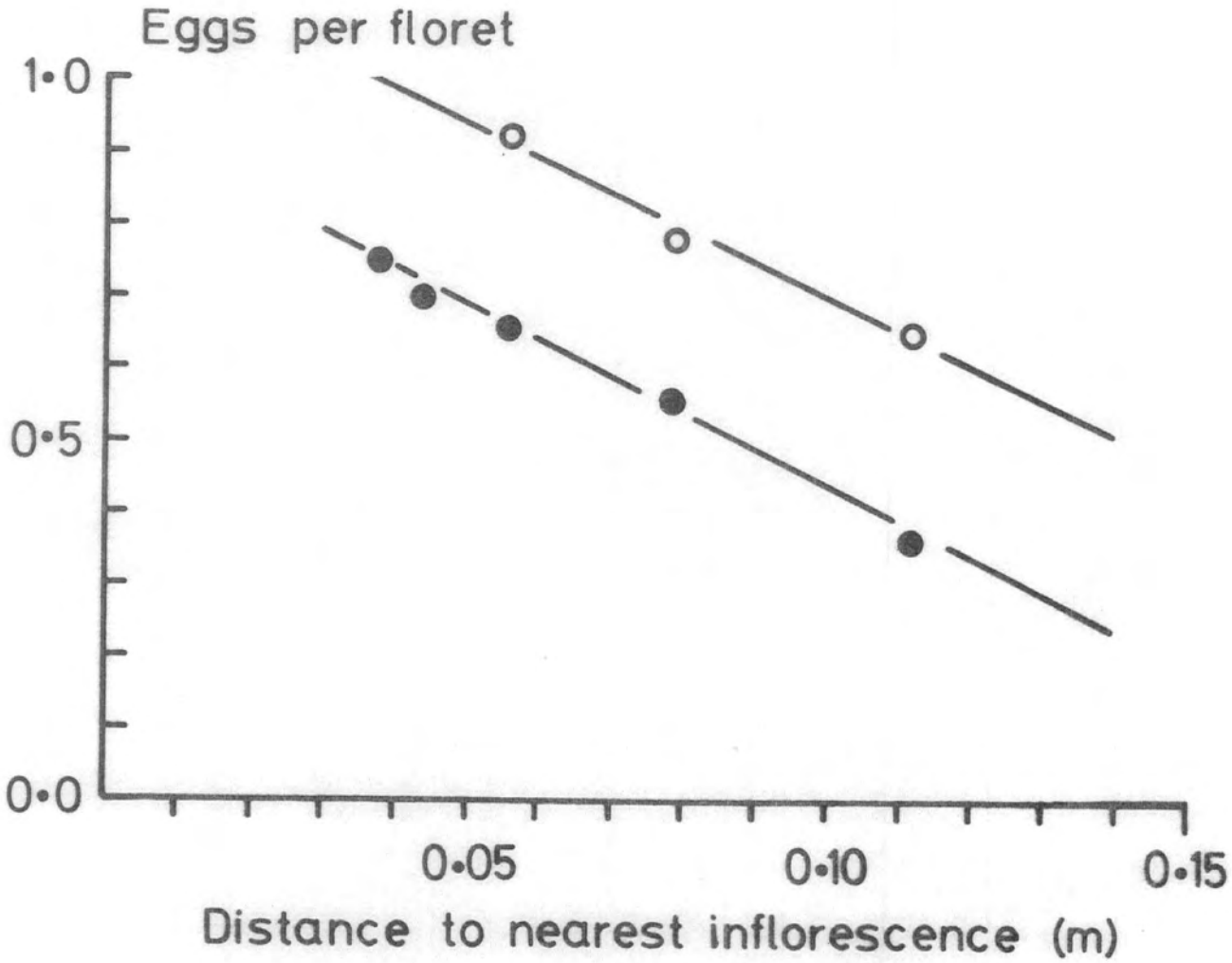
S.E. of slope = 0.5087

445m

$$y = 0.9399 - 5.0655x$$

$n = 5 \quad r = -0.9953 \quad P < 0.001$

S.E. of slope = 0.2847


Eggs per floret
1·0
0·5
0·0
0·05
0·10
0·15
Distance to nearest inflorescence (m)

oviposition periods did not vary with altitude, the date of the mid-point at each site was directly related to altitude. This could have been due to the adult moths emerging at progressively later dates under the cooler climatic regimes at the higher altitudes. Coulson *et al.* (1976), working on the annual life-cycles of two species of Tipulidae at various altitudes in this region, found that adult emergence was delayed at higher altitudes. They related this delay to the cooler climatic conditions affecting pupation. Both of these species of tipulid emerge in May and June, at a similar date to *Coleophora alticolella*. The emergence of *Molophilus ater* Meigen was delayed by about 7 days over a 300 metre increase in altitude, and *Tipula subnodicornis* Zett. by 11 days over the same altitudinal range. These values are similar to the delay in the oviposition period of *Coleophora alticolella*, which was 11.1 days per 300 metre rise.

These three species of insect have a quiescent phase during the winter months which for *Coleophora alticolella* is a true diapause. Diapause serves to synchronize all of the individuals at one developmental stage, by allowing the larvae at an earlier stage of development to catch up with those that are fully grown.

Photoperiod is a stimulus which is frequently used for the maintenance of diapause by insects. Many northern species are released from diapause by mid-winter, but the lower thermal thresholds for the start of post-diapause development are often higher than the environmental temperatures at this time. This can lead to a break between the end of diapause and post-diapause development (Tauber and Tauber 1976). Since all of the sites used in this research were at approximately the same latitude, *Coleophora alticolella* would be released from diapause on about the same date at each. However, the lower temperature threshold for recommencing development would be reached at a later date at the

higher altitudes. In addition, the lower temperatures at the higher sites would cause slower development during the pre-pupal and pupal stages. This results in the delayed emergence of imagos at higher altitudes. This delay is, however, advantageous because it enables the moth to be synchronized with the development of its food-plant.

When the eggs are being laid, there is apparently no way of telling which of the florets will develop into seed capsules. *Juncus squarrosus* is wind-pollinated (Welch 1966a) and so the adult moths cannot ensure its fertilization, as happens in the relationship between the yucca moth *Tegiticula yuccasella* (Riley) and its host plant *Yucca* spp.; or between the noctuid moth *Hadena bicruris* Hufn. and its larval food-plant, the white campion *Silene alba* (Mill.) (Brantjes 1976). In order to avoid competition between newly hatched larvae, and to ensure that at least some of the larvae find themselves on a floret that has developed seed, it would be advantageous for the *Coleophora alticolella* eggs to be distributed regularly with respect to the florets.

Overdispersion of eggs has been reported for other species of *Coleophora*. The distribution of the eggs of *C. laricella*, with respect to the needles of the western larch (*Larix occidentalis* Nutt.), has been studied in Idaho by Brown and Kulhavy (1978a). They found that 94% of the infected needles had one egg, 5.8% had two eggs and only 0.2% had more than two. *C. serratella* has a preponderance of single egg clutches on the leaves of birch (*Betula* spp.) (Coshan 1974). *C. alticolella* also lays single egg clutches and the majority of the oviposition sites have only one egg. But during the first half of the egg-laying period suitable oviposition sites are in short supply, which leads to an increase in the mean number of eggs per site as the total density increases. As the *Juncus squarrosus* florets open, more sites become available and fewer eggs are laid in groups.

Lawton (1978) has shown that the architecture of a plant can change as it develops. This alters the number of niches available to phytophagous insects. He suggests that this increase in spatial complexity of a plant could account for the increase in the diversity of species feeding on it, during the season. Increase in the spatial complexity is also responsible for changes in the egg-laying behaviour of *Coleophora alticolella*. This confirms Jordan's (1958) suggestion that the oviposition behaviour is affected by the developmental stage of the food-plant.

The density of eggs per floret changes with altitude, and is related to the density of ovipositing moths. Within one altitude site, there may be variation in the density of eggs, depending on the distribution of the *Juncus squarrosus* inflorescences. Areas with a lower density of inflorescences than the background density for the whole sward had fewer eggs per floret; areas with a comparatively high density of inflorescences had greater numbers of eggs per floret. The relationship between eggs per floret and inflorescence density was not linear, but increased to an asymptote. The number of eggs per floret for each density plot was indirectly related to the expected mean distance between nearest inflorescences.

Murdoch and Oaten (1975) have shown that, for predator-prey models when prey are distributed in spatially-separated patches, predators must spend time travelling from patch to patch, which could otherwise be spent searching for prey within a patch. Oaten (1977) has shown that this transit time is important in the stabilizing properties of the functional response. His model suggests that with high prey density within patches, less time must be spent travelling from patch to patch.

Hassell and May (1974) have discussed an aggregative response in predator-prey models; with a given predator staying in areas of high prey density for longer periods of time, and hence more predators occurring in these high density regions, at any instant of time.

There was little variation in the number of florets, and hence oviposition sites, per inflorescence of *Juncus squarrosus*, both within and between different density plots at the same altitude. Also the response of an individual female *Coleophora alticolella* to different densities of florets per inflorescence is not known, nor the density of adults searching in each plot. Consequently, it was not possible to test if *C. alticolella* behaves as a typical predatory or parasitic insect in its oviposition behaviour. However, the time that would have to be spent travelling between inflorescences in different densities of *Juncus squarrosus* seems to have a significant effect in limiting the number of eggs laid per floret.

CHAPTER 5

STUDIES ON THE LARVAE OF *COLEOPHORA ALTICOLELLA*

5.1 Introduction

From measurements of the head capsules, Jordan (1958) established that *Coleophora alticolella* has four larval instars. Similar measurements were made during this study and the mean head width of each instar was found not to differ significantly from Jordan's results.

The larvae feed on the seeds of *Juncus squarrosus* during the period of July to October. They hatch from eggs laid on the outside of the seed capsules and burrow through the pericarp to gain access to the seeds, at the beginning of the first instar. The first three instars are spent inside the initial seed capsule and Jordan *(loc. cit.)* found that this period lasted about six weeks in favourable conditions. Towards the end of the third instar or at the beginning of the fourth, each larva starts to construct a papery case (as shown in Plate I). This it carries around whilst searching for more food, having eaten the contents of its initial capsule. The larval case is impervious to water (Sich 1926) and Jordan (1958) suggested that this would prevent waterlogging; likewise it could protect the larva from desiccation whilst exposed on the outside of the capsules.

Jordan *(loc. cit.)* found that the larvae ate, on average, the contents of 2.3 seed capsules during their development. He also showed that they spent about three weeks feeding after they had produced their cases.

After feeding is completed, the larvae move down to the leaf-litter in order to pass the winter in diapause, although overwintering larvae are occasionally found adhering to the vegetation. This movement

of larvae to the ground layer in the autumn is referred to as larval migration; this is not to be equated to emigration from the population. The migrating larvae are still within the same population at each site; only their location has changed.

In this chapter, the larval density and distribution is examined in relation to the seed capsules at different altitudes. Survival, between the egg stage and larval establishment inside the food supply, is shown to be mainly dependent on the proportion of florets developing into seed capsules. The effect of this on the altitudinal distribution of the larvae is also discussed. In addition, larval development was measured in relation to altitude and the production of cases and their subsequent migration has been investigated.

5.2 Larval density in relation to the food supply

Larval density was measured over the whole transect in the August of each year. By this time, all of the eggs had hatched and the larvae had become established inside the seed capsules. Most of the larvae had grown and were second or third instars; this facilitated counting of individuals because the first larval instars were very small and easily overlooked. On the other hand, the larvae were not so far advanced as to have produced cases and moved from their initial seed capsule. (A summary of these results is given in Appendix 5.)

Samples were taken on 9, 10 and 11 August in 1977, and in 1978 on 10 and 11 August. In 1979 the larvae were later in developing and samples were collected on 23 and 24 August.

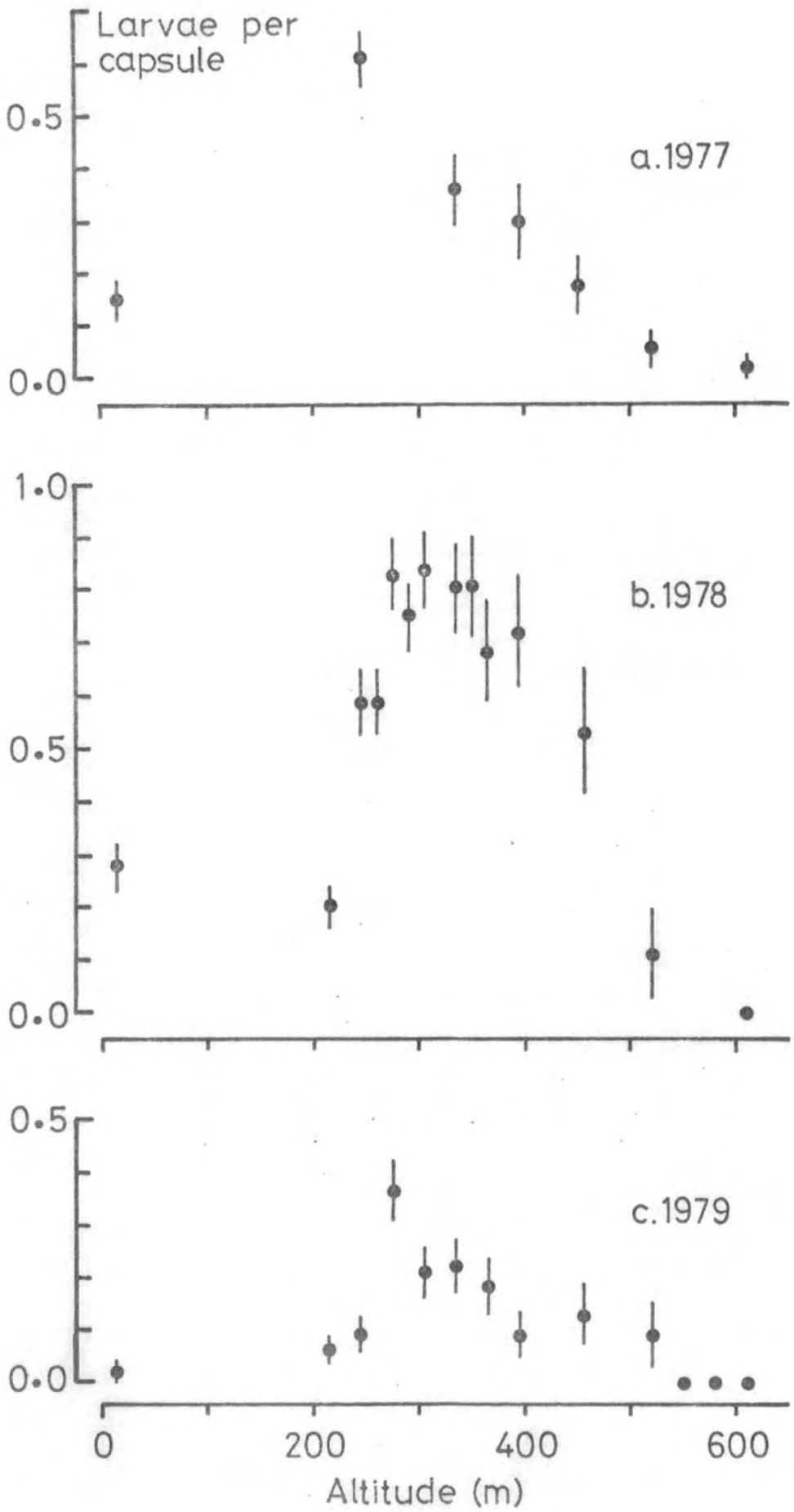
Figure 5.1 shows the mean number of larvae per seed capsule, with 95% confidence limits, at the different altitudes in the August of each year. These data show the relationship between the *Coleophora*

Figure 5.1 : The density of *Coleophora alticolella* larvae per seed capsule of *Juncus squarrosus* at different altitudes in August of the three years of this study. The mean values are shown with 95% confidence limits:

a. 1977

b. 1978

c. 1979


Larvae per capsule
0.5
0.0
a.1977
1.0
0.5
0.0
b.1978
0.5
0.0
c.1979
0
200
400
600
Altitude (m)

alticolella larvae and their food supply, and not the number per unit area of ground, an aspect which is covered whilst discussing the population dynamics in Chapter 7.

In 1977 the peak of larval density was at 245m, with a mean (± 95% confidence limits) of 0.614 ± 0.053 larvae per capsule (Figure 5.1a). Some larvae were found at 610m in 1977, but only at very low densities. The value for this site, shown in Figure 5.1a, is from two larvae in a sample of 30 inflorescences.

Samples were collected from many more sites in 1978. In this year the peak of larval density was between 275m and 350m, often with more than 0.8 larvae per capsule (Figure 5.1b). No larvae were found above 520m. Larval density was reduced below 275m, but did not reach zero; there was a mean of 0.278 ± 0.045 larvae per seed capsule at 15m.

1979 was characterized by very low larval densities. Again the peak densities were found at the middle altitudes (Figure 5.1c). The highest value was at 275m with 0.361 ± 0.057 larvae per capsule; the only other sites with more than 0.2 larvae per capsule were 305m and 335m.

To summarize the data shown in Figure 5.1, larval density in relation to the food supply was highest at the middle altitudes, falling to zero above 520m in 1978 and 1979, but with a few larvae at 610m in 1977. At the lowest altitude larval densities were low, but they were never reduced to extinction. Generally, densities in 1978 were the highest, and in 1979 the lowest (although there was no significant difference between the values for the 520m site). Most of the values for the 1977 sample season lay between those for the other two years.

5.3 Larval distribution in relation to the seed capsules

Samples taken in August 1978 were used to study the dispersion of the larvae in order to discover if they aggregated in successful seed-producing capsules. These samples had the highest densities of larvae and also the greatest range of different densities. Consequently, if crowding was to occur, it should be most evident in these conditions.

It is possible to test if a distribution departs from randomness by comparing its mean and variance. In a Poisson distribution, $s^2/\bar{x}$ is unity; a value significantly greater than one implies aggregation, and overdispersion is indicated by a value significantly less than one (Southwood 1966). This coefficient of dispersion can be tested with the formula:

$$\chi^2 = \frac{s^2 (n-1)}{\bar{x}}$$

where s^2 is the variance, n the number of sample units (in this case seed capsules) and $\bar{x}$ the mean number of larvae per seed capsule.

Table 5.1 gives the values for the coefficients of dispersion and the results of the χ^2 tests of the Null Hypothesis that the coefficients are not significantly different from unity.

All of the values for the coefficients of dispersion are less than unity, even at sites with more than 0.8 larvae per seed capsule. Below 500m the larvae were significantly overdispersed with respect to the capsules. There are fewer capsules with more than one larva, and fewer unoccupied capsules, than would be expected from a Poisson distribution with the same mean value at each site.

Although the larvae were overdispersed, some sharing of seed capsules did occur. Table 5.2 gives the number and percentage of larvae in each sample that were sharing capsules. These percentages are less

Table 5.1 : *The coefficients of dispersion of the* Coleophora alticolella *larvae in relation to the seed capsules of the food plant at different altitudes in August 1978. The results of* χ^2 *tests of the Null Hypothesis that the coefficients are not significantly different from unity are also given*

Altitude (m)	Larvae per seed capsule *(x)*	Coefficient of dispersion $s^2/\bar{x}$	Number of seed capsules *(n)*	χ^2 (*n*-1 d.f.)	*P*
15	0.278	0.789	432	340.1	<0.001
215	0.202	0.821	426	348.9	<0.001
245	0.592	0.606	360	217.6	<0.001
260	0.590	0.552	332	172.8	<0.001
275	0.829	0.427	350	149.0	<0.001
290	0.750	0.450	320	143.6	<0.001
305	0.839	0.419	286	119.4	<0.001
335	0.807	0.540	228	122.6	<0.001
350	0.817	0.538	241	129.1	<0.001
365	0.685	0.573	181	103.1	<0.001
395	0.723	0.613	148	90.8	<0.001
455	0.530	0.659	100	65.2	<0.001
520	0.111	0.889	54	47.1	Not significant

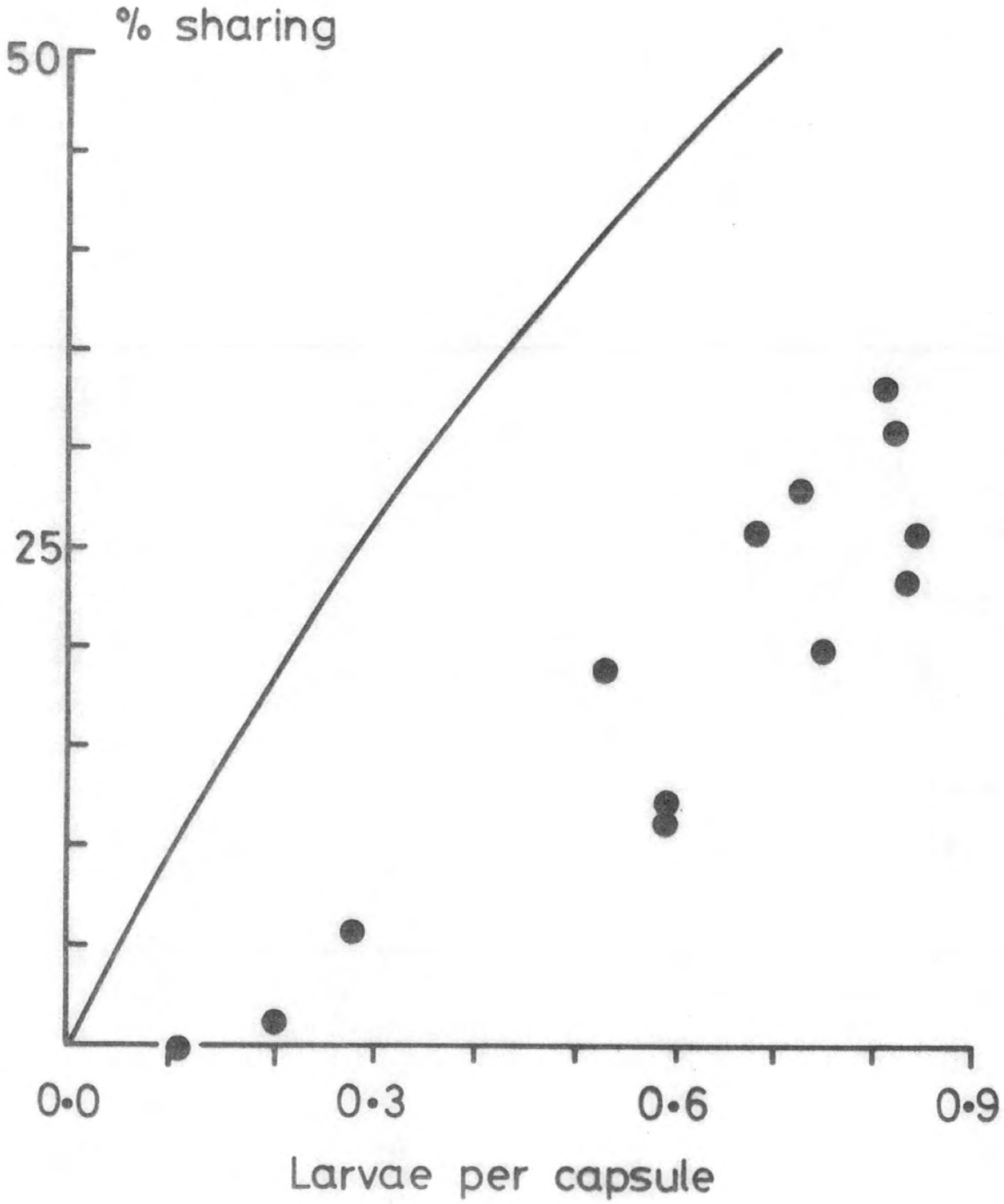
than would be expected from a Poisson distribution, but even so, in some samples over 30% of the larvae were inside capsules with one or more other individuals. The incidence of this crowding inside seed capsules is a density-related phenomenon, as can be seen from Figure 5.2. This graph shows that at high densities of larvae per seed capsule the percentage of larvae sharing the food supply increases.

Table 5.2 : *The total number of* Coleophora alticolella *larvae in each sample taken in August 1978; and the number and percentage of these larvae found to be inside seed capsules with other individuals*

Altitude (m)	Total larvae	Larvae sharing a seed capsule	% sharing
15	120	8	6.7
215	86	2	2.3
245	213	26	12.2
260	196	22	11.2
275	290	68	23.4
290	240	48	20.0
305	240	62	25.8
335	184	61	33.2
350	197	61	31.0
365	124	32	25.8
395	107	30	28.0
455	53	10	18.9
520	6	0	0.0

Both the eggs and the larvae of *Coleophora alticolella* are overdispersed on the food-plant. The newly hatched larvae are very small in relation to the structure and dimensions of the inflorescence, and probably have a very limited mobility. This reduces their ability to significantly alter their distribution pattern at this early stage in their life-cycle. The lack of a significant aggregation of larvae inside successful seed capsules suggests that the larvae burrow into the

Figure 5.2 : The percentage of *Coleophora alticolella* larvae sharing *Juncus squarrosus* seed capsules with one or more other individuals, at different densities of larvae per seed capsule in August 1978. The curve shows the expected values calculated from the Poisson distribution.


% sharing
50
25
0·0
0·3
0·6
0·9
Larvae per capsule

floret or seed capsule. This could have important consequences on the survival of these first instar larvae, particularly at the higher altitudes, as starvation would be expected in unsuccessful florets.

5.4 The survival of *Coleophora alticolella* from egg to establishment in the seed capsule

In Section 4.5 the density of the *Coleophora alticolella* eggs was discussed in relation to the number of *Juncus squarrosus* florets, i.e. the potential food supply. By using these data, and those for the subsequent density of larvae, it is possible to calculate the survival of *Coleophora alticolella* from the egg to the stage when the larvae are established inside the food supply. The percentage survival is calculated from the number of eggs and larvae per floret by the formula:

$$\% \text{ Surviving} = \frac{\text{Larvae per floret} \times 100}{\text{Eggs per floret}}$$

Table 5.3 gives the maximum density of eggs laid at each site in 1978 and the density of larvae per floret in the August sample. This table also shows the survival rates at each altitude. The values range from over 80% at 15m to less than 20% at 520m. The relationship between survival and altitude is not linear over the altitudinal range (Figure 5.3). It appears to be sigmoidal, with a greater reduction in the percentage surviving, with increasing altitude in the middle region of the transect.

Figure 5.3 : The percentage survival of *Coleophora alticolella* from eggs to larval establishment inside seed capsules, at different altitudes in 1978.

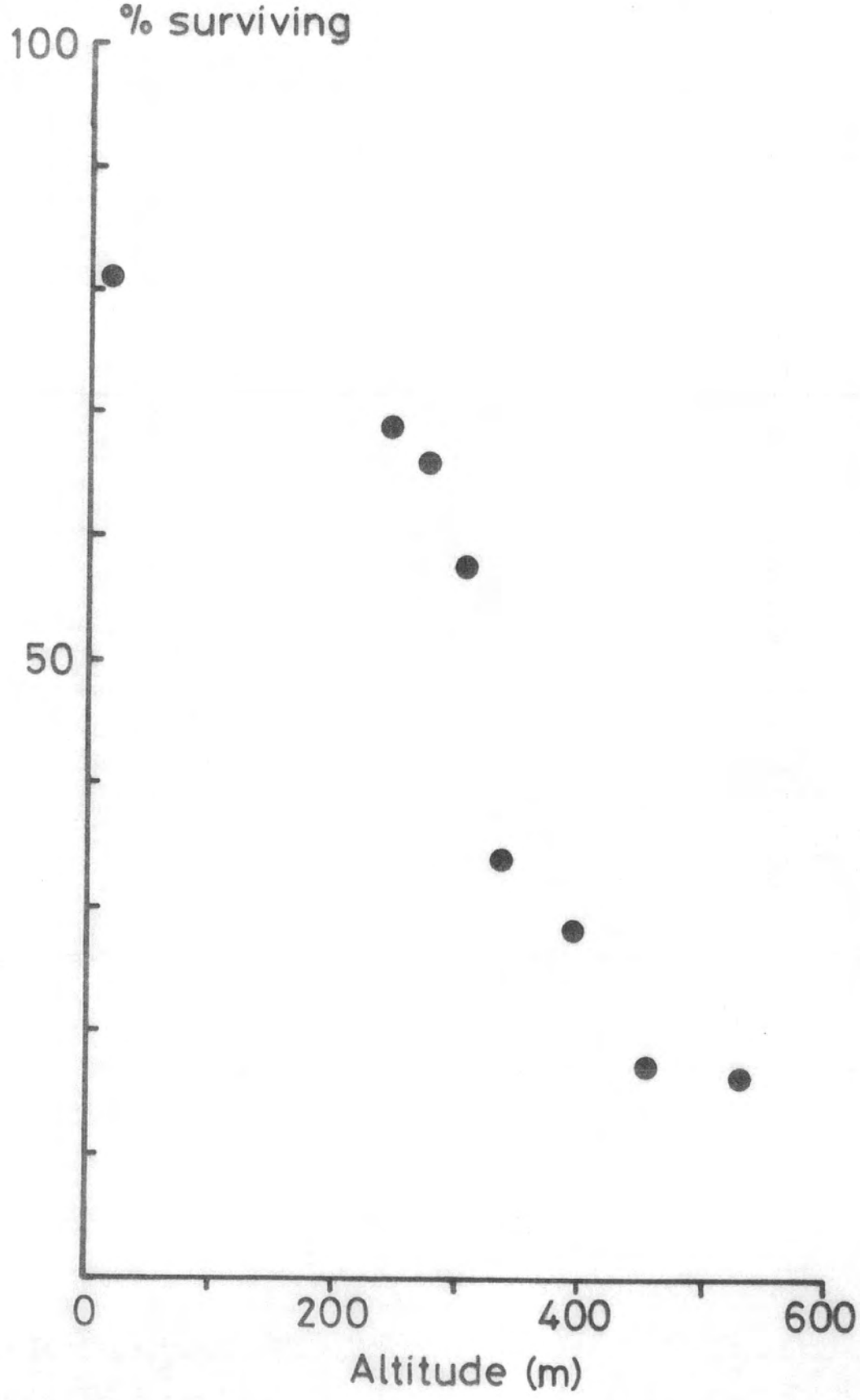

% surviving
100
50
0
200
400
600
Altitude (m)

Table 5.3 : *The density of eggs and larvae per floret of* Juncus squarrosus *at eight altitudes in 1978; with the percentage surviving calculated from these values*

Altitude (m)	Eggs per Floret	Larvae per Floret	% Surviving
15	0.287	0.232	80.8
245	0.735	0.508	69.1
275	1.038	0.687	66.2
305	0.929	0.532	57.3
335	1.120	0.383	34.2
395	0.899	0.257	28.6
455	0.794	0.138	17.4
520	0.102	0.017	16.7

The percentage surviving has been calculated from the densities of eggs and larvae per floret; in other words, from their relationship to the potential food supply at each altitude. If, as suggested earlier, the newly hatched larvae burrow into the nearest floret, then the proportion surviving should be dependent on the proportion of florets successfully developing into seed capsules. This assumes that a larva which burrows into a floret that has not developed into a seed capsule is unable to leave and try others in its quest for food. This is a reasonable assumption because an ability to reject unproductive florets and continue searching would lead to aggregation of the larvae inside seed capsules on a much larger scale than has been shown to occur.

Seed capsule production has been discussed in a previous chapter. However, values for the proportion of florets developing into seed capsules

are summarized in Table 5.4 for the altitudes under consideration. These data are calculated from the number of florets and seed capsules in the August 1978 samples; the same samples as used in assessing larval densities. By this time all of the capsules that were to develop had done so.

Table 5.4 : *The number of florets, and the proportion that had developed into seed capsules, in samples of 30 inflorescences of* Juncus squarrosus *from eight altitudes in August 1978*

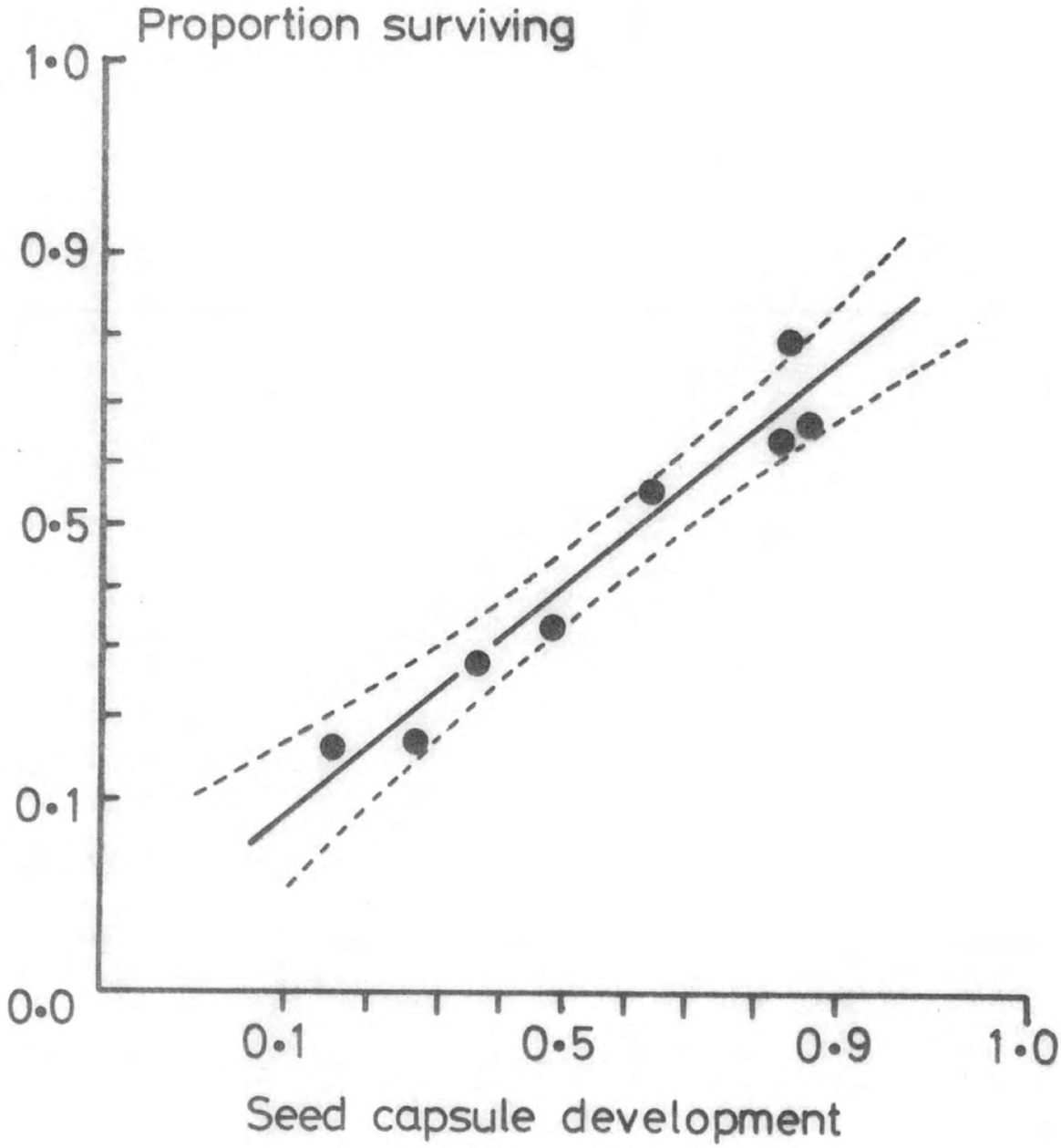
Altitude (m)	Number of florets	Seed capsules as a proportion of florets
15	517	0.836
245	419	0.859
275	422	0.829
305	451	0.634
335	481	0.474
395	416	0.355
455	384	0.260
520	359	0.150

The values for *Coleophora alticolella* survival and seed capsule production were converted to angles by the arcsin transformation and plotted against each other in Figure 5.4. This graph shows that survival at this stage in the life-cycle is directly related to the proportion of the florets developing into seed capsules. The relationship can be described by the regression line:

Figure 5.4 : The proportion of *Coleophora alticolella* surviving from the egg stage to larval establishment (y) plotted on an angular scale against the proportion of florets developing into seed capsules (x). The equation of the regression line is :

$$\arcsin \sqrt{y} = 0.851 \arcsin \sqrt{x} + 1.543$$

$n = 8$, $y = 0.972$, S.E. of slope = 0.084, $P < 0.001$. The 95% confidence belt for the regression line is shown by the broken lines.


Proportion surviving
1·0
0·9
0·5
0·1
0·0
0·1
0·5
0·9
1·0
Seed capsule development

$$\arcsin \sqrt{y} = 0.851 \arcsin \sqrt{x} + 1.543$$

where x is the proportion of florets developing into seed capsules and y is the proportion of *Coleophora alticolella* surviving from egg to larval establishment. The figure shows this line with the 95% confidence belt for the dependent variables. An extrapolation of this relationship to the point where all of the florets develop into seed capsules indicates that survival of *C. alticolella* would be between 87.0% and 99.8%. However, with 90% seed capsules development, which is nearer to the maximum shown in Table 5.4, the survival rate would lie between 68.1% and 87.5%. In fact, the line equivalent to the simple relationship $y = 0.8x$ lies entirely within the 95% confidence belt, for all values of x below 0.95. This implies that the survival rate is around 80% of the seed capsule production rate over the observed range of x.

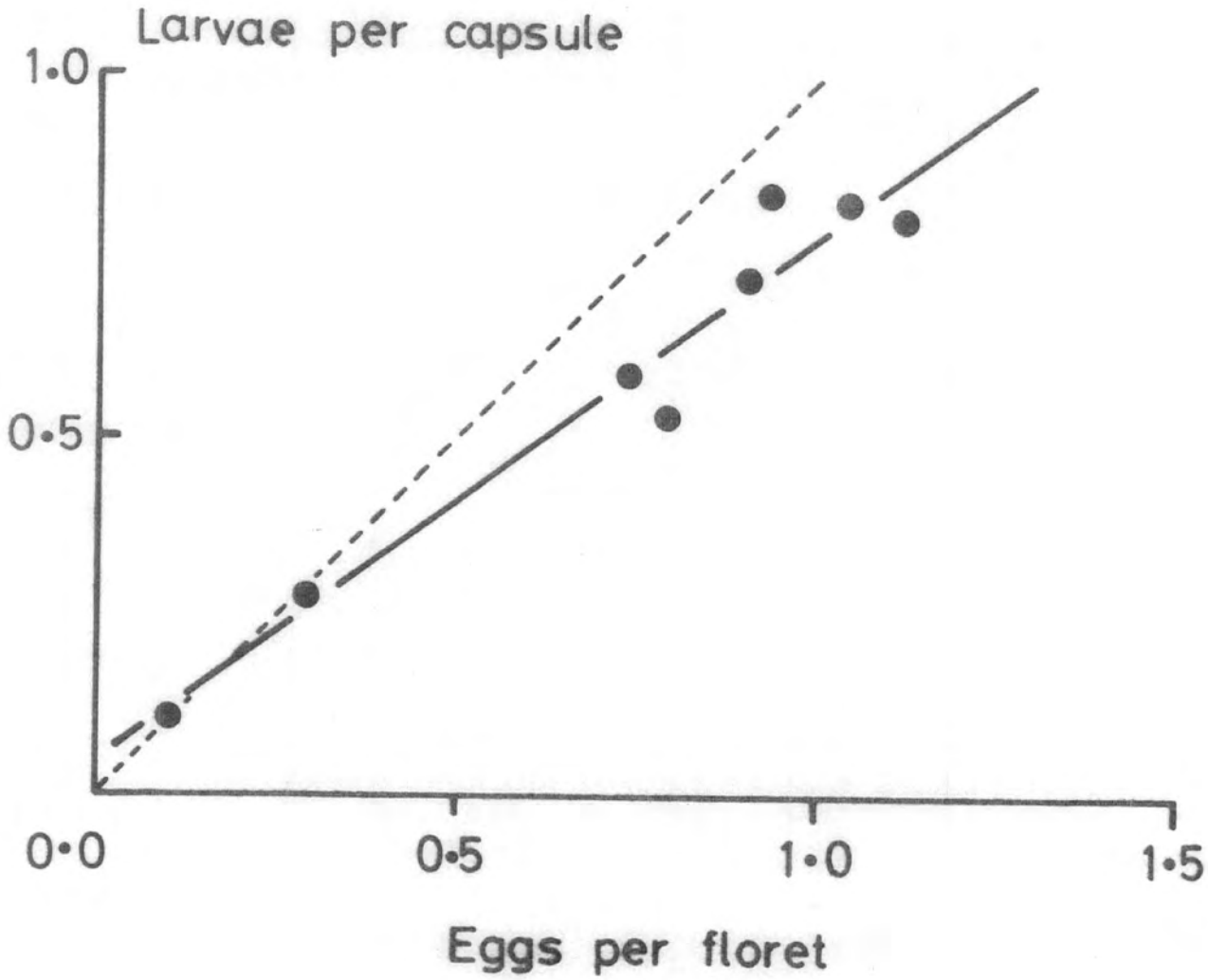
If survival during this period is entirely determined by seed capsule production, then the ratio of larvae per seed capsule to eggs per floret would be expected to be unity. A ratio greater than unity would indicate that the newly hatched larvae could select florets that had produced seed capsules, in preference to the unsuccessful ones. A ratio less than unity would indicate that some of the mortality was due to factors other than seed capsule failure. Figure 5.5 shows the mean number of larvae per capsule plotted against the number of eggs per floret, at the eight altitude sites. The regression line is coincidental with the 1:1 relationship at low densities, but at the higher densities survival is lower than expected. The regression coefficient is significantly less than unity ($t = 3.799$, $n = 8$, $P < 0.01$). This suggests that there is another component of mortality at this stage, apart from seed capsule failure, and that it increases with an increase in the number of eggs per floret.

Figure 5.5 : The density of *Coleophora* larvae per seed capsule (y) plotted against the density of eggs per floret (x). The solid line has the formula :

$$y = 0.732x + 0.048$$

$n = 8$ $r = 0.973$ S.E. of slope = 0.071 $P < 0.001$

The broken line shows the ratio $y = x$.


Larvae per capsule
1·0
0·5
0·0
0·5
1·0
1·5
Eggs per floret

Failure of seed capsules does not explain all of the mortality prior to larval establishment. Additional mortality factors may not be related to food availability; for example, infertility of eggs or failure of the larvae to hatch, although no eggs were found in samples later in the season to substantiate this suggestion. Neither parasitoids nor predators of eggs or newly hatched larvae were detected. Cannibalism or the destruction of eggs by older larvae could occur, especially at high densities or in large egg groups. Cannibalism has been recorded for other Lepidoptera (e.g. Brower 1961; Fox 1975), but has not been observed for *Coleophora alticolella*.

Notwithstanding these other possibilities, the major mortality factor acting on *C. alticolella*, between the egg stage and when the larvae become established inside the food supply, is starvation caused by the failure of florets to develop into seed capsules (at least at the densities encountered during this research). Consequently, at the higher altitudes on the Little Dun Fell transect, where seed capsule production is much reduced, this factor is very important, and in 1978 resulted in over 80% mortality above 500 metres.

5.5 The upper altitudinal limit of larval distribution

Table 5.5 gives data for the upper altitudinal limits of seed setting by *Juncus squarrosus* and also *Coleophora alticolella* larval distribution, from this and other studies. Previous authors (Jordan 1962; Reay 1959; Welch 1965) have used data for the sites on Little Dun Fell and near Knock Ore Gill (an area 5km to the south, see Fig. 2.2) to illustrate the changes in this upper limit.

Jordan (1962) concluded that the upper limit of the moth larvae is determined by the upper limit of seed-setting by the food plant.

Table 5.5 : *The upper altitude limits for* Coleophora alticolella *larval distribution and* Juncus squarrosus *seed capsule production for some years during the period 1942 to 1979. All localities, apart from those used by Pearsall, are on the western escarpment of the Pennines; Knock Ore Gill is about 5km to the south of the Little Dun Fell transect (see Fig. 2.2). The data from Pearsall and Welch are based only on the presence of larval cases.* * *Indicates years when the reduction in the larval limit was caused by a reduction in the upper limit of seed capsule production.*

Year	Upper limit of seed capsules (m)	Upper limit of *C.alticolella* infestation (m)	Locality	Source of reference
1942/44/45	762 - 823	550	Central Lake District	Pearsall 1950
1947	>823	610	Saddle Back Lake District	,,
1947	1036	463	Ben Wyvis Rothiemurchus	,,
1952	753	564	Little Dun Fell	Jordan 1955
1953	753	564	Little Dun Fell	,,
* 1954	410	410	Little Dun Fell	,,
1955	>455	427	Little Dun Fell	Reay 1959
1956	>455	427 - 440	Little Dun Fell	,,
1957	>455	455	Little Dun Fell	,,
1963	>600	410	Knock Ore Gill	Welch 1964
1964	>600	427	Knock Ore Gill	,,
	Expected altitude with 5% capsule production			
1977	678	610	Little Dun Fell	This study
* 1978	551	520	Little Dun Fell	,,
1979	596	520	Little Dun Fell	,,

However, this only occurs in years when the seed capsule production is reduced to an altitude below the upper limit of egg laying. He suggested that in a year of good seed-setting following a bad year, the limits of the larvae and seed should not coincide,due to the poor dispersal of ovipositing adults and thus a slow recolonization rate. This was corroborated by Reay (1959) who found that in 1955, the year following the fall noted by Jordan, seeds were produced at a higher level than larval distribution. The slow recolonization rate was obvious, with the larvae only gaining altitude by some 45 metres in the next three seasons.

By the time my studies had started, the upper limit was around 610 metres, but in 1978 seed production was reduced at the high altitudes (the table shows the predicted altitude with 5% capsule production, because of the asymptotic approach to zero). This resulted in a reduction in the upper altitude limit of the larvae. In 1979 the larvae had not gained ground, despite considerable seed capsule production above the level of larval distribution in the previous year.

Welch (1965) suggested that low seasonal temperatures may also be important in the change of the upper altitudinal limit of *C.alticolella*, causing a slower larval development, and then an adult emergence too late for oviposition on the food plant. This seems unlikely, because natural selection should have resulted in a characteristic trigger to initiate post-diapause development that would enable the emerging moths to be synchronized with their food-plant (Tauber and Tauber 1976). Also, during this study, eggs were found to have been laid at all stages of floret development, so any later emergence would not preclude oviposition. More likely is Pearsall's (1950) suggestion that an adverse climate could cause a slower development of the seed capsules, after oviposition, so that larvae may hatch before seed production, a situation similar to that described in Section 5.4.

The present research has shown that a lowering of the upper altitude limit of *Coleophora alticolella* is not a sudden cut-off, but is a result of a gradual decline in larval survival, concomitant with the decline in the success of seed capsules at higher altitudes.

5.6 A comparison of larval development at 15m and 455m in 1978

The development of the *C. alticolella* larvae at the lowest sample site was compared with that at 455m. The larvae were removed from the seed capsules and examined for evidence of parasitization, or to find if they had died prior to collection. The parasitized and 'dead' larvae were excluded from the following analyses. The remaining larvae were assigned to different age-classes, after measuring the width of their head capsules. The number of eggs present on each inflorescence was also recorded. (These data are available in Appendix 6.)

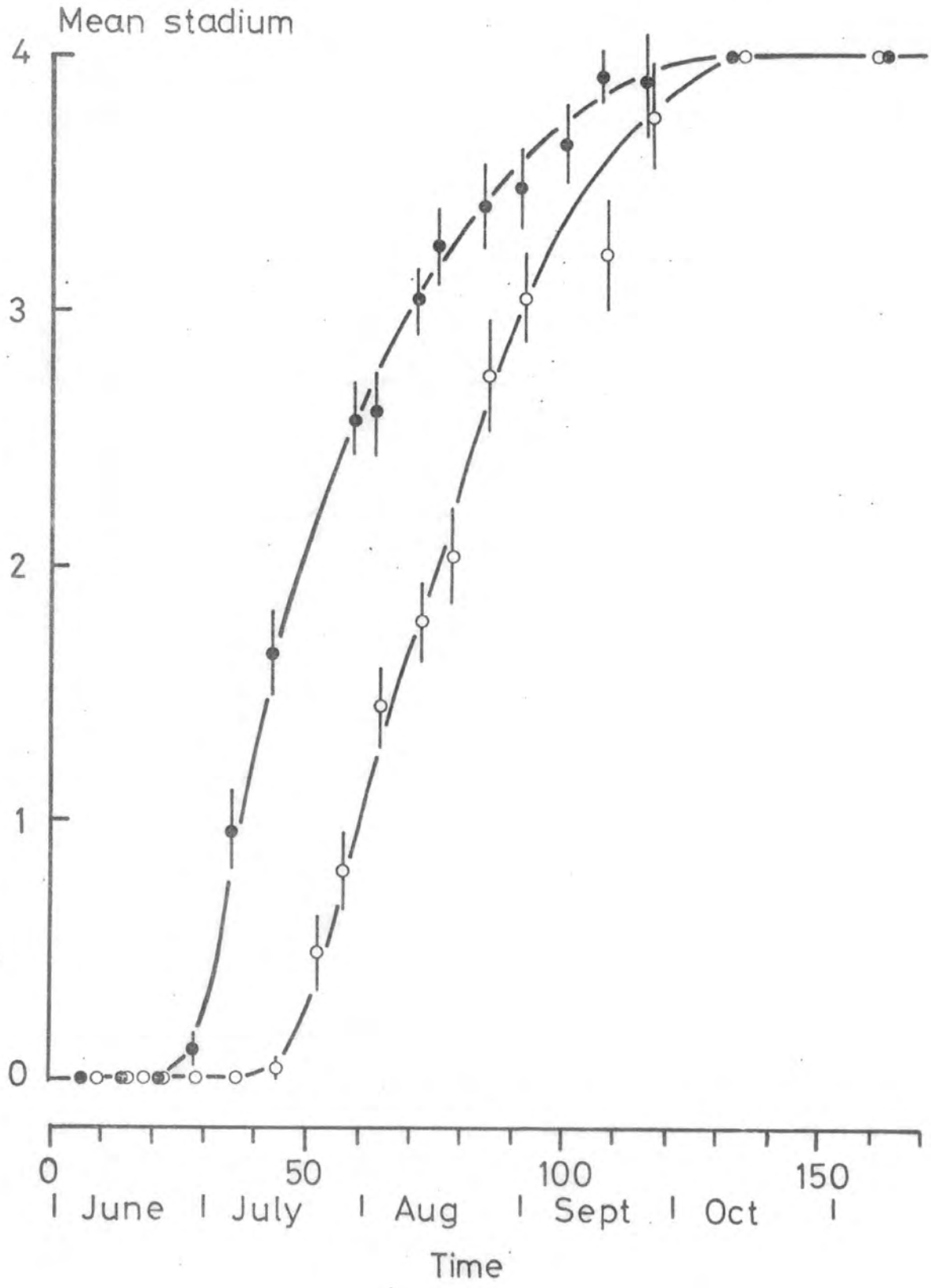
Larval development is expressed as the mean stadium present in each sample, calculated by using the values 0 to 4 for the egg and four larval instars. The results are given in Table 5.6. Only eggs were present from 30 May until 21 June at 15m, and from 9 June until 6 July at 455m. At the end of the sampling season, all of the surviving larvae were fourth instars. Very few larvae were present on the last two sample dates at 15m and none was found in the samples from 455m in either October or November. By this late stage most of the larvae had finished feeding and had already moved down to the leaf-litter.

Figure 5.6 shows the mean instars plotted against the date of each sample for both sites; the two curves have been fitted by eye. The values for the 455m site lie to the right of these from 15m, indicating that larvae at the higher altitude were at an earlier stage in their development throughout the season.

Table 5.6 : *The mean instar calculated from the number of eggs and live larvae present in samples from the 15m and 455m sites during the 1978 field season. (Mean instar of 0 occurs when only eggs are present.)*

15m Date	Mean instar	Standard deviation	Sample size	455m Date	Mean instar	Standard deviation	Sample size
30 May	0.000	0.000	9				
6 June	0.000	0.000	85	9 June	0.000	0.000	32
14 June	0.000	0.000	96	15 June	0.000	0.000	51
				18 June	0.000	0.000	58
21 June	0.000	0.000	116	22 June	0.000	0.000	125
28 June	0.106	0.311	123	29 June	0.000	0.000	129
5 July	0.965	0.695	86	6 July	0.000	0.000	201
13 July	1.653	0.679	72	14 July	0.039	0.201	158
				22 July	0.484	0.567	62
29 July	2.570	0.658	79	27 July	0.804	0.543	46
2 Aug	2.585	0.701	65	3 Aug	1.447	0.542	47
10 Aug	3.043	0.650	94	11 Aug	1.774	0.575	53
16 Aug	3.254	0.595	63	17 Aug	2.031	0.537	32
23 Aug	3.413	0.583	46	24 Aug	2.739	0.542	23
30 Aug	3.475	0.506	40	1 Sept	3.050	0.394	20
8 Sept	3.649	0.487	37				
15 Sept	3.920	0.275	25	16 Sept	3.217	0.518	23
24 Sept	3.889	0.333	9	25 Sept	3.765	0.437	17
11 Oct	4.000	0.000	5	12 Oct	(4.000)	0.000	0
8 Nov	4.000	0.000	3	7 Nov	(4.000)	0.000	0

Figure 5.6 : The development of *Coleophora alticolella* larvae, from egg to the fourth instar, at the 15m site (○) and the 455m site (○) during 1978. The values are expressed as the mean stadium (with 95% confidence limits) present on each sampling date; time is in days, 1 = 1 June 1978.


Mean stadium
4
3
2
1
0
0
50
100
150
June
July
Aug
Sept
Oct
Time

The two curves do not appear to be of the same shape. At 15m the gradient of the line, after about 60 days, is less than either earlier in the season at the same site, or compared with the same stages of development at 455m. This convergence of the two lines seems to indicate a slower development of the larvae, from the second to the fourth instar, at the lower site. However, this may be attributed to the older larvae having moved to the leaf-litter, and to mortality of larvae due to parasitoids, which attack at 15m but not at 455m. The loss and death of the older larvae leads to an exaggeration of the proportion of the younger larvae in the samples. The rate of development will also appear to decrease towards the end of the season because the mean value can only reach 4 when there are no younger larvae present. For these reasons it is not possible to calculate the duration of the third instar with accuracy.

Approximations to the duration of the earlier stadia are possible, by interpolation of the graphs in Figure 5.6, and from the median oviposition dates as given in the last chapter. The mean hatching date corresponds to the time when the mean instar is 0.5; this is when half of the population is in the first instar and half are still in eggs. The difference between this value and the median date of the oviposition period gives an estimate of the duration of the egg stage. Similarly, the duration of the first instar is from the mean hatching date to mid-way between mean instars 1 and 2 (i.e. 0.5 to 1.5). These mean dates are given in Table 5.7 with the values for the duration of each stage.

The values given in Table 5.7 must be treated with caution as they have no confidence limits. However, the first period, from oviposition to hatching, took one month at 455m but only 25 days at 15m. The duration of the first instar was shorter, being only 10 days at 15m and 13 days at 455m. The duration of instar II was similar at both sites, but a little

Table 5.7 : *The mean date for the start of each instar and the median date of the oviposition period at 15m and 455m in 1978; the duration of each stage and the differences between the dates at the two altitudes are also given*

Mean instar	Stage	15m		455m		Difference between sites (days)
		Mean date	Duration of each stage (days)	Mean date	Duration of each stage (days)	
Oviposition		8 June		23 June		15
	Egg		25		31	
0.5		3 July		24 July		21
	Instar I		10		13	
1.5		13 July		6 Aug		24
	Instar II		15		16	
2.5		28 July		22 Aug		25
	Instar III		30		22	
3.5		27 Aug		13 Sept		17

longer than instar I. The effect of the convergence of the two graphs after 60 days is evident from the apparent longer duration of the third instar at the lower site; but the value of 30 days for the duration of instar III at 15m is an overestimate.

It is surprising that, apart from the longer duration of the egg stage at 455m, there was little effect of altitude on larval development. The final column of Table 5.7 shows that the time lag between equivalent mean instars increases from a 15 day delay in oviposition to 21 days on hatching but then remains at a similar level to the beginning of instar III.

The last samples containing eggs were collected on 5 July at 15m compared with 3 August at 455m. The first occurrence of fourth instars in samples from 15m was on 29 July and on 24 August at 455m. Table 5.8 gives the developmental rate per day between these sample dates, calculated by dividing the difference between mean instars on the two dates by the time interval in days. This rate was of the same order at both altitudes, but only slightly slower at 455m.

Table 5.8 : *The development rate per day of the larvae of* Coleophora alticolella *at 15m and 455m in 1978; calculated from the change in mean instar for the period from the last sample with eggs until the first sample with fourth instars*

		15m	455m
Last sample with eggs			
	Date	5 July	3 August
	Mean instar	0.965	1.447
First sample with fourth instars			
	Date	29 July	24 August
	Mean instar	2.570	2.739
Time between samples (days)		24	21
Development rate (change in mean instar per day)		0.067	0.062

The effect of increasing altitude on the developmental rates of different stages can be examined by calculating temperature coefficients ($^{*}Q_{10}$), assuming that temperature is the only factor affecting development over this range. The altitudinal difference of 440m between the two sites is equivalent to a $3^{\circ}C$ temperature difference. The following formula can be used to calculate the Q_{10} when the rates are not exactly $10^{\circ}C$ apart (Schmidt-Nielsen 1979):

$$\log Q_{10} = (\log R_2 - \log R_1) \cdot \frac{10}{T_1 - T_2}$$

where R_1 and R_2 are the rates at the two temperatures T_1 and T_2.

The values of the two developmental rates from Table 5.8 substituted into this equation give a Q_{10} of 1.30. If a similar approach is taken for the duration of the egg stages at the two altitudes (25 days at 15m and 31 days at 455m) the resulting Q_{10} is 2.10.

Thus, the development rate per day of eggs would be doubled with an altitudinal decrease equivalent to a temperature increase of $10^{\circ}C$. However, there is remarkably little effect of temperature on the developmental rate during the early larval instars.

5.7 Larval case production and larval migration

5.7a Methods

During frequent visits to the sample sites in 1977 and 1978 the production of the larval cases and the subsequent migration from the food-plant to the leaf-litter was studied. Permanent quadrats, measuring 2m by 2m, were staked out at several altitudes; 15m, 245m,

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* Q_{10} is temperature-dependent; the mean daily temperatures at Moor House (558m) during the summer of 1978 were: June, $9.1^{\circ}C$; July, $10.0^{\circ}C$; August, $10.7^{\circ}C$.

335m, 395m and 455m. (This procedure was also carried out at 520m but, due to low larval numbers, the results from this site are not included.) The larval cases on the inflorescences within the quadrats were marked with a quick-drying waterproof ink, a different colour code for each sample date. By this method, the number of larvae that had produced cases since the previous sample date could be recorded. In addition, the larvae that had been marked on a previous occasion and were still present were counted. These values have been expressed as the number of cases per inflorescence and are tabulated in Appendix 7.

The difference between the cumulative total cases produced and the number present on each sample date gives the number of larvae that had left the inflorescence and moved down to overwinter; this is the number migrating and the values are also given in Appendix 7.

The relationships between the cumulative total of cases produced, and also the number of larvae migrating, at each site were both sigmoidal with respect to time. These data have been analysed by describing them with logistic equations computed by the least-squares method of regression. Some examples of the results of these analyses are shown graphically in Appendix 8.

5.7b Case production

The results of the regression analysis of cumulative total cases produced against time of sample are given in Table 5.9. Apart from at 15m in 1978, over 99% of the variation in the number of cases produced per inflorescence is accounted for. The values of k are the upper asymptotes of the equations and represent the total number of larval cases produced per inflorescence at each site.

Table 5.9 : *The results of regression analyses to describe the relationship between the number of larval cases produced per inflorescence (y) and time (x, in days with 1 = 1 June) by logistic equations with the formula:*

$$y = \frac{k}{1 + \exp(a-bx)}$$

Altitude	k	a	b	F	degrees of freedom	P	R^2
1977							
15	1.4734	8.1901	0.1102	1251.3	2,10	<0.001	0.995
245	4.1671	14.9198	0.1726	882.1	2,8	<0.001	0.994
335	1.9331	16.9657	0.1810	1284.3	2,6	<0.001	0.997
395	1.3982	17.8918	0.1879	2951.3	2,6	<0.001	0.999
455	0.5158	15.1453	0.1523	1285.7	2,6	<0.001	0.997
1978							
15	0.8609	8.9314	0.0998	1154.0	2,9	<0.001	0.952
245	1.5821	18.8674	0.1853	1467.7	2,5	<0.001	0.998
335	3.0699	23.7327	0.2449	3599.8	2,5	<0.001	0.997
395	1.7735	20.6624	0.1997	1554.6	2,5	<0.001	0.998
455	0.3672	22.4258	0.2207	424.9	2,4	<0.001	0.993

Table 5.10 : *The mean date of production of the larval cases during 1977 and 1978; measured in days, 1 = 1 June*

Altitude (m)	Mean production date (1 = 1 June)	Calendar date	Standard deviation (days)	Standard error (days)	Number produced
1977					
15	74.3	13 Aug	15.1	0.50	918
245	86.4	25 Aug	9.7	0.53	327
335	93.7	2 Sept	9.2	0.39	555
395	95.2	3 Sept	8.9	0.43	429
455	99.4	7 Sept	10.9	0.69	220
1978					
15	89.5	28 Aug	16.7	1.48	127
245	101.8	10 Sept	9.0	0.69	169
335	96.9	5 Sept	6.8	0.30	508
395	103.5	11 Sept	8.4	0.53	246
455	101.6	10 Sept	7.6	0.91	69

The mean date of case production at each of these altitudes has been calculated as the point of inflexion from these equations. These values are given in Table 5.10, with their standard deviations. There was a direct relationship between the mean date of case production and altitude in 1977 (Figure 5.7a). This can be described by the equation:

$$y = 0.057x + 73.277$$

where x is the mean date in days after 31 May and y is altitude in metres. The regression coefficient is significantly ($P < 0.001$) greater than zero and indicates that case production was delayed by 5.7 ± 0.9 days for every 100m increase in altitude.

Although the mean date of case production was delayed at some of the higher sites in 1978, the regression coefficient was not significantly different from zero (Figure 5.7b).

The mean date of case production was later at each altitude in 1978 than in 1977. Table 5.11 gives the results of *t*-tests on these differences, which proved significant at each altitude, apart from at 455m. The delay was similar for both the 15m and 245m sites, with the mean date being a little over 15 days later in the second year. The differences at the higher sites were not so great.

Table 5.11 : *t-tests of the differences between the mean dates of larval case production in 1977 and 1978 at five altitudes*

Altitude (m)	Difference 1978 - 1977 (days)	*t*	*P*
15	15.2	9.730	<0.001
245	15.4	17.700	<0.001
335	3.2	6.504	<0.001
395	8.3	12.161	<0.001
455	2.2	1.926	>0.05

Figure 5.7 : The mean date of larval case production, with 95% confidence limits, at different altitudes. The regression equations are given with the mean date, y, in days (1 = 1 June) and altitude, x, in metres

a. 1977

$$y = 0.057x + 73.277$$

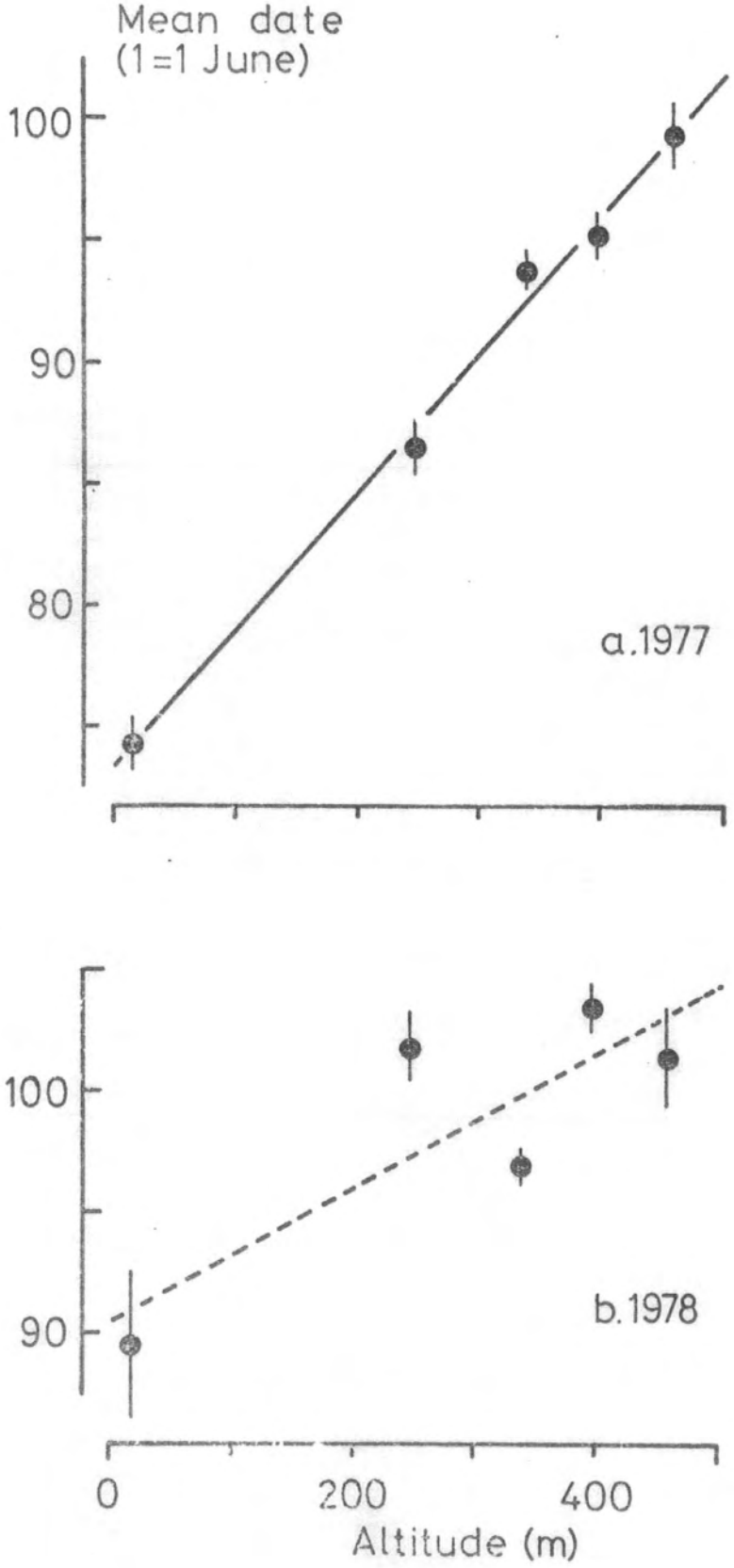
$n = 5$ $r = 0.996$ S.E. of slope = 0.003 $P < 0.001$

b. 1978

$$y = 0.028x + 90.592$$

$n = 5$ $r = 0.844$ S.E. of slope = 0.010 $0.05 < P < 0.10$

The regression coefficient is not significantly different from zero; the trend is shown in the figure by a broken line.


Mean date
(1=1 June)
100
90
80
a.1977
100
90
b.1978
0
200
400
Altitude (m)

The standard deviations are measurements of the synchrony of case production at each site. The 15m site had the largest spread in both years, with 95% (2 x 1.96σ) of the cases being produced over a 59 day period in 1977 and over 65 days in 1978 (Table 5.12). The production of 95% of the cases at the other altitudes took an appreciably shorter time, with values ranging from 35 to 43 days in 1977 and 27 to 35 days in 1978. In contrast to the 15m site, these values were lower in the second of the two years at each site.

Table 5.12 : *The number of days taken for the production of 95% of the larval cases at different altitudes in 1977 and 1978*

Altitude (m)	1977	1978
15	59	65
245	38	35
335	36	27
395	35	33
455	43	30

The spread of case production will be determined primarily by the synchrony of larval development. This will depend on the length of the oviposition period, assuming that all eggs have an equal chance of survival to the case production stage, irrespective of the time that they were laid during the oviposition period. 95% case production at the Little Dun Fell sites took on average 35 days, which was about the same length as the oviposition period in 1978. It is not known why there was such a large spread of case production at 15m; it is unlikely, from the evidence of the data on egg-laying, that the oviposition period at this site was very much longer than those at other sites in 1978.

Although ultimately dependent on the length of the oviposition period, the synchrony of case production may be modified by other factors. Figure 5.8 shows that, at the Pennine sites, there was an inverse relationship between the standard deviation of case production date and the density of larvae per seed capsule. The 95% confidence limits of the standard deviations are shown in this figure and have been calculated by the formula given by Snedecor and Cochran (1967; p. 74). The linear relationship at these sites can be described by the formula:

$$y = 10.960 - 4.183x$$

where y is the standard deviation of the case production dates and x the number of larvae per seed capsule at each site. The relationship is significant at the 5% level of probability.

At the higher densities of larvae per seed capsule, the percentage of larvae sharing seed capsules increases (Figure 5.2). Consequently, the time taken to produce the cases could be modified by food availability. If the larvae produce their cases when the food supply in their first capsule is exhausted, those larvae sharing capsules with other individuals should produce cases earlier in the season, relative to solitary larvae at the same stage of development.

This hypothesis was tested using data from a sample of 20 inflorescences collected from the 335m sample site on 1 September 1978. This has been shown to be a site with high larval density, and consequently a high proportion of larvae sharing seed capsules. By this sample date, larval case production had started, although only two fully formed cases were present; most were small and thin and had obviously been newly initiated. A 2 x 2 contingency table was constructed to test the Null Hypothesis that the number of larvae in a seed capsule has no effect on the proportion of larvae with cases. The results can be seen in Table 5.13,

Figure 5.8 : The standard deviation of the case production dates at different densities of larvae per seed capsule:

□ 15m site in 1977

□ 15m site in 1978

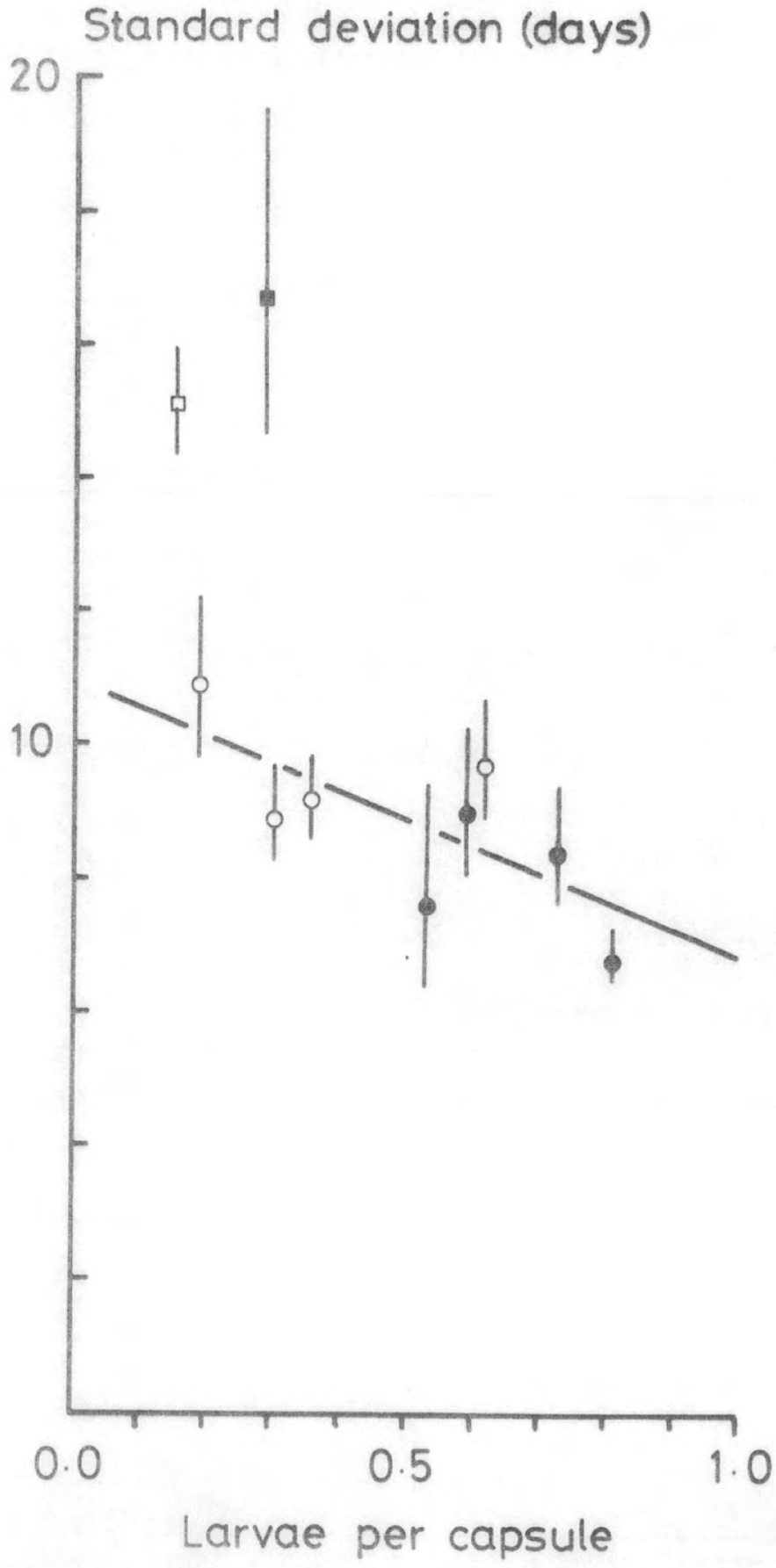
○ Little Dun Fell sites in 1977

○ Little Dun Fell sites in 1978

The regression line has been calculated from the data for the Little Dun Fell sites (circles) and has the equation:

$$y = 10.960 - 4.183x$$

$n = 8$ $r = -0.719$ S.E. of slope = 1.651 $P < 0.05$


Standard deviation (days)
20
10
0·0
0·5
1·0
Larvae per capsule

which shows a significantly greater proportion of the larvae that were sharing seed capsules had started to produce their cases, than those larvae in capsules by themselves; thus disproving the Null Hypothesis at the 5% probability level.

Table 5.13 : *A 2 x 2 contingency table to test the Null Hypothesis that the number of larvae in a seed capsule has no effect on the proportion of larvae with cases. The value of* χ^2 *has been calculated using Yates' correction.*

	Single larvae in capsule	>1 larva in capsule	
No case	42	19	61
Case	25	29	54
	67	48	115

$\chi^2 = 5.101$ $P < 0.05$ Null Hypothesis rejected.

5.7c Larval migration

The difference between the cumulative total of cases produced and the number still present on each sample date was used as a measure of the number of larvae that had migrated to the leaf-litter. (These values are also given in Appendix 7.) It is assumed that all of these missing larvae are those that have finished feeding, and have left the inflorescences to seek refuges for overwintering. Some of this disappearance could have been due to predation, although no evidence was found for this, and none has been reported in the previous studies. Thorough searching of the inflorescences outside the boundary of the permanent quadrats

showed that a few of the marked larvae had moved out of the area to the surrounding plants. This emigration was not on a large enough scale to be responsible for the changes seen here. Also, assuming random movements of larvae between inflorescences, emigration from the quadrats should equal immigration, and thus have no effect on the number of cases present at one time.

Logistic curves have been fitted to the data to describe the migration of the larvae during this period. Table 5.14 shows the results of these analyses. All of the equations explain at least 95% of the variation in the number of larvae that migrated, with most being over 99%.

The values for the parameter k are the maximum number of larvae migrating at each sample site. Comparison of these values with those for the number of cases produced (Table 5.9) shows that the predicted total number migrating is always less than the number produced. This reflects the real situation; by definition the migrating larvae must have produced cases first. The differences between the numbers of cases produced and larvae migrating are caused by mortality of the larvae after case production; these values are used later in discussing the population dynamics of this moth.

The data given in Table 5.14 were treated in the same way as those for larval case production, to calculate the mean migration dates. The results are given in Table 5.15.

In 1977 there was a direct relationship between the mean date of larval migration and altitude (Figure 5.9a). This can be described by the formula:

$$y = 0.114x + 81.000$$

where y is the mean date of migration in days (1 = 1 June) and x is the altitude in metres. The regression coefficient is significantly ($P < 0.01$)

Table 5.14 : *The results of regression analyses to describe the relationship between the number of larvae per inflorescence migrating (z) and time (x, in days with 1 = 1 June) by logistic equations with the formula:*

$$z = \frac{k}{1 + \exp(a - bx)}$$

	Altitude (m)	k	a	b	F	degrees of freedom	P	R^2
1977								
	15	0.6481	8.2582	0.0965	1055.5	2,10	<0.001	0.994
	245	2.5980	12.6109	0.1214	581.6	2,8	<0.001	0.991
	335	1.8302	19.7533	0.1712	10788.3	2,6	<0.001	0.999
	395	1.3779	10.7924	0.0834	700.5	2,6	<0.001	0.994
	455	0.4944	9.7868	0.0725	399.0	2,6	<0.001	0.990
1978								
	15	0.2353	8.7838	0.0867	143.5	2,9	<0.001	0.963
	245	0.8335	26.7461	0.2259	8252.6	2,5	<0.001	0.999
	335	2.9051	28.2873	0.2550	1006.9	2,5	<0.001	0.997
	395	1.6255	24.8590	0.2100	1462.6	2,5	<0.001	0.998
	455	0.3319	18.5413	0.1606	159.7	2,4	<0.001	0.981

Table 5.15 : *The mean date of larval migration in 1977 and 1978; measured in days with 1 = 1 June*

	Altitude (m)	Mean migration date (1 = 1 June)	Calendar date	Standard deviation (days)	Standard error (days)	Number migrating
1977						
	15	85.6	25 Aug	17.3	0.87	398
	245	103.9	12 Sept	14.0	0.99	199
	335	115.4	23 Sept	9.8	0.43	530
	395	129.4	7 Oct	19.9	1.01	391
	455	135.0	13 Oct	23.1	1.72	181
1978						
	15	101.3	9 Sept	19.4	3.32	34
	245	118.4	26 Sept	7.4	0.79	89
	335	110.9	19 Sept	6.5	0.29	496
	395	118.4	26 Sept	8.0	0.55	213
	455	115.4	23 Sept	10.5	1.32	63

Figure 5.9 : The mean date of larval migration, with 95% confidence limits, at different altitudes. The regression equations are given with the mean date, y, in days (1 = 1 June) and altitude, x, in metres.

a. 1977

$$y = 0.114x + 81.000$$

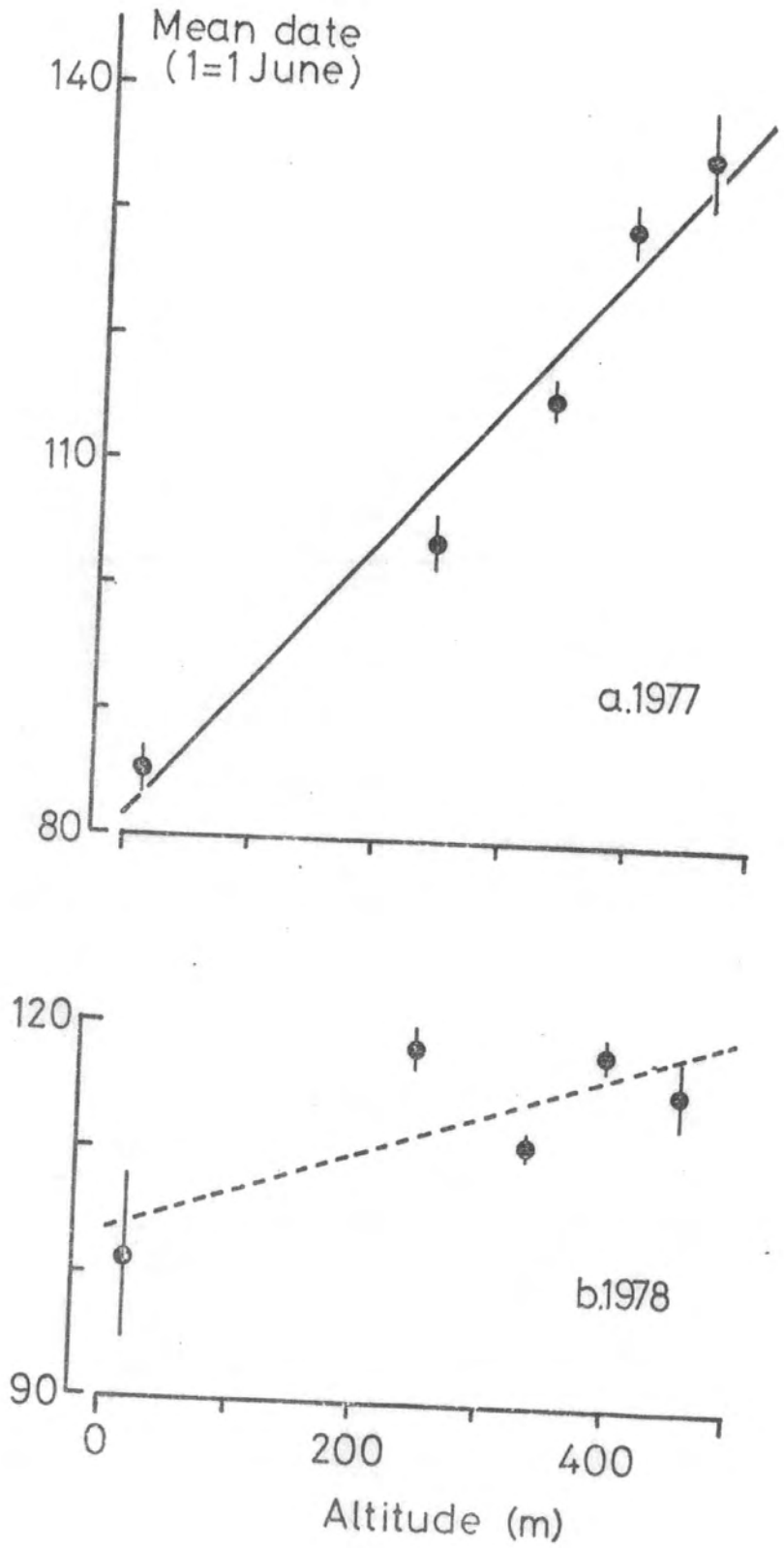
$n = 5$ $r = 0.979$ S.E. of slope = 0.014 $P < 0.01$

b. 1978

$$y = 0.033x + 103.463$$

$n = 5$ $r = 0.784$ S.E. of slope = 0.015 $P > 0.10$

The regression coefficient is not significantly different from zero; the trend is shown in the figure by a broken line.


Mean date
(1=1 June)
140
110
80
a.1977
120
90
b.1978
0
200
400
Altitude (m)

greater than zero and shows that migration was delayed by 11.4 ± 4.3 days for every 100m increase in altitude.

As with case production, there was no significant relationship between larval migration and altitude in 1978 (Figure 5.9b).

Table 5.16 shows that the mean larval migration date in 1978 was significantly earlier than in 1977 at 335m, 395m and 455m; but that at the two lowest altitudes larval migration, like case production, was later in the second of the two years. In fact, the differences between the mean dates of larval migration at 15m and 245m were similar to those for case production, being about 15 days later in 1978.

Table 5.16 : *t-tests of the differences between the mean dates of larval migration at five altitudes in 1977 and 1978. Negative values indicate an earlier mean date in 1978 than 1977*

Altitude (m)	Difference 1977-1978 (days)	*t*	*P*
15	+ 15.7	4.574	<0.001
245	+ 14.5	11.448	<0.001
335	- 4.5	8.676	<0.001
395	- 11.0	9.565	<0.001
455	- 19.6	9.040	<0.001

Calculation of the synchrony of larval migration at these altitudes (Table 5.17) showed that this period was much longer in 1977 than in 1978 for each sample site; apart from at 15m, where 95% of the migration was over a period of 76 days in 1978 compared with 68 days in 1977.

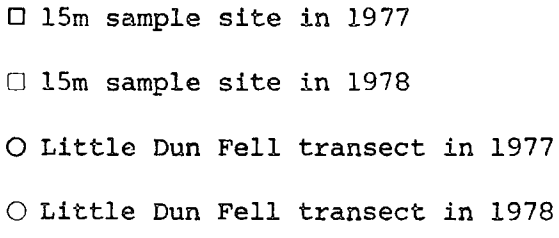
Table 5.17 : *The time taken, in days, for 95% of the* Coleophora alticolella *larval migration, at different altitudes in 1977 and 1978*

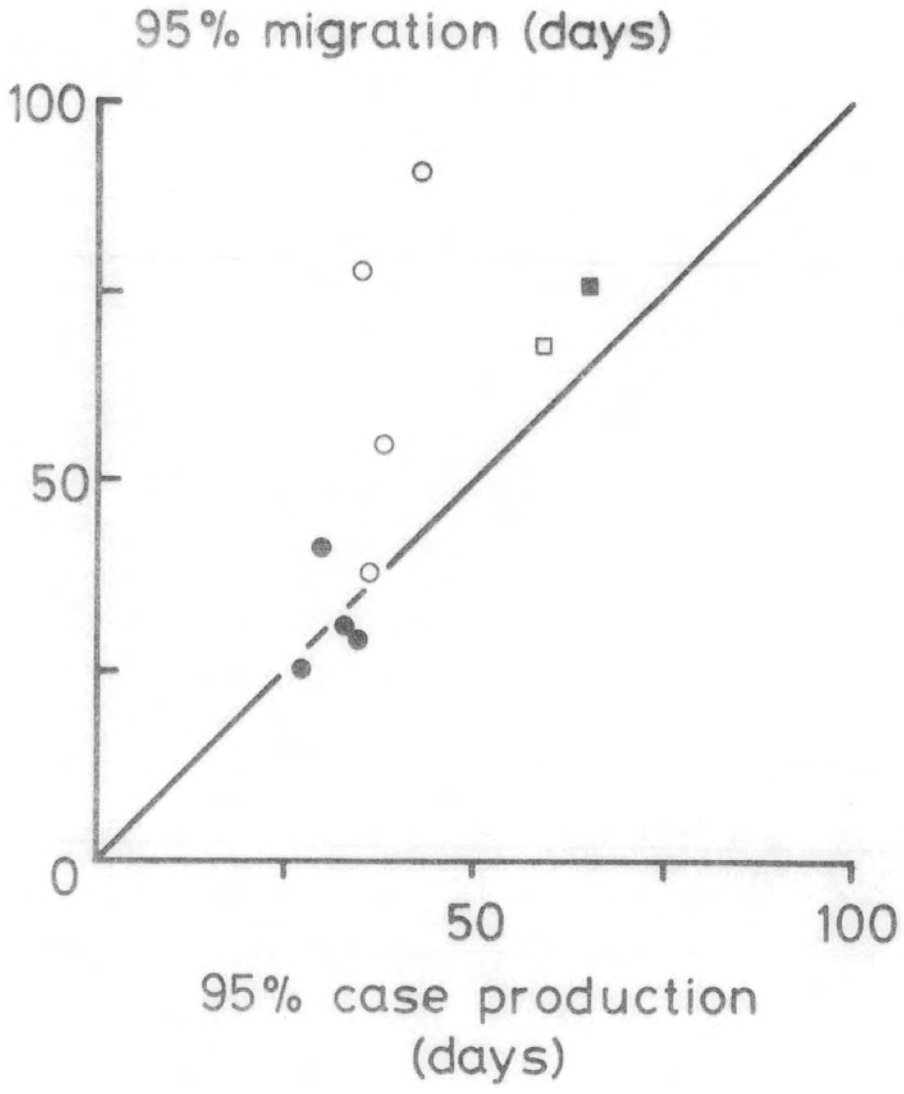
Altitude (m)	1977 (days)	1978 (days)
15	68	76
245	55	29
335	38	25
395	78	31
455	91	41

In both years, migration occurred over a shorter time period at the 335m sample site, and the longest were at 15m in 1978 and 455m in 1977. The value of 91 days at the 455m site for 1977 is a very large spread about the mean date, and would indicate that migration continued until the end of November. This is an overestimate, from the evidence of observations made in the field.

The synchrony of migration will depend, to some extent, on the synchrony of case production, because larvae cannot migrate until after they have produced their cases. As with case production, the greatest synchrony was at sites with the highest densities of larvae per seed capsule. Figure 5.10 shows the time taken for 95% migration plotted against the time for 95% case production. Only three points lie below the line of equality. These were 245m, 335m and 395m in 1978; the value for 335m in 1977 is very near to this line. At sites where larval density was lower, the spread of migration was greater than that of case production.

Figure 5.10 : The time taken for 95% migration of *Coleophora alticolella* larvae plotted against the time for 95% case production. The diagonal line shows equality in both parameters.




95% migration (days)
100
50
0
50
100
95% case production
(days)

5.8 Larval feeding after case production

The difference between the mean date of larval case production and the mean date of migration to the leaf-litter is an estimate of the average time that the larvae spend feeding on the seed capsules, whilst in their cases. Of course, not all of this time will be spent eating seeds; the larvae must move from one capsule to another, for example. Rather it is a measure of the whole of this feeding period.

The larval migration date may not be independent of the case production date, because they are both calculated from the same data. However, a comparison of the two regression coefficients for 1977 (Figures 5.7a and 5.9a) shows that the slope for migration is significantly greater than that for case production (t = 4.120, with 6 degrees of freedom; $P < 0.01$). Thus the larvae at the higher altitudes spent longer between producing their cases and migrating than those at the low altitudes, in 1977.

Figure 5.11 shows the values for the length of time spent in this stage, plotted against altitude; and also these same values expressed as the percentage rate per day, from the formula:

$$\% \text{ rate per day} = \frac{100}{\text{Migration date} - \text{Production date}}$$

The 1977 data is shown in Figure 5.11a and is similar to a typical temperature-dependent development-rate plot, bearing in mind that the cooler temperatures are at the higher altitudes and lie to the right. The inverse linear relationship between the reciprocal x 100 of the feeding time and altitude has the formula:

$$100/y = 9.118 - 0.0143x$$

Figure 5.11 : The average number of days that larvae spent feeding on the seed capsules after case production (○), and the percent feeding rate per day (○), in relation to altitude in:

a. 1977

and

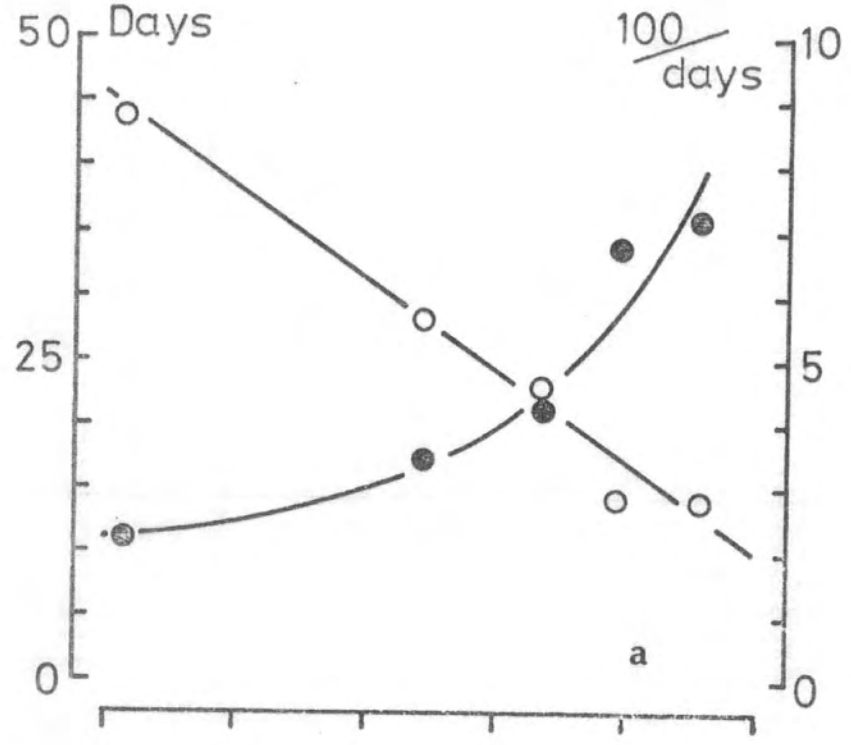
b. 1978

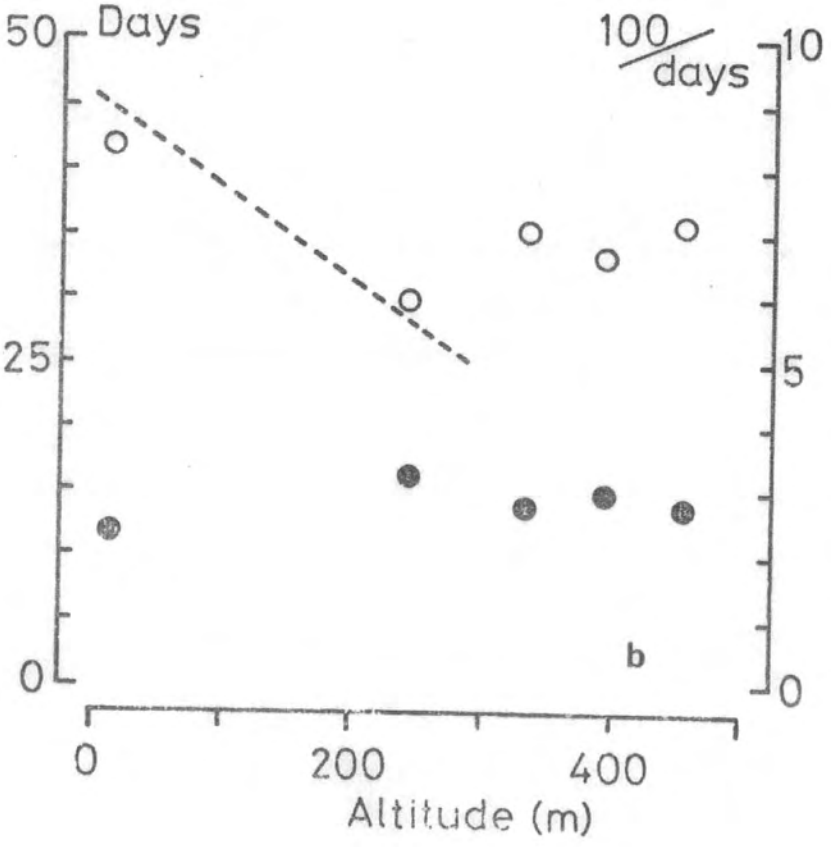
The regression of percent feeding rate per day ($^{100}/_{y}$) on altitude (x) in 1977 is:

$$^{100}/_{y} = 9.118 - 0.0143x$$

$n = 5$, $r = -0.991$ S.E. of slope = 0.001 $P < 0.001$

There was no significant relationship between feeding rate per day and altitude in 1978; the broken line in Figure 5.11b shows the relationship calculated from the 1977 data.


50
Days
100/days
10
25
5
0
0
a


50
Days
100/days
10
25
5
0
0
b
0
200
400
Altitude (m)

This indicates that between 15m and 455m the duration of this period corresponds to the hyperbola:

$$6993 = y(637.6 - x)$$

In these equations y is the number of days between case production and larval migration, at each altitude, x in metres.

A temperature-time curve for insect development approximates to a hyperbola for only a very narrow temperature range, departing widely from it at either end, and is often better described by a logistic curve (e.g. Davidson 1942, 1944). However, Andrewartha and Birch (1954) suggest that the hyperbola may be accepted as descriptive of this type of relationship, within the limited range of temperatures encountered under field conditions, as opposed to laboratory experiments. In the present study, the altitude range between 15m and 455m is equivalent to a difference in mean temperatures of about $3^{o}C$. Humpesch and Elliott (1980) have successfully used power-law equations ($Y = aX^{-b}$) as empirical models to describe the relationship between temperature and hatching time of various Ephemeroptera. The hyperbolic equation is comparable to the power-law equation with $b = 1$ and X = the difference between the experimental temperature (T) and the lower developmental threshold (t) (i.e. $Y = a/(T - t)$).

In 1978 (Figure 5.11b) there was no relationship between the length of this period and altitude along the transect. However, the broken line on this graph, which is the trend calculated from the 1977 data, shows that the rates at 15m and 245m were similar in both years. Above this altitude these feeding times were much shorter than in the previous year.

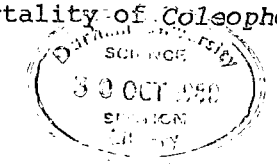
It is not known why the relationship between feeding time and altitude did not hold for the higher sites in 1978, but it may have been

due to food shortage. I have shown previously that the food supply can affect larval case production. When larval density is high, all of the excess food available to the cased larvae would be eaten soon after the early cases had been produced. This would force the later larvae from the inflorescence and result in an earlier and more synchronised migration, with all of the larvae disappearing very soon after case production.

Jordan (1958) showed that on average the larvae eat the contents of 2.3 seed capsules. Therefore at densities higher than about 0.435 larvae per seed capsule, food shortage could be expected. Competition for the excess seed capsules would not be so severe at the 245m site, even though the density of larvae in the August of both years was greater than this value, because parasitization, negligible at higher sites, would reduce the larval density both before and after case production.

5.9 Discussion

Climatic changes along the altitudinal gradient affect *Coleophora alticolella* both indirectly, through its food supply, and directly, on the speed of its development. Larval density and distribution, in relation to the seed capsules, is dependent on the distribution and abundance of eggs but is modified by food-plant success. Newly-hatched larvae do not move very far, but burrow into one of the nearest florets. Subsequent larval survival depends on whether this has developed into a seed-bearing capsule on which it may feed. Establishment of larvae in a suitable food supply can be a critical stage in the life-cycle of an insect, particularly when the eggs are laid on the surface of the food-plant (Waloff 1968). Very high mortality can sometimes occur in this situation. The failure to set seed by *Juncus squarrosus* has been shown to be responsible for 80% of the mortality of *Coleophora alticolella*,



before larval establishment, and this is the most important factor contributing to a lowering of the upper altitudinal limit of the distribution of this moth.

Insects, being poikilothermic, depend on environmental temperatures for their growth and development. This relationship has been well established by many studies which have shown a faster development from egg to adult at higher temperatures. Fewer studies have examined particular stages of the life-cycle separately. Those that have done so have usually investigated the immobile stages; eggs (e.g. Davidson 1942; Humpesch and Elliott 1980) or pupae (e.g. Nielsen and Evans 1960). These studies have confirmed the expected relationship between temperature and development. The temperature relationships of the more active, larval stages have rarely been studied in isolation. However, there is evidence to show that the relationship between development and temperature is not constant throughout an insect's life, but may change at different stages (e.g. Birch 1945). Data given by Butterfield (1976), for the development rates of the cranefly *Tipula subnodicornis*, show that the egg and pupal stages are highly sensitive to temperature, but that the larval stages are usually less affected, with Q_{10} values of one or even less.

Acclimatization, or long-term physiological adjustment to environmental temperatures, occurs in insects (Wigglesworth 1972). This is distinct from the temperature-independent metabolism which has been reported for some poikilotherms (mostly intertidal invertebrates) (e.g. Newell 1966, 1970). When acclimatized, an animal retains its temperature-dependence, but its response curve is shifted to compensate for the prevailing conditions. If fully compensating, the metabolic rates of animals held at the temperatures to which they are acclimatized will be the same (Schmidt-Nielsen 1979).

Coulson *et al.* (1976) have shown that the larval development of the tipulid *Molophilus ater* is not related to the temperature difference over a large range of altitudes in the northern Pennines. The development of the larvae of *Coleophora alticolella* inside the seed capsules of its food-plant is also constant in different parts of its altitudinal range, despite the differences in environmental temperatures. However, the development of the eggs was faster at the low altitudes, where temperatures were warmer, and it is probable that the pupal period was also shorter at these sites. Of course, these relationships between larval growth and altitude are not completely analogous to controlled experiments on the effects of temperature on development; other factors such as differential mortality or genetical differences, in the different parts of the insect's range, may also be responsible for an apparent temperature-independence. Further studies would be necessary to show if these effects were due to acclimatization to temperatures in the field; and, if there is acclimatization, whether it occurs only during the larval stages, and not during the egg or pupal stages.

Despite phases of apparent compensation for different environmental temperatures, the overall development of insects is slower in cooler conditions. However, there are other mechanisms by which insects can circumvent the effects of adverse environmental temperatures and yet still maintain seasonality, thus enabling them to inhabit a wide geographical range. These include: a change from an annual to a biennial life-cycle in colder areas, for example in the eggar moth, *Lasiocampa quercus* (L.) (Ford 1972); pupation at a small size in cooler temperatures, as in the garden chafer, *Phyllopertha horticola* (L.) (Laughlin 1963); or even the insertion of extra larval instars at higher temperatures, as Geyspits and Zarankina (1963) recorded for the pale tussock moth,

Dasychira pudibunda (L.). Geographical populations of the same species have also evolved in response to latitudinal differences in climate (Danilevskii 1965; Beck 1968).

One of the commonest mechanisms enabling insects to be synchronized with their food supply, or with other events occurring over a short period of time, is diapause (Tauber and Tauber 1976). The use of a winter diapause in the maintenance of an annual life-cycle by *Coleophora alticolella*, over the whole of its altitudinal range, is clearly demonstrated by the results given in this and the preceding chapters. In 1977, larval case production was delayed by 5.7 days and larval migration by 11.4 days, for every 100m increase in altitude. The following spring, the median date of the oviposition period was delayed by only 3.7 days per 100m. Consequently, between 15m and 455m, the 50 day delay in larval migration was reduced to only a 16 day delay in oviposition. Thus the moth is able to compensate for much of the delay caused by the retarded development at the higher sites.

CHAPTER 6

STUDIES ON THE PARASITOIDS OF *COLEOPHORA ALTICOLELLA*

6.1 Introduction

One host species is often attacked by a number of different parasitoids which may range from host-specific, monophagous species to polyphagous species attacking a variety of different hosts. Zwölfer (1971) has reviewed the structure of such parasitoid complexes in an attempt to discover what mechanisms exist to allow this competitive co-existence. Root (1967) used the term 'guild' to define a group of species that exploit the same class of environmental resources in a similar way. He developed this concept from his studies on insectivorous birds gleaning insects from the foliage of oak leaves. Since then, the concept has been applied to studies of insects (e.g. Rathcke 1976). Price (1971) has shown that the members of the guild of parasitoids attacking the cocoons of the sawfly *Neodiprion swainei* Midd. have different responses to microhabitat changes, such as moisture and host density. This enables them to co-exist on the same host.

Jordan (1958, 1962) and Reay (1959) both reared hymenopterous parasitoids from *Coleophora alticolella* larvae collected from low altitudes, but found them to be absent in areas with harsher climatic conditions. Cragg (1961) thought it unlikely that these natural enemies could have a significant effect on the population dynamics of *C. alticolella* at Moorhouse. Coulson and Whittaker (1978) suggest, however, that they could exert some regulating influence at the lower altitudes.

The two previous studies on *C. alticolella* were confined to sites above 195m and sampling during the periods of parasitization was infrequent. This aspect of the ecology of *C. alticolella* has now been

studied in greater detail, especially with the inclusion of the low altitude sample site at Drigg.

The different species of insect parasitoids reared from *C. alticolella* are listed in this chapter, followed by the results of some more detailed studies on some of the commoner species. The effects of the increasing climatic harshness on the parasitoids and their relationship with their host were also investigated. Finally, the changes in the complexity of the parasitoid guild along the altitudinal gradient are demonstrated and the competitive abilities of the parasitoids are discussed.

6.2 The species of parasitoids attacking *Coleophora alticolella*

Six species of primary parasitoid and one hyperparasitoid were reared from *Coleophora alticolella* larvae feeding on *Juncus squarrosus* during this study. All of the parasitoids were Hymenoptera and there are no records of parasitic Diptera from this host.

Primary parasitoids:

Scambus brevicornis (Gravenhorst)	Ichneumonidae, Pimplinae
Gonotypus melanostoma (Thomson)	Ichneumonidae, Campopleginae
Gelis sp.	Ichneumonidae, Phygadeuontinae
Elachertus olivaceus (Thomson)	Eulophidae, Eulophinae
Euderus viridis Thomson	Eulophidae, Euderinae
Pteromalus (Habrocytus) semotus (Walker)	Pteromalidae, Pteromalinae

Hyperparasitoid:

Tetrastichus endemus (Walker)	Eulophidae, Tetrastichinae

Scambus brevicornis was one of the commonest species of parasitoid reared from *Coleophora alticolella* by Jordan (1958) and Reay (1959). Askew (1964) has pointed out that the species of eulophid referred to in these earlier studies as "a genus near *Miotropis*" is, in fact, *Elachertus olivaceus*. Jordan and Reay both reared pteromalids from this host. Reay (1959) named his as *Habrocytus* sp. and I assume that they were *Pteromalus semotus (Habrocytus* is now a subgenus of *Pteromalus* (Fitton *et al*. 1978)). Reay also found a *Euderus* species.

Gelis instabilis (Foerster) has been recorded as a natural enemy of rush-feeding *Coleophora* by Morley and Rait-Smith (1933). The individuals reared from *C. alticolella* during this research were not identified to species because the systematics of this genus are confused at present and are undergoing review (M. Fitton pers. comm.). There is much host-mediated structural modification in the species of *Gelis;* often males and females have been described as separate species (Zwart 1978). The male *Gelis* that I reared from *Coleophora alticolella* had fully formed wings but the females were apterous.

Coleophora alticolella is a new host record for *Gonotypus melanostoma*. Only one male and one female were reared during this study, from samples taken at Drigg on 24 August 1977. This parasitoid has previously been recorded from the moths *Assara terebrella* (Zincken) and *Cydia strobilella* (L.) (Hedwig 1943).

Tetrastichus endemus is hyperparasitic, attacking *Elachertus olivaceus*.

Braconidae were not recorded as parasitoids of *Coleophora alticolella* during this study; although Jordan (1958) found *Bracon* sp., and Thompson (1945) listed two species, *Microbracon obscurator* Nees and *M. osculator* Nees.

Samples of *Coleophora alticolella* collected at various times during the summer of 1977, and cultured in an outhouse subject to normal winter conditions, did not produce any other parasitoids which may have had to undergo diapause before emergence.

6.3 *Elachertus olivaceus*

Elachertus olivaceus was one of the commonest parasitoids of *Coleophora alticolella* found during the study. It is a slightly gregarious ectoparasite and is oligophagous, being recorded from other species of rush-feeding *Coleophora* (Askew 1968; Bouček and Askew 1968). Jordan (1958) gives the impression that *Elachertus olivaceus* only attacked the host larvae that had produced cases, but during this study it was also found feeding on second, third and fourth instar hosts; they were often found inside the seed capsules before case production.

E. olivaceus were observed ovipositing on hosts in the field and in the laboratory. When laying eggs on the early host instars, the female walks over the seed capsule tapping it with her antennae. If a suitable host is found, she injects her ovipositor through the pericarp to lay on the larva within. The ovipositor of such a small species is very short and will not be able to reach a host feeding on seeds in the middle of the capsule; only those which are near to the pericarp will be susceptible to attack.

Sich (1923) suggested that the minute species of Hymenoptera might gain access to the *Coleophora* larvae by squeezing between the apical valves of the case. This seems unlikely as all of the *Elachertus olivaceus* females that I observed ovipositing on the older larvae did so by piercing the case with the ovipositor.

Examination of the host larvae parasitized by *Elachertus olivaceus* in the laboratory revealed that they were paralysed by the ovipositing female, a condition from which they never recovered. No evidence was found for more than one female ovipositing on the same host, and all of the parasite larvae on a host were at the same stage of development.

E. olivaceus overwinter as pupae. However, cast pupal skins in association with the remains of parasitized *Coleophora alticolella* larvae, inside the seed capsules,indicated that some of the individuals emerge before the winter. None of the other parasitoids pupated until the following spring. These observations corroborate an earlier suggestion by Askew (1964) that *Elachertus olivaceus* has two generations per year; a conclusion he gained from the distribution of the flight periods.

Jordan (1958) recorded up to three pupae of this species per host. I occasionally found four or even five fully formed pupae on one host, all of which emerged successfully in the laboratory. The number of *E. olivaceus* supported by the host larvae was investigated in more detail.

6.3a The number of *Elachertus olivaceus* per parasitized host

The number of *E. olivaceus* pupae found on each host larva was recorded and the results divided into groups depending on the age of the host. Two age-classes of host were used; young hosts which had not produced larval cases, and older, bigger hosts with larval cases. Table 6.1 shows that most of the smaller host larvae had only one *E. olivaceus*, and never more than two. The older larvae could support more individuals.

Table 6.1 : *The frequencies of* Coleophora alticolella *larvae, of two age-classes, with different numbers of* Elachertus olivaceus *pupae in 1977 and 1978*

	Pupae per host				
	1	2	3	4	5
1977					
Host without larval case	56	8	0	0	0
Host with larval case	55	47	22	8	1
1978					
Host without larval case	93	7	0	0	0
Host with larval case	24	34	5	2	0

Hosts attacked *E. olivaceus* before case production were never found with more than two eggs, larvae, or pupae. Therefore the difference in the average number of pupae per host, in relation to host size, cannot be attributed to competition between the developing parasitoid larvae causing a reduction in their numbers. There was, however, considerable variation in the size of the pupae on different hosts.

6.3b The length of *Elachertus olivaceus* pupae

The length of the *E. olivaceus* pupae, from the 15m and 245m sample sites, was measured microscopically. The results were separated into groups according to whether the pupae had been found on host larvae attacked before or after case production; and within these two groups,

into the lengths of pupae in different brood sizes. (For the purpose of this investigation, a brood is defined as the number of parasitoids on each host.) The results for 1977 and 1978 were combined as there were no significant differences between equivalent means. The mean lengths of pupae from different categories of host are later used in calculating pupal volume.

Table 6.2 shows that the maximum mean length of the pupae was a little over 1.8mm, and that the minimum mean length was less than three-quarters of this value, 1.333mm (the range of values was from 1.179mm to 2.051mm). The mean pupal lengths are consistently greater at 15m, but at each altitude there is variation depending on the size of the host and the number in each brood.

The differences between the mean lengths of pupae in different brood sizes, but on the same stage of host, at the two altitudes, are given in Table 6.3. There was no significant difference between the lengths of pupae in broods of one and broods of two, when *Elachertus olivaceus* parasitized larvae before they had produced their cases at the 15m sample site; but at 245m the pupae in broods of two were 16.6% shorter than solitary pupae. The difference was significant ($P < 0.01$). Similarly, when the host larvae were parasitized after they had produced cases, the pupae were found to be significantly shorter in double broods than in single broods at 245m, but not at 15m. It was not until there were four pupae in a brood that there was any significant reduction of the mean pupal length at the lower site.

Table 6.2 : *The mean lengths (mm) of* Elachertus olivaceus *pupae at two altitudes. The values are categorized according to the developmental stage of the host larva and the different brood sizes of the parasitoid*

Brood size (pupae per host)		15m		245m	
		Developmental stage of host		Developmental stage of host	
		without case	with case	without case	with case
1	$\bar{x}$	1.786	1.808	1.598	1.776
	s	0.147	0.095	0.175	0.138
	n	6	4	42	20
2	$\bar{x}$	1.756	1.714	1.333	1.624
	s	0.077	0.323	0.205	0.166
	n	4	13	6	34
3	$\bar{x}$		1.802		1.658
	s		0.149		0.213
	n		20		19
4	$\bar{x}$		1.586		1.410
	s		0.083		0.174
	n		8		8
5	$\bar{x}$				1.472
	s				0.418
	n				5

Table 6.3 : *The differences between the mean lengths of* Elachertus olivaceus *pupae, from different brood sizes on the same stage of host, at 15m and 245m*

Altitude (m)	Stage of host	Brood sizes compared	Difference (mm)	S.E. of difference (mm)	*t*	d.f.	*P*
15	Without case	1 - 2	+0.030	0.071	0.423	8	N.S.
	With case	1 - 2	+0.094	0.101	0.931	15	N.S.
	With case	1 - 3	+0.006	0.058	0.103	22	N.S.
	With case	1 - 4	+0.222	0.056	3.964	10	<0.01
245	Without case	1 - 2	+0.265	0.088	3.011	46	<0.01
	With case	1 - 2	+0.152	0.042	3.619	52	<0.001
	With case	1 - 3	+0.118	0.058	2.034	37	<0.05
	With case	1 - 4	+0.366	0.069	5.304	26	<0.001

Table 6.4 : *The differences between the mean lengths of* Elachertus olivaceus *pupae on hosts at different stages of development (with case - without case), but with the same brood size at 15m and 245m*

Altitude (m)	Brood size (pupae per host)	Difference (mm)	S.E. of difference (mm)	*t*	d.f.	*P*
15	1	+0.022	0.076	0.289	8	N.S.
15	2	-0.042	0.098	0.429	15	N.S.
245	1	+0.178	0.041	4.341	60	<0.001
245	2	+0.291	0.088	3.307	38	<0.01

Table 6.5 : *The differences between the mean lengths of* Elachertus olivaceus *pupae at different altitudes (15m - 245m), but on the same stage of host development with the same brood sizes*

Stage of host	Brood size (pupae per host)	Difference (mm)	S.E. of difference (mm)	*t*	d.f.	*P*
Without case	1	+0.188	0.066	2.848	46	<0.01
Without case	2	+0.423	0.092	4.598	8	<0.01
With case	1	+0.032	0.057	0.561	22	N.S.
With case	2	+0.090	0.094	0.957	45	N.S.
With case	3	+0.144	0.059	2.441	37	<0.05
With case	4	+0.176	0.068	2.588	14	<0.05

At 245m solitary *Elachertus olivaceus* pupae on large hosts were 11.1% longer than on the younger host larvae and, in broods of two, the pupae were 21.8% longer on the older hosts, and both differences were significant (Table 6.4). At 15m, however, there were no significant differences between the mean pupal lengths in relation to the developmental stage of the host.

Table 6.5 shows the results of *t*-tests comparing the equivalent mean pupal lengths between altitudes. Solitary *E. olivaceus* pupae that fed on host larvae before case production at 245m were 10.5% shorter than those at 15m. The pupae in broods of two on the younger hosts were 24.1% shorter at the higher sample site. Both of these differences were significant ($P < 0.01$). There were no significant differences between the mean lengths of pupae in broods of one or two on the larger hosts, but the pupae in the larger broods at 245m were significantly ($P < 0.05$) shorter than their counterparts at 15m.

6.3c Pupal volume

Length is only one measurement of the size of pupae, and on its own cannot show the full effect of brood size and host developmental stage on this parasitoid. The pupae are ellipsoid but flattened dorso-ventrally, such that they are wider than deep. Measurements were taken of the length, width and depth of twelve pupae, to enable calculation of the pupal volume.

The relationships between pupal width and length and pupal depth and length can be seen in Figure 6.1. The regression equations of width (w) on length (l) and depth (d) on length are:

$$w = 0.475l - 0.174 \qquad (6.1)$$

$$d = 0.530l - 0.486 \qquad (6.2)$$

Figure 6.1 : The relationships between *Elachertus olivaceus* pupal width and length (○) and pupal depth and length (○)

The regression of width (w) on length (l) has the equation:

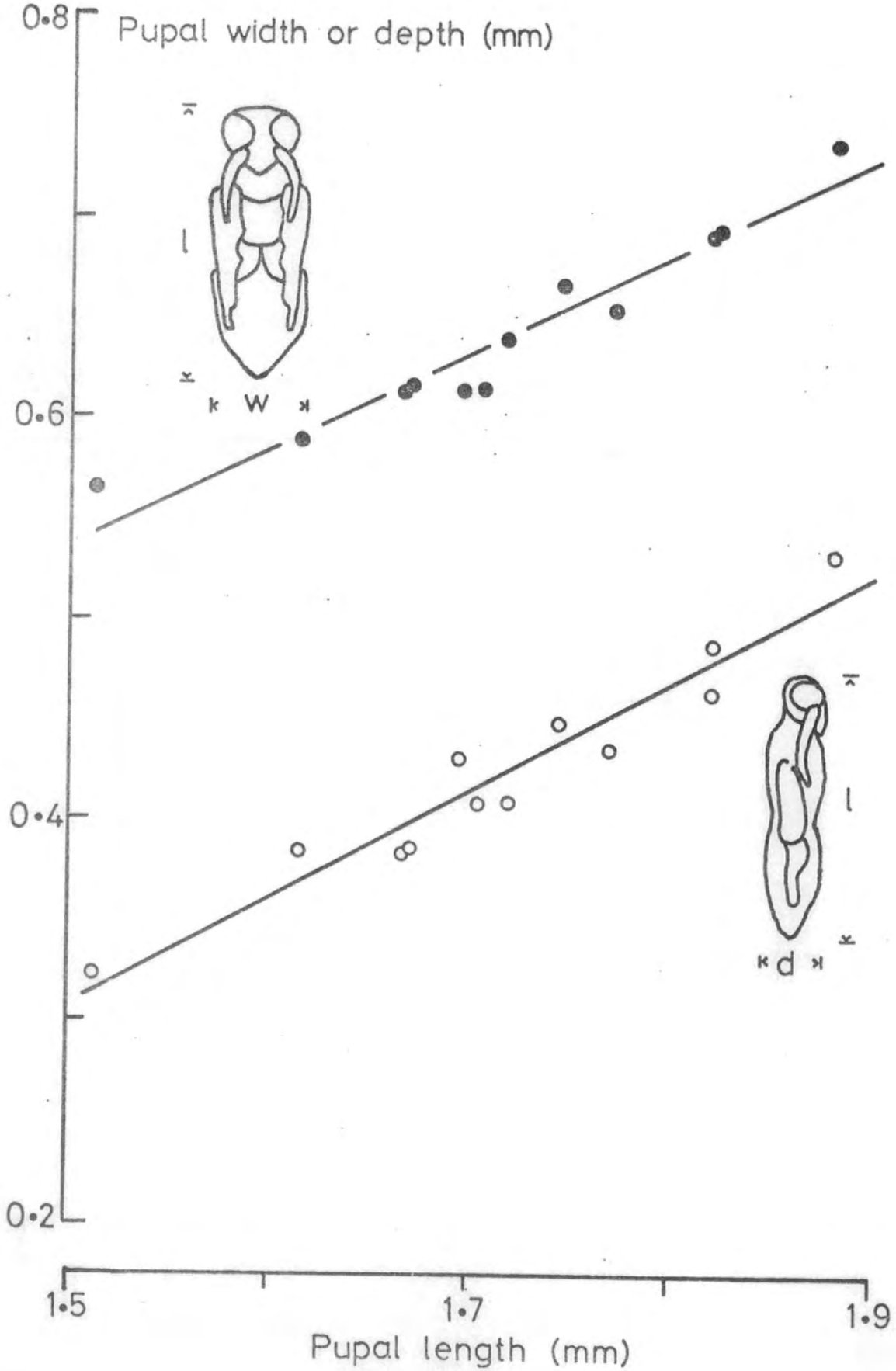
$$w = 0.475l - 0.174$$

$n = 12$, $r = 0.971$, $P < 0.001$, S.E. of slope = 0.037

The regression of depth (d) on length (l) has the equation:

$$d = 0.530l - 0.486$$

$n = 12$, $r = 0.958$, $P < 0.001$, S.E. of slope = 0.050


0·8
Pupal width or depth (mm)
l
W
0·6
0·4
d
0·2
1·5
1·7
1·9
Pupal length (mm)

The regression coefficients are not significantly different from each other (t = 0.884, d.f. = 20, $P > 0.05$) which indicates that there is a constant relationship between length, width and depth.

The volume of the pupae can be estimated as

$$\text{Volume} = {}^{4\pi}/_{3} \left({}^{l}/_{2}\right)\left({}^{w}/_{2}\right)\left({}^{d}/_{2}\right) \qquad (6.3)$$

Therefore, by substituting the values for the mean pupal lengths, from the different categories of host given in Table 6.2, into the equation

$$\text{Volume} = {}^{\pi}/_{6}\ (l)(0.475l - 0.174)(0.530l - 0.486) \qquad (6.4)$$

the volume of the pupae on the different hosts can be found. These values are given in Table 6.6. The maximum pupal volume, calculated from these mean lengths, was $0.306mm^3$ for single pupae on large hosts at the 15m site. The minimum volume was less than a quarter of this maximum, being only $0.071mm^3$ for broods of two on hosts without cases at the 245m site.

Table 6.6 : *The volume (mm^3) of* Elachertus olivaceus *pupae in different brood sizes and on hosts at different stages of development at 15m and 245m, calculated by substituting the values of mean pupal length, given in Table 6.2, into equation (6.4)*

Brood size (pupae per host)	15m		245m	
	Developmental stage of host		Developmental stage of host	
	Without case	With case	Without case	With case
1	0.291	0.306	0.177	0.284
2	0.270	0.243	0.071	0.190
3		0.302		0.209
4		0.171		0.096
5				0.119

6.3d Conclusions

It is usual for parasitic chalcids to paralyse their hosts before oviposition. This prevents the eggs from being dislodged or damaged and stops the host body from decaying before it is finally killed (Askew 1971). This is the case for *Elachertus olivaceus*, and consequently the size of the host at the time of oviposition determines the amount of food available to the parasitoid larvae.

The ovipositing female is able to regulate, to some extent, the number of eggs that she lays on a host in relation to its size (or perhaps its situation). The majority of *Coleophora alticolella* larvae attacked before case production can only support one *Elachertus olivaceus* larva, but the large, older hosts can sustain up to five of these parasitoids. Although there is no evidence for intraspecific competition causing the mortality of supernumaries, where it does occur, the limitations of the food supply result in the *E. olivaceus* pupating at a smaller size.

At the lower of the two altitudes, the *E. olivaceus* pupae were of maximum mean length and not restricted by the food supply, either on small hosts with one or two per brood, or on large hosts until there were four per brood. In comparison, at 245m the maximum mean length was only attained by single individuals on the larger of the two host types. Here the pupae on younger, smaller hosts were significantly shorter than those that had fed on the bigger hosts, as were the pupae in large broods compared with solitary pupae on either host type.

The volume of the pupae is related to their length. The pupal volume, calculated from the mean pupal length of *E. olivaceus* on the different categories of host, shows that there can be a four-fold difference in the size of pupae, depending on the brood size and host age.

The pupae of *Elachertus olivaceus* on the different categories of host were consistently smaller at 245m than their counterparts at 15m. It will be shown in Section 6.10 that there was no real difference between the first recorded date of parasiziation of *Coleophora alticolella* by *Elachertus olivaceus* at the two altitudes. Consequently, due to the progressive delay in the development of *Coleophora alticolella* with increasing altitude, host larvae will be smaller at 245m than at 15m on any given date. Thus the food supply at the higher altitude is, on average, less than at the lower site. This results in the parasitoids pupating at a smaller size at 245m.

I suggest that *C. alticolella* larvae inside the seed capsules are parasitized by the first generation of *Elachertus olivaceus* each year. The progeny emerge later that same summer, when the remaining hosts have produced cases. The second generation then develops on the larger hosts, which are able to support larger broods. There will, of course, be some overlap between the two generations, but by the end of the summer the majority of the *E. olivaceus* that were feeding on the younger hosts will have emerged, leaving only those on fourth instar larvae. This may have led to the misinterpretation of the parasitoid's life-cycle by previous authors.

6.4 *Scambus brevicornis*

Scambus brevicornis was the most widely distributed of the *Coleophora alticolella* parasitoids. It is highly polyphagic; Aubert (1969) gives a list of 23 host species from eight families of Lepidoptera, not including *C. alticolella*.

Stuart (1957) has given an account of the biology of this species, with reference to it as a parasitoid of the diamond back moth, *Plutella xylostella* (L.). He found that at 20°C the developmental

period from egg to emergence was about 16 days, followed by some seven to ten days for the maturation of eggs before oviposition. When parasitizing *Coleophora alticolella* in the field, the developmental period was much longer because it overwintered as a larva. Despite not pupating until the spring, they could be induced to emerge earlier if brought into the warmer conditions of the laboratory.

Scambus brevicornis is an ectoparasite, and virtually all of the *Coleophora alticolella* larvae attacked by this species were fourth instars. The larva of this parasitoid was usually found with the remains of its host inside the *C. alticolella* larval case; this it would use as a template for its own cocoon, which is spun inside.

Female *Scambus brevicornis* were observed ovipositing on *Coleophora alticolella* larvae in the field in late August and September. The host searching behaviour was similar to that described by Stuart (1957), but they were never seen to pierce the larval case with the ovipositor, as they did when parasitizing *Plutella xylostella*. The ovipositor was usually inserted through holes or gaps in the seed capsule wall, or through other weak points such as the junction between the larval case and capsule. Occasionally they were seen injecting the ovipositor between the valves at the apex of the larval case.

When a suitable host had been located it was paralysed and then the egg was laid. I never found more than one ichneumonid egg on a parasitized host, although Jordan (1958) reported finding more than one larva, of which only one survived.

Many female parasitic Hymenoptera eat the body fluids of some of their hosts, during adult life; this has been shown to speed up or ensure the maturation of the eggs (Askew 1971). *Scambus brevicornis* is no exception, and during this study adult females were seen eating *Coleophora alticolella* larvae. They usually attacked the larvae that were inside the thin, newly constructed cases. These

would be torn open with the mandibles and the prey partially removed, often with the ovipositor being used as a lever. The body fluids would then be eaten, leaving the empty larval skin and chitinous head-capsule.

6.5 *Euderus viridis*

Euderus viridis was another common parasitoid of *Coleophora alticolella*. Only one individual was found per parasitized host; it attacked early in the season and was found on second or third instars. The larvae of this parasitoid were always inside the seed capsule and only rarely had their hosts started to produce cases. There was only one generation per year and the larvae did not pupate until the spring. *Euderus viridis* was not observed ovipositing in the field, but adults were collected by sweep-netting at many of the sites where it was later found parasitizing *Coleophora alticolella*.

As well as parasitizing *Coleophora* species associated with *Juncus*, Bouček and Askew (1968) list it as a probable parasitoid of the moth *Glyphypterix cramerella* Fabr. and it is also found on *Dactylis*.

6.6 *Pteromalus semotus*

Pteromalus semotus was only found infrequently. It is polyphagic; a list of other hosts has been given by Graham (1969) in his description of the species. *P. semotus* has been recorded from other species of *Coleophora*, for example from *C. serratella* by Gepp (1975), and its life-history on *C. frischella* L. has been described by Delucchi and Verbeke (1953). It is a solitary parasitoid of *C. alticolella* and usually attacks this host after case production.

Graham (1969) has recorded that *Pteromalus semotus* is sometimes hyperparasitic and I have reared it from *Scambus brevicornis* larvae

inside *Coleophora alticolella* cases. Adults were swept from some of the sample sites, but none was observed ovipositing.

6.7 *Gelis* sp.

These were solitary parasitoids and the larvae are probably ectophagous. Although they do not pupate until the spring, they could be easily identified in the late summer because at that time the fully grown larva spins a dark grey or black cocoon inside the *Coleophora alticolella* case.

Gelis sp. was a much commoner parasitoid of *Coleophora* feeding on *Juncus effusus* and *J. conglomeratus* than on nearby *J. squarrosus*. This may have been due to a difference in the method of search by the females; being apterous, they are unable to fly between the widely dispersed *J. squarrosus* inflorescences. They probably aggregate on the large clumps of the other two rush species because here they can walk between the closer groups of flowers.

Two other parasitoids were found to attack *Coleophora* larvae feeding on *Juncus effusus* and *J. conglomeratus*; they were both eulophids: *Dicladocerus westwoodii* Westw. and *Miotropis unipuncta* Nees. Neither of these species were recorded from samples of *Juncus squarrosus*. A more detailed investigation into the parasitization of *Coleophora alticolella* on its different food-plants would provide more information on the subject of avoidance of competition among parasitic insects attacking the same host species.

6.8 Hyperparasitization by *Tetrastichus endemus*

Tetrastichus endemus is a solitary endophagous parasitoid of the eulophid *Elachertus olivaceus*. It was observed as a larva inside the pupa of its host. It pupates and emerges in the spring, leaving its host pupa by a hole in the 'tail-end'. There appears to be only one generation per year on *E. olivaceus*, and it was only found in the early pupae, inside the seed capsules.

Hyperparasitization by *Tetrastichus endemus* was only recorded at the lowest sample site. Very few of these hyperparasitoids were found during 1977, but many more in 1978. The percentage parasitization, given in Table 6.7, has been calculated using the number of first generation *E. olivaceus* pupae present (i.e. those inside seed capsules), plus those that had emerged. The number of potential hosts that had escaped parasitization and emerged could be assessed by the cast pupal skins with the remains of parasitized *Coleophora alticolella* larvae, inside the seed capsules. These values are from samples of 30 inflorescences gathered in November 1977 and 50 inflorescences in November 1978. The percentage hyperparasitization was about three times higher in 1978 than in the previous year.

Table 6.7 : *The number of first generation* Elachertus olivaceus *pupae present inside seed capsules and the number that had emerged, with the number that had been parasitized by* Tetrastichus endemus, *in the samples taken at Drigg in November 1977 and 1978. The percentage of the total first generation parasitized is also given.*

	1977	1978
E. olivaceus pupae present	4	28
E. olivaceus emerged	8	7
Number parasitized by *T. endemus*	2	21
% parasitization	17	60

The density of *Juncus squarrosus* inflorescences was appreciably lower in 1978 than in 1977. Table 6.8 shows the density of *Elachertus olivaceus* inside the seed capsules (live plus parasitized and emerged) and those inside the *Coleophora alticolella* cases, as well as the density of *Tetrastichus endemus*; the values are given as number per m^2.

Table 6.8 : *The number of* Elachertus olivaceus *inside seed capsules and inside host larval cases, with the number of the hyperparasitoid* Tetrastichus endemus, *from samples of* Juncus squarrosus *taken at Drigg in November 1977 and 1978. The densities are also given as the number per* m^2, *calculated from the density of inflorescences*

	1977		1978	
	Number in sample	Density (m^{-2})	Number in sample	Density (m^{-2})
J. squarrosus inflorescences	30	157	50	38
E. olivaceus inside seed capsules (generation I)	12	63	35	27
E. olivaceus pupae inside host cases (generation II)	25	131	11	8
T. endemus	2	10	21	16

The density per m^2 of the *Elachertus olivaceus* inside the seed capsules was lower in 1978 than in the previous year, but the density of *Tetrastichus endemus* was slightly higher. The high incidence of parasitization of the first generation of *Elachertus olivaceus* in 1978 resulted in a much lower density of the second generation (those inside

Coleophora alticolella cases). As Table 6.8 shows, there were more than sixteen times as many *Elachertus olivaceus* pupae per square metre inside the host cases in 1977 than in 1978.

6.9 The parasitoid sex-ratios

Female Hymenoptera are generally produced from fertilized eggs and are diploid, whereas males develop from unfertilized haploid eggs; this reproductive system is termed arrhenotokous parthenogenesis (Askew 1971). Thelytokous parthenogenesis is an alternative mechanism in which females develop from unfertilized diploid eggs and males are usually absent or rare. These reproductive systems allow considerable modification of the sex-ratio, which may be highly variable under different environmental conditions (Clausen 1939; Flanders 1962).

The sex-ratios of the adult parasitoids bred from *Coleophora alticolella* larvae are shown in Table 6.9. These differ greatly between species, from virtually all males of *Scambus brevicornis* to almost totally females of *Elachertus olivaceus*. There were significantly more females of *Euderus viridis* than would be expected from a 1:1 sex-ratio ($\chi^2_1 = 5.252$, $P < 0.05$). The other three species did not show significant deviations from the unity sex-ratio.

Table 6.9 : *The sex-ratios of adult parasitic Hymenoptera reared from* Coleophora alticolella *larvae*

	Females	Males	% Females
Scambus brevicornis	8	245	3.2
Elachertus olivaceus	168	1	99.4
Euderus viridis	72	47	60.5
Pteromalus semotus	7	12	36.8
Gelis sp.	10	7	58.8
Gonotypus melanostoma	1	1	50.0

Scambus brevicornis is biparental. Morley (1908) recorded that females were very common throughout northern and central Europe but that males were scarce. However, both Thorpe (1930) and Stuart (1957) found males to be in the majority when *S. brevicornis* was bred from the pine-shoot moth *(Rhyacionia buoliana* Schiff.) and the diamond back moth.

Male *Scambus brevicornis* were predominant in the samples of parasitized *Coleophora alticolella* larvae, but only females were collected by sweep-netting. The females ovipositing on *C. alticolella* in the field were very large in comparison with the males and the few females that were reared from the samples. Table 6.10 gives mean values for the wing and ovipositor lengths of these two groups of females and also the mean wing lengths of the males.

The wings and ovipositors of females laying eggs on *Coleophora alticolella* were both significantly longer ($P < 0.001$) than of the females bred from this host. These larger females must have developed on different host species. During July and August, female *Scambus brevicornis* were observed searching and probing with their ovipositors into the flower-heads of the thistles *Cirsium palustre* (L.) Scop. and *C. arvense* (L.) Scop., growing near to the stands of *Juncus squarrosus*. However, parasitoids were not successfully reared from samples of these thistles.

Chewyruev (1913) and Arthur and Wylie (1959) found that, in experiments on ichneumonids of the sub-family Pimplinae, females were in the majority when bred from large hosts, but that males predominated from small hosts. This disparity in the sex-ratios has been attributed to selective oviposition by the females. Flanders (1939) has shown that the ovipositing female is able to control the fertilization

Table 6.10 : *The mean wing length and ovipositor length of female* Scambus brevicornis *collected from* Juncus squarrosus *in September and of those bred from* Coleophora alticolella, *with the mean wing length of males also bred from this host*

	Females collected from *Juncus squarrosus* in September		Females reared from *Coleophora alticolella* larvae		Males reared from *Coleophora alticolella* larvae
	Ovipositor length (mm)	Wing length (mm)	Ovipositor length (mm)	Wing length (mm)	Wing length (mm)
$\bar{x}$	3.97	5.87	2.44	3.90	3.49
s	0.13	0.23	0.25	0.24	0.23
n	4	4	5	5	10

of the eggs, and thus govern the sex of her offspring. He suggests that an environmental stimulus, host size for example, could cause the release and activation of sperm from the spermatheca; hence fertilizing the egg if it is being laid on a host suitable for the development of a female. Therefore the sex-ratio of the next generation will be determined by the proportions of large and small hosts available for oviposition.

It seems likely that *Scambus brevicornis* lays mostly unfertilized eggs on *Coleophora alticolella* because this host does not provide sufficient food to allow the females to grow to maximum size. It was not possible to calculate the sex-ratio for the whole population of this species because the alternative hosts were not found.

Elachertus olivaceus will oviposit and develop on *Coleophora alticolella* larvae in the laboratory. Several generations of this parasitoid were reared during the study, and it was evident that this species can reproduce parthenogenetically. Uniparental bisexuality does occur, with males as well as females being produced by unfertilized females. The males of *Elachertus olivaceus* are very rare (Askew 1964); only one was found from a total of 169 individuals bred from samples taken from the field during this study. However, in the laboratory cultures, a higher percentage of males was produced (11.6% of a total of 129).

Flanders (1945) noted that changes of the sex-ratio of uniparental species are often correlated with the type of habitat or the season in which the previous generation developed. For example, males of *Encarsia formosa* Gahan, a parasitoid of the greenhouse whitefly *Trialeurodies vaporium* (Westw.), appear in the autumn, being progeny of females that developed during the warm summer. Cyclical parthenogenesis (heterogony), resulting in alternating sexually and asexually

reproducing generations in different seasons, is well-documented for other groups of animals (White 1977); it occurs in many Hymenoptera and is perhaps best-known in the gall-wasps (Cynipidae) (e.g. Cameron 1903).

The higher percentage of male *Elachertus olivaceus* may have occurred in the laboratory cultures because the females developed in warm conditions. The collection of this species from locations with summer temperatures higher than in northern England would show if males are produced in the field as a result of the thermal history of the parental females.

6.10 The phenology of parasitoid attack

For this investigation, samples of twenty *Juncus squarrosus* inflorescences were collected from 15m and 245m each week. These samples were usually collected on consecutive days at the two sites, first at 15m, then 245m. The inflorescences were placed into ventilated containers and cultured in the laboratory. The adult parasitoids were removed soon after they had emerged, to prevent further parasitization of remaining hosts. By this method it was possible to record the week in which each species of parasitoid first attacked the *Coleophora alticolella* larvae. Only the three commonest species were analysed in this way. The results are given in Table 6.11.

The difference of one day between the samples in which *Elachertus olivaceus* was first recorded at the two sites is due to sampling on consecutive dates. In 1978 they were first recorded from samples taken at a later date than in 1977. This difference between years was, however, the same as the time between samples, so the real difference between years may have been less than the seven days indicated by this method.

Table 6.11 : *The sample date on which three species of parasitoid were first recorded from* Coleophora alticolella *at two sites in 1977 and 1978*

	15m		245m	
	1977	1978	1977	1978
Elachertus olivaceus	3 Aug	10 Aug	4 Aug	11 Aug
Euderus viridis	26 July	29 July	11 Aug	9 Sept
Scambus brevicornis	17 Aug	8 Sept	9 Sept	25 Sept

Adult *E. olivaceus* were taken in sweep-net samples at all sites up to and including 305m on 11 August in 1978; a further indication that there was no appreciable delay at the higher altitudes.

Euderus viridis occurred earlier at the 15m site than at 245m in both years. There was little difference between years at 15m, but at 245m it was first recorded almost a month later in the second year. *E. viridis* first attacked the hosts earlier than *Elachertus olivaceus* at 15m, but later at the higher altitude.

Scambus brevicornis was about three weeks earlier at the lower sample site and also about three weeks later in 1978 than in 1977. Its first occurrence was always later than that of the two eulophids. This is expected because *S. brevicornis* attacked the larvae with cases whereas the two eulophids were found on younger hosts.

The appearance of the different parasitoids in the samples of *Coleophora alticolella* need not necessarily be correlated with their emergence in the field. They may have been present at an earlier date but not detected because they were unable to attack the much younger host larvae.

There was a delay of three to four weeks between the production of the first larval cases and the first records of *Scambus brevicornis*, which indicated that this parasitoid was not limited by first appearance of the susceptible stage. Whether this was due to the female *S. brevicornis* emerging later than *Coleophora alticolella* case production, or to the utilization of alternative hosts until the start of attack, is not known.

Host-parasitoid synchrony is more important for monophagous or oligophagous species than for those with a wider host range (Hassell 1976). The polyphagous species, such as *Scambus brevicornis*, can be more opportunistic, ovipositing on whatever is abundant at the time. On the other hand, the two eulophids have a very limited host range, probably relying entirely on *Coleophora alticolella* in the study areas. Parasitization by *Euderus viridis* was delayed at the higher of the two altitudes. However, there was no such delay for *Elachertus olivaceus* and this slight asynchrony resulted in the production of smaller progeny at the higher altitude.

6.11 Parasitization of *Coleophora alticolella* larvae in relation to altitude

The parasitization of *Coleophora alticolella* can be considered in two phases. Some of the larvae are attacked whilst still inside the seed capsules, before case production. This occurs from the beginning of August and most of these parasitized larvae are of the third instar. The second phase of attack is later in the larval development, when they are parasitized after they have produced their cases and are mainly of the larger fourth instar. These two phases are not entirely separated, for the host population as a whole, because

larval cases are produced over a period of several weeks, so both young and old host larvae will be present at the same time for much of the summer.

Table 6.12 shows the number of parasitized *Coleophora alticolella* larvae found in samples taken in early November 1977. The data are separated according to the two age-classes of host larva and are expressed as the number of parasitized *C. alticolella* larvae per 1000 seed capsules

Table 6.12 : *The number of parasitized* Coleophora alticolella *larvae per 1000 seed capsules of* Juncus squarrosus *at different altitudes in November 1977. Values for the number attacked before and after case production are given separately (5 November at 15m; 6 November, Little Dun Fell)*

Altitude (m)	Parasitized larvae per 1000 seed capsules (without cases)	Parasitized larvae per 1000 seed capsules (with cases)	Total number of parasitized larvae in each sample
15	27.2	41.5	48
215	16.0	182.6	87
245	13.0	97.5	93
275	4.1	43.6	47
305	0.0	32.6	28
335	0.0	7.0	5
365	0.0	6.6	4
395	0.0	4.1	1
455	0.0	0.0	0

of *Juncus squarrosus*. The number of parasitized larvae in both situations shows an overall decrease with increasing altitude,

although there were fewer parasitized larvae with cases at the 15m site than at the first three sites on Little Dun Fell. There was always a higher proportion of the older host larvae parasitized than the ones before case production at each altitude. Parasitized larvae were not found inside seed capsules above 275m, whereas some of the older hosts were found to be parasitized as high as 395m.

In November 1978, samples of *Juncus squarrosus* were collected from more sites than in the previous year. The data from these samples (Table 6.13) also show that there is a reduction in the number of larvae parasitized, with increasing altitude. However, in 1978, parasitized larvae inside seed capsules were recorded at 305m, 30m higher than in the previous year, but parasitized larvae inside host cases did not occur above 365m. In addition, at 15m, 215m and 290m, the greater proportion of the parasitoids were found on the younger host larvae. The occurrence of parasitized larvae inside seed capsules at the higher altitudes may have been due to the delayed case production by the larvae in 1978.

Parasitization is expressed as a percentage of the number of *Coleophora alticolella* larvae present in August; that is, near to the beginning of the parasitization period. The percentage has been calculated from the total number of parasitized larvae present per seed capsule (including those that had emerged) in the November samples; i.e. at the end of the parasitization period. This can be summarized by the formula

$$\% \text{ Parasitized} = \frac{\text{Parasitized larvae per seed capsule in November}}{\text{Larvae per seed capsule in August}} \times 100$$

The densities of larvae per seed capsule in August are those used in Section 5.2, and are given in Appendix 5.

Table 6.13 : *The number of parasitized* Coleophora alticolella *larvae per 1000 seed capsules of* Juncus squarrosus, *at different altitudes in November 1978. Values for the numbers parasitized before and after case production are given separately. (Sample dates: Little Dun Fell, 7 Nov; 15m, 8 Nov.)*

Altitude (m)	Parasitized larvae per 1000 seed capsules (without cases)	Parasitized larvae per 1000 seed capsules (with cases)	Total number of parasitized larvae in each sample
15	119.7	50.2	193
215	72.1	31.2	53
245	48.3	75.7	137
260	33.6	38.4	49
275	16.6	39.5	89
290	27.3	11.7	30
305	0.6	16.3	29
335	0.0	2.6	5
350	0.0	0.0	0
365	0.0	0.6	1
395	0.0	0.0	0
455	0.0	0.0	0
520	0.0	0.0	0

Larval densities were measured at only a few sites in the August of 1977, but over the complete altitude range in August 1978. Table 6.14 shows the percentages of larvae parasitized at the major sample sites in both 1977 and 1978. The complete range of values for the percentage parasitization at the different altitudes in 1978 are shown in Figure 6.2.

Table 6.14 : *The percentage of* Coleophora alticolella *larvae parasitized at the major sample sites in 1977 and 1978*

Altitude (m)	% Parasitized 1977	1978
15	46.1	61.1
245	18.0	21.0
335	1.8	0.3
395	1.4	0.0
455	0.0	0.0
520	0.0	0.0

Table 6.14 shows that there was a dramatic reduction in parasitization with increasing altitude. Although parasitization at 15m was lower in 1977, there was little difference between the two years on the Little Dun Fell transect. Parasitization was also high at the 215m site in 1978 (Figure 6.2). This figure shows that the precipitous reduction of parasitization started around this altitude, falling from 51% to 2% with a 90m increase in altitude. The sites on the lower slopes of Little Dun Fell were close together, the 215m and 305m sites being separated by a distance of only 4km.

Both Jordan (1962) and Reay (1959) found that there was a reduction in the incidence of parasitization of *C. alticolella* with increasing altitude along this transect. In 1953 for example, Jordan recorded parasitization of 31.8% and 31.3% at 198m and 228m respectively, but found that only 7.6% were parasitized at 320m.

Figure 6.2 : The percentage parasitization of *Coleophora alticolella* larvae plotted against altitude, for samples taken in early November 1978

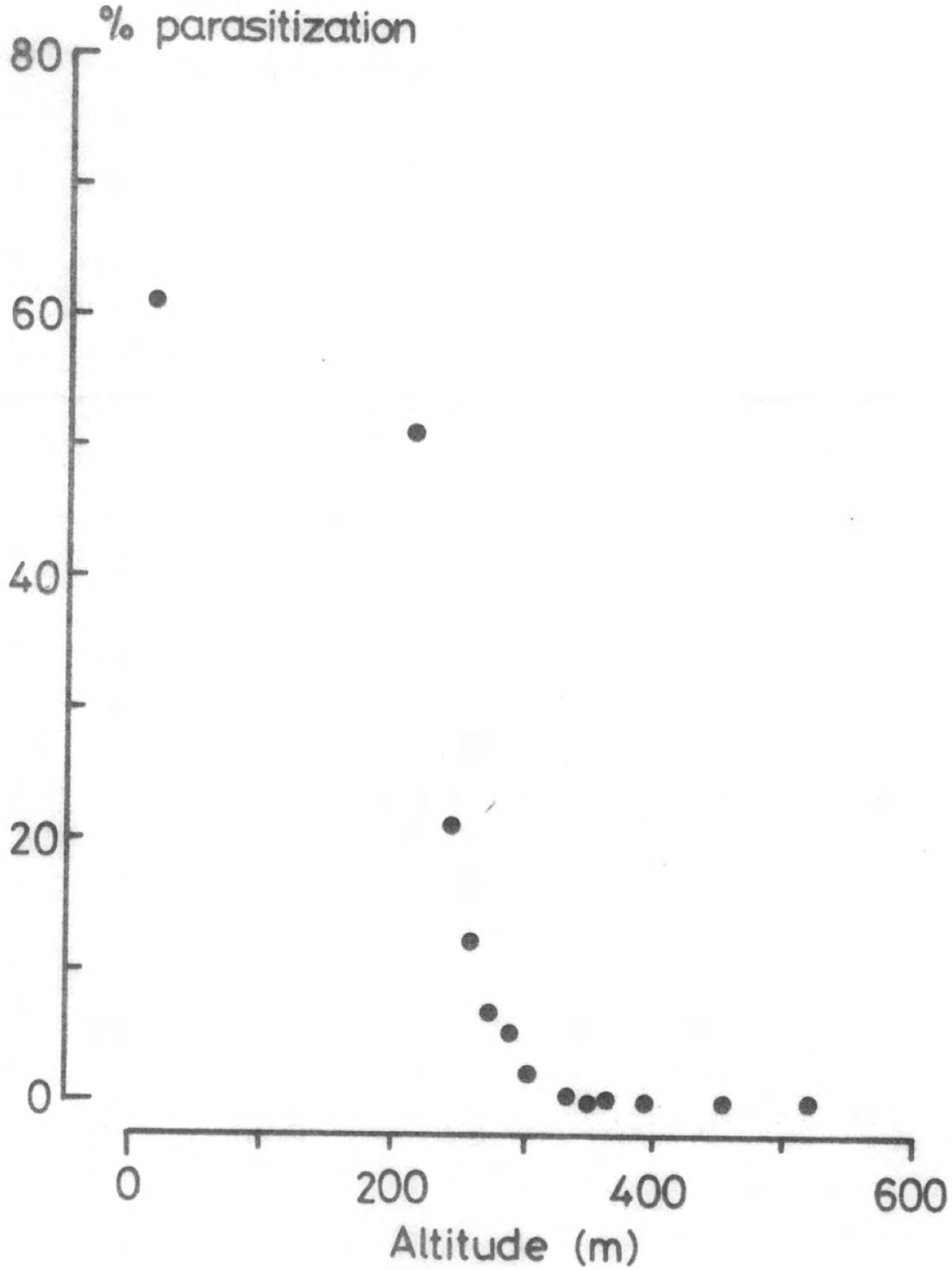

% parasitization
80
60
40
20
0
0
200
400
600
Altitude (m)

Table 6.15 gives different measurements of the density of host larvae at three sites, and shows that the number of larvae per m^2 was highly variable, both between years and between sites, but that this was not related to the percentage parasitization. On a micro-scale, larvae per inflorescence or per seed capsule was generally higher at the higher sites than at Drigg. There is insufficient data from any one site to tell if the percentage parasitization is directly related to host density or whether it acts as a delayed density dependent factor. However, it is clear from this data and the evidence of previous authors that the reduction in parasitization with increasing altitude is not directly related to the changes in host density along the transect.

6.12 The diversity of the parasitoid guild in relation to altitude

Not all of these natural enemies were recorded parasitizing *Coleophora alticolella* larvae at each site. Table 6.16 shows that the number of different species bred from the host larvae is reduced with increasing altitude.

The species that was found attacking *C. alticolella* furthest up the transect was the largest of the parasitoids, the ichneumon *Scambus brevicornis;* this was recorded from *Coleophora alticolella* at 395m in 1977 and 365m in 1978. *Elachertus olivaceus* was the chalcid with the greatest altitudinal range, as it was bred from host larvae collected at 305m in both years. This was closely followed by *Euderus viridis,* whose upper limit was 290m in 1978. *Pteromalus semotus* and *Gelis* sp. were occasionally found at 275m and below, but *Gonotypus melanostoma* and the hyperparasitoid *Tetrastichus endemus* were only recorded at the lowest sample site.

Table 6.15 : *The percentage parasitization of* Coleophora alticolella *larvae, at three altitudes in 1977 and 1978, in relation to different measurements of larval density in August*

Altitude (m)	Year	Larvae per m^2	Larvae per inflorescence	Larvae per seed capsule	% parasitization
15	1977	566	2.70	0.149	46.1
	1978	241	4.00	0.278	61.1
245	1977	482	8.17	0.614	18.0
	1978	174	7.10	0.592	21.0
335	1977	335	4.31	0.356	1.8
	1978	602	6.13	0.807	0.3

Table 6.16 : *The species of parasitic Hymenoptera reared from* Coleophora alticolella *larvae collected at different altitudes in 1977 and 1978*

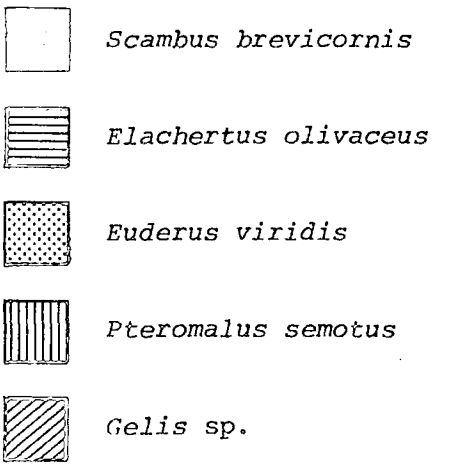
	Altitude (m)	*Scambus brevicornis*	*Elachertus olivaceus*	*Euderus viridis*	*Pteromalus semotus*	*Gelis* sp.	*Gonotypus melanostoma*	*Tetrastichus endemus*
1977	15	+	+	+	+	+	+	+
	215	+	+	+	+			
	245	+	+	+	+	+		
	275	+	+	+		+		
	305	+	+					
	335	+						
	365	+						
	395	+						
	455							
1978	15	+	+	+	+	+		+
	215	+	+	+				
	245	+	+	+	+	+		
	260	+	+	+		+		
	275	+	+	+	+			
	290	+	+	+				
	305	+	+					
	335	+						
	350							
	365	+						
	395							
	455							

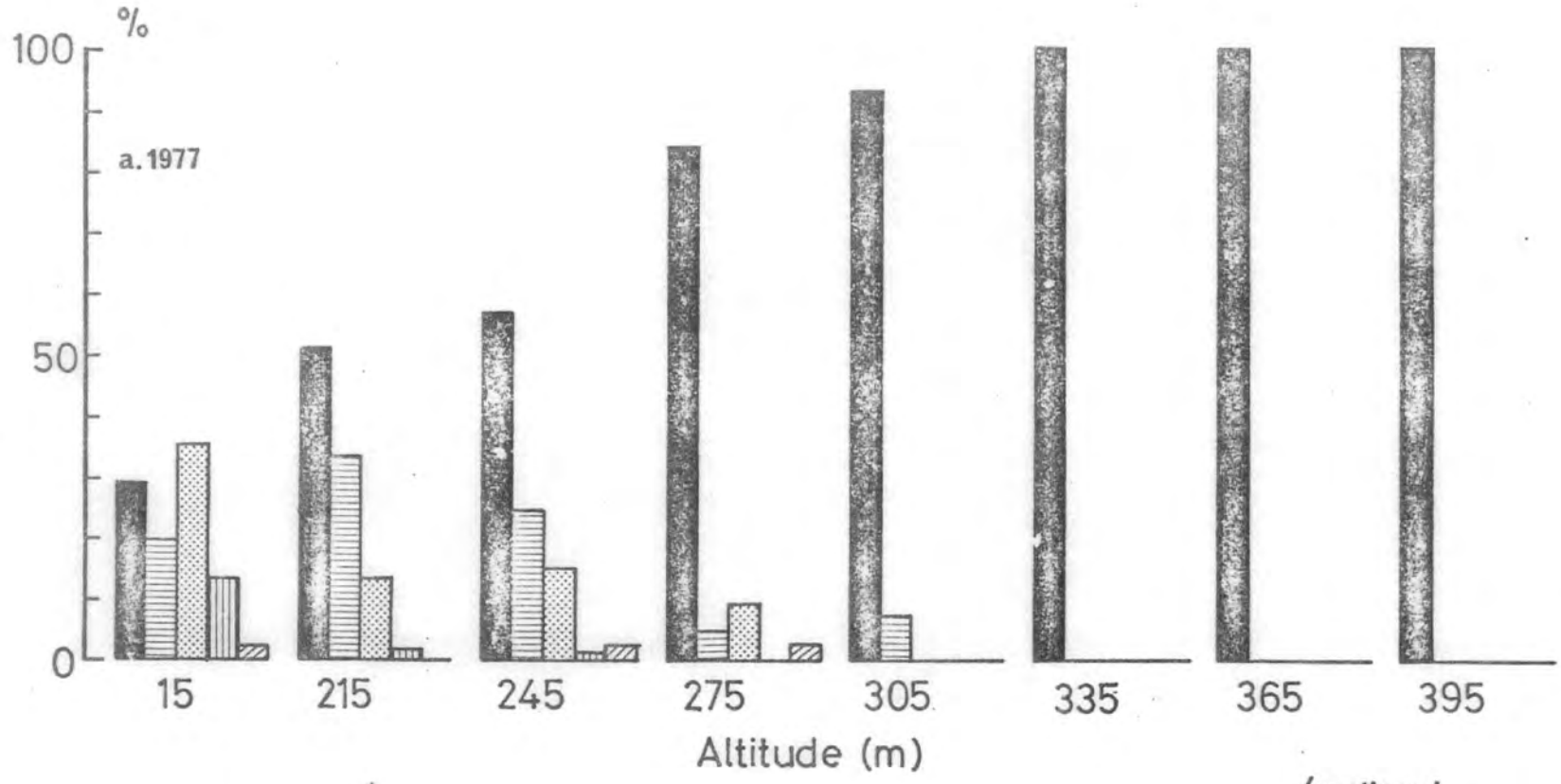
Table 6.16 was constructed on a presence or absence basis for the natural enemies and as such gives equal weight to all species. Although this gives some indication of the species diversity, it does not show the relative proportions of the different species at each of the sites. The percentages of each component species in the guild of *Coleophora alticolella* larval parasitoids, from the November samples, are shown as histograms in Figure 6.3a for 1977 and Figure 6.3b for 1978. They do not include the incidence of the hyperparasitoid, which has been discussed elsewhere.

Apart from the reduction in the number of species of parasitoid with increasing altitude, the main feature shown by these figures is the increase in the dominance of *Scambus brevicornis* at the higher altitudes. Obviously it represents 100% of the species composition when it is the only parasitoid present, but at altitudes where other species were recorded it was often the most numerous. This dominance by *S. brevicornis* was particularly noticeable in 1977, whereas in 1978 some of the other species were more frequent on the Little Dun Fell transect. Despite the dominance of *S. brevicornis* at high altitudes, its density is lower at these sites.

S. brevicornis accounted for less than 30% of the parasitized hosts at 15m in both years, *Euderus viridis* being the dominant member of the guild at this site. *Elachertus olivaceus* was the commoner of the two eulophids at most of the sites on Little Dun Fell and contributed to over 50% of the total *Coleophora alticolella* parasitized at 215m in 1978. The two remaining species, shown on these graphs, contributed little to the total parasitization even at the lowest altitude. *Gonotypus melanostoma* is not shown in these figures as it was absent from the November samples.

Figure 6.3 : The composition of the parasitoid guild at different altitudes in (a) 1977 and (b) 1978. The contribution made by each species is shown as a percentage of the total parasitized *Coleophora alticolella* larvae.





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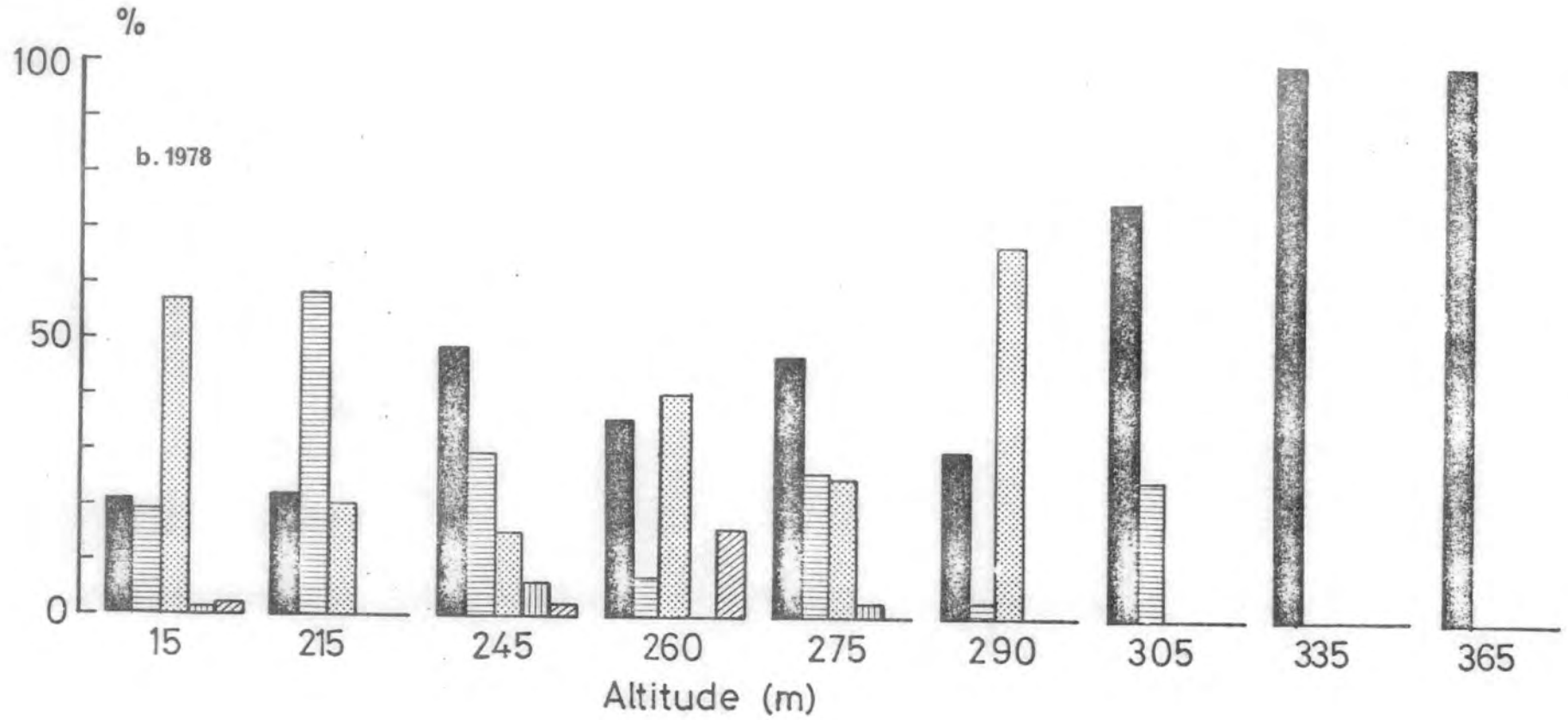

%
100
50
0
b. 1978
15
215
245
260
275
290
305
335
365
Altitude (m)

The eulophids were more sensitive to the harsher conditions at the higher altitude than was *Scambus brevicornis*. This was responsible for the decrease in the proportion of parasitized larvae found inside seed capsules compared with those in cases (Tables 6.12 and 6.13) and finally resulted in only the older hosts being attacked towards the upper limit of parasitoid distribution.

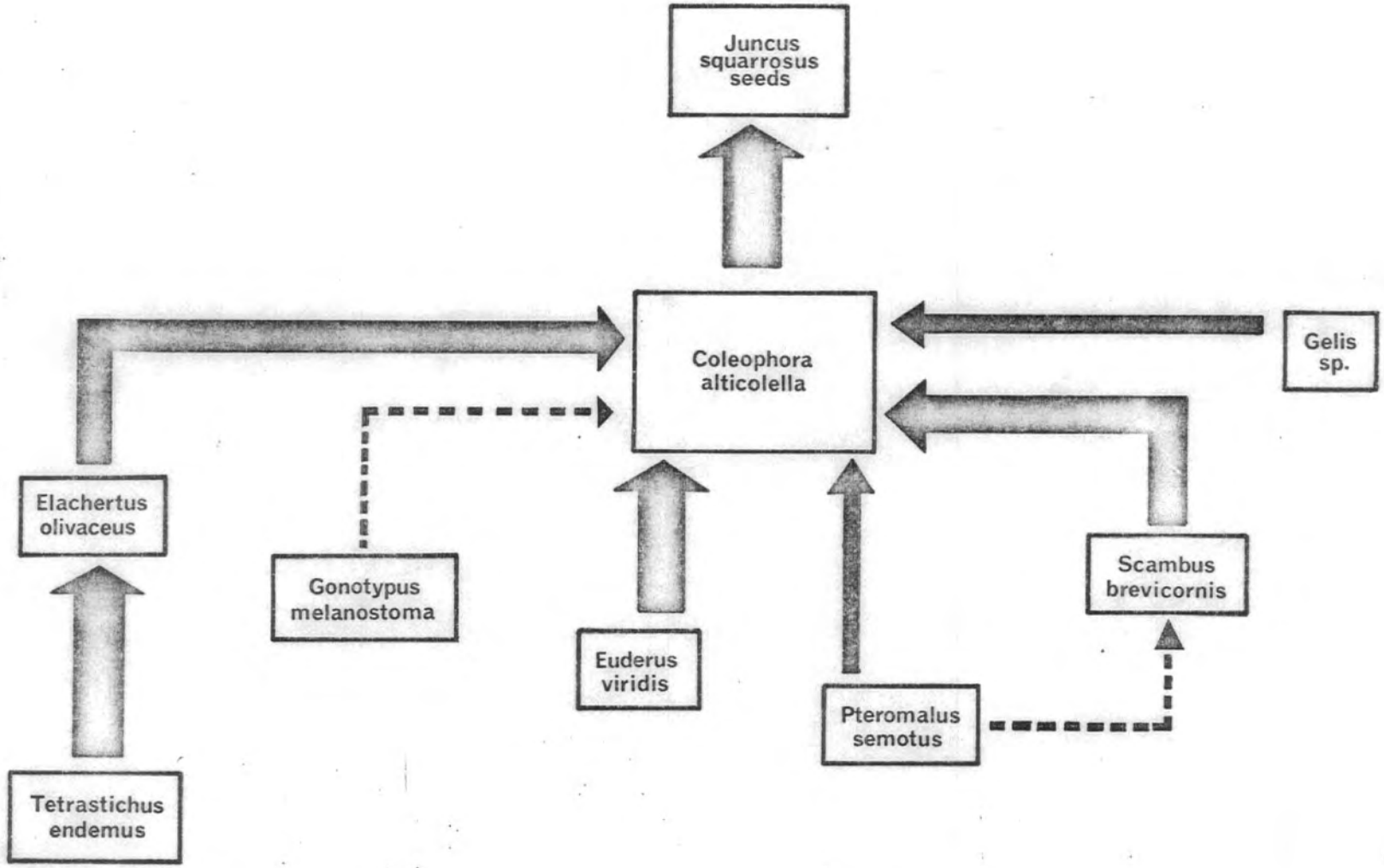
6.13 A summary of the relationships between *Coleophora alticolella* and its larval parasitoids

A summary diagram of the relationships between the parasitoids and their host is shown in Figure 6.4. This has been constructed from data for the 15m sample site, where the food-web was most complex. The thickness of each arrow for the primary parasitoids ranks their abundance in 1978. *Gonotypus melanostoma* is shown with a broken arrow as it was only recorded in 1977. The link between *Pteromalus semotus* and *Scambus brevicornis* is also shown as a broken line because this was a very infrequent relationship, being recorded on only three occasions during the whole study.

6.14 Discussion

Parasitic Hymenoptera and Diptera are under-represented in the insect faunas of moorlands (Coulson and Whittaker 1978). Whittaker (1965, 1971) found that the parasitoids of the spittle bug *Neophilaenus lineatus* (L.) were absent from Moor House but were present in a low altitude population in southern England. The absence of parasitoids of other insects on moorlands has been demonstrated at Moor House; e.g. the tipulid *Molophilus ater* (Hadley 1971) and the carabid beetles (Houston 1970) were never attacked by these natural enemies. If it does occur, parasitization is at a low level; e.g. the dipteran

Figure 6.4 : The relationships between *Coleophora alticolella* and its larval parasitoids based on data from the 15m sample site.


Juncus squarrosus seeds
Coleophora alticolella
Gelis sp.
Elachertus olivaceus
Gonotypus melanostoma
Euderus viridis
Scambus brevicornis
Pteromalus semotus
Tetrastichus endemus

Siphona genticulata (Degeer) attacking the larvae of the crane fly *Tipula subnodicornis* Zett. (Coulson 1962) or the eulophid *Tetrastichus actis* (Walker) parasitizing the heather psyllid *Strophingia ericae* (Curtis) (Hodkinson 1973).

Similar altitudinal effects have been found in Scandinavia. Studies of the invertebrate fauna on the branches of birch showed a reduction in the proportion of predators and parasitoids with increasing altitude (Hågvar 1976), and in alpine habitats in southern Norway the chrysomellid beetle *Melasoma collaris* L. was never attacked by parasitoids (Hågvar 1975).

Although the searching and oviposition rates of parasitic Hymenoptera are reduced at low temperatures (e.g. Burnett 1951, 1954; Boldt 1974), these observed reductions of parasitization at high altitude cannot be entirely attributable to cooler conditions. The parasitization of *Coleophora alticolella* was reduced from over 50% to less than 2% with an altitudinal increase of only 90 metres; this is equivalent to a fall in temperature of only $\frac{1}{2}^{o}C$. Temperature is only one of many climatic variables. Other effects of weather conditions on parasitoids have been reported; for example, rain and heavy dew cause reductions in oviposition (Burnett 1954, 1956), flight activity is reduced in windy conditions (Juillet 1960, 1964) and humidity can affect searching rates (Boldt 1974). During this research it was noted that the ichneumon *Scambus brevicornis* stopped searching and ovipositing when it rained. These effects of weather are severe limitations in upland areas like the Pennines, where there is much rain and it is frequently misty. In addition, there is little shelter from the high winds which blow over the moors.

Other factors, apart from the effects of climate on searching efficiency, will reduce the parasitoids' rates of increase. Synchrony

with the host is important if a parasitoid has a short adult life or if it can only attack at a particular stage of host development. The start of attack by *Elachertus olivaceus* was not delayed with increasing altitude and it was able to parasitize some of the small hosts even at the higher sites. However, the accessibility of the younger larvae may have been a limiting factor. At the low altitudes the relatively larger third instars will occupy more space inside the seed capsules and will, therefore, be closer to the pericarp, through which the adult parasitoid oviposits. At the higher sites the same instar will, on average, be smaller and more difficult to locate among the seeds. This problem is not solved entirely by delaying the time of attack at the higher altitudes, as *Scambus brevicornis* does. The preferred stage of host may be more abundant later in the year, but this is also when the conditions are less favourable, with cooler and wetter weather, and also shorter day length, which together reduce the searching efficiency. The effects of the approaching winter will, of course, be more noticeable and relatively earlier at higher altitudes.

As a consequence of the lack of synchrony with its host, the *Elachertus olivaceus* were smaller at the higher site. This reduction of body size could result in a lower fecundity, reduced powers of dispersal and a shorter adult life.

Host parasitoid synchrony will be more important for the oligophagous species, which probably relied entirely on *Coleophora alticolella* on Little Dun Fell. *Scambus brevicornis* is polyphagous and may have other generations on a variety of hosts. Indeed, this parasitoid must use other hosts for the production of females. If these alternatives are absent from a site, the use of *Coleophora alticolella* as a host may be prevented. The diversity of invertebrate

species is reduced with increasing altitude (Hågvar 1976; Coulson and Whittaker 1978; Coulson and Butterfield, pers. comm.). Consequently, despite the abundance of *Coleophora alticolella*, the alternative hosts on which *Scambus brevicornis* depends for its summer generation and, more importantly, for the production of females, may be scarce at the higher altitudes. It is possible that the large alternative hosts were absent altogether from the higher sites. If this were the case, the parasitization of *Coleophora alticolella* could be entirely due to the immigration of a few females. (They could be easily blown up the hillside as no great distance is involved.) They would lay unfertilized eggs on the small hosts and only males would emerge the following year. Extinction of the parasitoid would then follow until the next influx of females.

The complexity of the parasitoid guild is reduced under harsher climatic conditions, with the hyperparasitoid being the first to drop out. Coulson and Whittaker (1978) have noted that the virtual absence of top predators, to which obligate hyperparasitoids are analogous, results in the simplified food chains characteristic of moorlands. The parasitoids with the greater host specificity were dominant in the areas with the more stable climatic conditions, whereas the opportunistic polyphage penetrated to the higher altitudes.

Zwölfer (1971) has suggested that in order to co-exist, competing parasitoids may counter-balance the efficiency of exploiting the host population (by better searching abilities or higher reproductive capacities) against improved competitive abilities in direct interactions (by successful hyperparasitism for example). He illustrated this theory of 'counter-balanced competition' with several examples, including the parasitoid complex of the European pine sawfly (*Neodiprion serfiter* Geoffr.).

Similar conclusions about competition among parasitoids were being drawn in America (Force 1970). Here they were later viewed within the framework of r- and K- selection, as proposed by MacArthur and Wilson (1967) and further elaborated by Pianka (1970). Force (1972, 1974) compared four parasitoids of the cecidomyiid gall midge *Rhopalomyia californica* Felt, and found that their reproductive capacities were inversely related to their competitive abilities. He was able to order them along an r - K continuum, and showed that the least competitive (r-selected) was commonest in the earliest stages of succession and where environmental conditions were severest.

Price (1973) contributed further to this type of analysis with his studies on the parasitoids of the sawfly *Neodiprion swainei* Midd. He showed that the r-strategists predominated towards the edges of the host range. They were also found in newly colonised areas, from where they were displaced by the competitively superior K-selected species, as succession continued.

Price (1970, 1971, 1973) showed that the better competitors were those that attacked the cocoons of the sawfly; they were often hyperparasitic through the enemies of the host larvae. The parasitoids that attacked the larvae had the higher reproductive rates. It is not always the case that the later attacking species are better competitors. They may not be able to attack a host that has been previously parasitized (Force 1970). This will result in a lowering of the density of hosts available to these later species, causing a reduction in their rate of increase (Beddington *et al.* 1976; Hassell 1978).

There are limitations to this type of analysis as it is not always possible to compare parasitoids of different families (Barbosa 1977) and the intensity of competition may change, depending upon the trait under consideration (Force 1975). However, the three commonest

parasitoids of *Coleophora alticolella* can be seen to differ in their competitive abilities. The eulophids attack the young host larvae. This prevents case production and therefore reduces the density of available hosts for *Scambus brevicornis*. On the other hand, *S. brevicornis* can tolerate a wider range of environmental conditions and has a greater range of hosts than its competitors. *Elachertus olivaceus* can produce more progeny per individual host than *Euderus viridis* and it has two generations per year on *Coleophora alticolella*.

CHAPTER 7

POPULATION STUDIES ON *COLEOPHORA ALTICOLELLA*

7.1 Introduction

In the previous chapters data were presented on the amount of food available to the *Coleophora alticolella* larvae, the density of their eggs and larvae, and the effects of parasitization. This chapter is a synthesis of these data in the form of age-specific life-tables for the moth population at different altitudes.

The analysis of life-tables can reveal the causes of fluctuations in animal numbers and the limits between which these fluctuations occur. This is achieved by the identification of the key factors responsible for population change and the appraisal of density-dependent factors responsible for population regulation (e.g. Varley, Gradwell and Hassell 1973).

Southwood (1966) has pointed out that data from different areas should be analysed separately, as the level of the population and the roles of different factors may vary from locality to locality. In this chapter, the analysis of life-tables for *Coleophora alticolella* shows that the mortality factors vary with altitude and that different factors could play a key role in determining population change in different parts of the altitudinal range.

7.2 The life-tables

The life-tables for *Coleophora alticolella* at six sites of different altitudes are presented in Table 7.1a-f. They cover the period from eggs in 1977 to larvae in seed capsules in 1979, which is a little over two generations. Data have been based on the number of each stage

present per seed capsule, and then converted to the density per square metre to enable comparisons between years.

The data for the 1978 season are the most complete and have been used as a framework for the calculation of some of the values in other years; the values that were measured directly are indicated. The density of larvae was measured at all of the sites in the August of each year (Section 5.2 and Appendix 5). These values have been used as the starting point for the rest of the calculations.

The values for the k-factors have been calculated in the usual way by the formula

$$k_i = \log N_i - \log N_{i+1}$$

where N_i is the density of *Coleophora alticolella* before a mortality factor and N_{i+1} is the density after that factor has acted; common logarithms have been used throughout.

a. Eggs

The number of eggs laid at each site was measured in 1978 and the resulting larval densities showed that survival, from the egg stage to establishment inside the seed capsules, was mainly dependent on seed capsule development. The calculations in Chapter 5 showed that the survival rate in 1978 was approximately 80% of the proportion of florets developing into seed capsules. To calculate the density of eggs laid in 1977 and 1979 it has been assumed that survival was similarly related to seed capsule production. The survival rate is therefore calculated from the formula

$$S = 0.8R$$

where S is the proportion of *C. alticolella* surviving to establishment inside the seed capsules and R is the proportion of florets developing

Table 7.1 : *Life tables for* Coleophora alticolella *at*

a. 15 metres

b. 245 metres

c. 335 metres

d. 395 metres

e. 455 metres

f. 520 metres

l_x The density per square metre at the start of each stage (x)

d_x The number dying from different mortality factors

k The mortality in each stage

The values in italics are those measured directly; the rest have been calculated from these.

An explanation of the terms and the methods of calculation of the values is given in the text.

Table 7.1a : *Life-table for* Coleophora alticolella *at 15m (numbers per* m^2*)*

Stage (x)	Mortality	l_x	d_x	k
1977				
Eggs		762		
	Seed capsule failure		196	0.129
Larvae established in seed capsules		566		
	Grazing		0	0.000
	Parasitoids		103	0.087
	Dead in capsule		164	0.190
Larvae with cases		299		
	Parasitoids		158	0.326
	Dead in case		11	0.035
	Grazing		0	0.000
Larvae migrating to leaf-litter		130		
Potential eggs		5850		
1978	Egg shortfall		5548	1.287
Eggs		302		
	Seed capsule failure		57	0.091
Larvae established in seed capsules		245		
	Grazing		4	0.007
	Parasitoids		104	0.245
	Dead in capsule		70	0.311
Larvae with cases		67		
	Parasitoids		44	0.464
	Dead in case		5	0.106
	Grazing		0	0.000
Larvae migrating to leaf-litter		18		
Potential eggs		810		
1979	Egg shortfall		733	1.022
Eggs		77		
	Seed capsule failure		25	0.170
Larvae established in seed capsules		52		
	Grazing		0	0.000

Table 7.1b : *Life-table for* Coleophora alticolella *at 245m (numbers per* m^2*)*

Stage (x)	Mortality	l_x	d_x	k
1977				
Eggs		838		
	Seed capsule failure		272	0.170
Larvae established in seed capsules		566		
	Grazing		84	0.070
	Parasitoids		10	0.009
	Dead in capsule		130	0.140
Larvae with cases		342		
	Parasitoids		77	0.111
	Dead in case		56	0.103
	Grazing		162	0.648
Larvae migrating to leaf-litter		47		
Potential eggs		2115		
1978	Egg shortfall		1700	0.707
Eggs		415		
	Seed capsule failure		129	0.162
Larvae established in seed capsules		286		
	Grazing		112	0.216
	Parasitoids		14	0.036
	Dead in capsule		74	0.270
Larvae in cases		86		
	Parasitoids		22	0.128
	Dead in case		19	0.153
	Grazing		14	0.162
Larvae migrating to leaf-litter		31		
Potential eggs		1395		
1979	Egg shortfall		1235	0.940
Eggs		160		
	Seed capsule failure		38	0.118
Larvae established in seed capsules		122		
	Grazing		85	0.518

Table 7.1c : *Life-table for* Coleophora alticolella *at 335m (numbers per m^2)*

Stage (*x*)	Mortality	l_x	d_x	k
1977				
Eggs		816		
	Seed capsule failure		327	0.222
Larvae established in seed capsules		*489*		
	Grazing		*154*	0.164
	Parasitoids		*0*	0.000
	Dead in capsule		115	0.183
Larvae with cases		*220*		
	Parasitoids		*6*	0.012
	Dead in case		4	0.008
	Grazing		*16*	0.034
Larvae migrating to leaf-litter		*194*		
Potential eggs		8730		
1978	Egg shortfall		6968	0.695
Eggs		*1762*		
	Seed capsule failure		1160	0.466
Larvae established in seed capsules		*602*		
	Grazing		*0*	0.000
	Parasitoids		*0*	0.000
	Dead in capsule		259	0.244
Larvae with cases		*343*		
	Parasitoids		*2*	0.003
	Dead in case		3	0.004
	Grazing		*0*	0.000
Larvae migrating to leaf-litter		*338*		
Potential eggs		15210		
1979	Egg shortfall		14752	1.521
Eggs		458		
	Seed capsule failure		143	0.163
Larvae established in seed capsules		*315*		
	Grazing		*94*	0.154

Table 7.1d : *Life-table for* Coleophora alticolella *at 395m (numbers per* m^2*)*

Stage (x)	Mortality	l_x	d_x	k
1977				
Eggs		834		
	Seed capsule failure		490	0.385
Larvae established in seed capsules		*344*		
	Grazing		*97*	0.144
	Parasitoids		*0*	0.000
	Dead in capsule		68	0.140
Larvae with cases		*179*		
	Parasitoids		*3*	0.007
	Dead in case		13	0.033
	Grazing		*36*	0.108
Larvae migrating to leaf-litter		*127*		
Potential eggs		5715		
1978	Egg shortfall		5040	0.928
Eggs		*675*		
	Seed capsule failure		482	0.544
Larvae established in seed capsules		*193*		
	Grazing		*16*	0.038
	Parasitoids		*0*	0.000
	Dead in capsule		89	0.303
Larvae with cases		*88*		
	Parasitoids		*0*	0.000
	Dead in case		12	0.064
	Grazing		*2*	0.012
Larvae migrating to leaf-litter		*74*		
Potential eggs		3330		
1979	Egg shortfall		3164	1.302
Eggs		166		
	Seed capsule failure		61	0.199
Larvae established in seed capsules		*105*		
	Grazing		*51*	0.289

Table 7.1e : *Life-table for* Coleophora alticolella *at 455m (numbers per* m^2*)*

Stage (x)	Mortality	l_x	d_x	k
1977				
Eggs		533		
	Seed capsule failure		338	0.437
Larvae established in seed capsules		*195*		
	Grazing		*45*	0.114
	Parasitoids		*0*	0.000
	Dead in capsule		73	0.290
Larvae with cases		*77*		
	Parasitoids		*0*	0.000
	Dead in case		14	0.087
	Grazing		*7*	0.051
Larvae migrating to leaf-litter		*56*		
Potential eggs		2520		
1978	Egg shortfall		1781	0.533
Eggs		*739*		
	Seed capsule failure		611	0.761
Larvae established in seed capsules		*128*		
	Grazing		*11*	0.039
	Parasitoids		*0*	0.000
	Dead in capsule		70	0.396
Larvae with cases		*47*		
	Parasitoids		*0*	0.000
	Dead in case		4	0.039
	Grazing		*10*	0.115
Larvae migrating to leaf-litter		*33*		
Potential eggs		1485		
1979	Egg shortfall		1233	0.770
Eggs		252		
	Seed capsule failure		164	0.475
Larvae established in seed capsules		*88*		
	Grazing		*25*	0.145

Table 7.1f : *Life-table for* Coleophora alticolella *at 520m (numbers per m^2)*

Stage (x)	Mortality	l_x	d_x	k
1977				
Eggs		97		
	Seed capsule failure		51	0.324
Larvae established in seed capsules		*46*		
	Grazing		*0*	0.000
	Parasitoids		*0*	0.000
	Dead in capsule		23	0.301
Larvae with cases		*23*		
	Parasitoids		*0*	0.000
	Dead in case		4	0.083
	Grazing		*10*	0.325
Larvae migrating to leaf-litter		*9*		
Potential eggs		405		
1978	Egg shortfall		214	0.326
Eggs		*191*		
	Seed capsule failure		160	0.790
Larvae established in seed capsules		*31*		
	Grazing		*0*	0.000
	Parasitoids		*0*	0.000
	Dead in capsule		20	0.450
Larvae with cases		*11*		
	Parasitoids		*0*	0.000
	Dead in case		4	0.196
	Grazing		*3*	0.243
Larvae migrating to leaf-litter		*4*		
Potential eggs		180		
1979	Egg shortfall		111	0.416
Eggs		69		
	Seed capsule failure		55	0.693
Larvae established in seed capsules		*14*		
	Grazing		*1*	0.032

into capsules at each site. The density of eggs is then calculated from the formula

$$\text{Eggs}.\text{m}^{-2} = \frac{\text{Larvae}.\text{m}^{-2}}{S}$$

b. The first period of grazing

The density of the *Juncus squarrosus* inflorescences is reduced by grazing (Section 3.7). The loss of inflorescences during this first period is the difference between the number produced and the number remaining in August, when samples were taken to assess the larval densities. Grazing is assumed to be random with respect to the inflorescences; it does not affect the survival of the larvae on the remaining inflorescences but reduces their density per square metre.

c. Parasitoids inside the seed capsules

The parasitoids start to attack the *Coleophora alticolella* larvae while these hosts are still inside their first seed capsule, but after the initial period of grazing. The number attacked at this stage is given in Section 6.11 and is calculated from the evidence of parasitization in the November samples.

d. Dead in capsule

This is the residual mortality between the larvae surviving the first bout of parasitization and the density of larval cases produced. This failure to produce larval cases was not measured directly and, for the purposes of the construction of these life-tables, it is assumed to act after parasitization.

e. Parasitoids of larvae in cases

Values for the second period of parasitization are also given in Section 6.11. The number surviving parasitization is calculated as the difference between the number of cases produced and the number of these larvae parasitized.

f. Larvae dead in cases

This mortality is calculated as the difference between the number of cased larvae per seed capsule that survived parasitization and the number of larvae per seed capsule that migrated to the leaf litter at the end of the summer. By considering the numbers per seed capsule in this way, it is possible to exclude the reduction due to the second period of grazing.

g. The second period of grazing

As with the first grazing period, this mortality factor only affects the density per square metre and does not affect the larvae on the remaining inflorescences. This period of grazing results in the reduction in the density of inflorescences after August each year; these data have been discussed in Section 3.7. Although the sheep graze the inflorescences throughout this period, these calculations assume that this mortality factor acts after the parasitization of the larvae in their cases but before they migrate to the leaf litter to overwinter.

h. Potential eggs

The density of potential eggs has been calculated from the density of larvae migrating at the end of each season. These values have been multiplied by 0.5 to calculate the density of females, assuming an equal sex ratio.

Jordan (1958) found that newly emerged females contained ten to twenty eggs which appeared ready for immediate oviposition, but that the ovaries contained many smaller eggs which would mature later. He estimated that the maximum number of eggs per female was about 90 and considered that the majority would be deposited during the course of the oviposition period, since the females taken at the end of the egg-laying period had only a few eggs left. The density of the females has been multiplied by 90 to calculate the potential egg density. These calculations can be summarized as

$$\text{Potential Eggs} = \text{Larvae Migrating} \times 0.5 \times 90$$

i. Egg shortfall

The egg shortfall is the difference between the potential egg density and the real density of eggs laid the following year. It is not strictly a measure of mortality, but is the reduction in natality.

7.3 Analysis of the life-tables

The generation mortality, K, is the sum of the values for all the k-factors. For the following analyses, the generation mortality is calculated from egg to egg. A summary of the k-factors for the 1977-78 and 1978-79 generations at the six sites is given in Table 7.2, with the values for K.

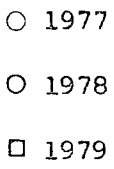
Figure 7.1 shows the density of eggs at each site, based on the data from the life-tables. In 1977 the eggs were at similar densities at all sites below 400 metres, while the density was lower above this altitude. In the following year the density of eggs was highest at 335 metres (higher than in the previous year). At the two lowest sites the density was reduced in 1978 and was less than that at 455 metres.

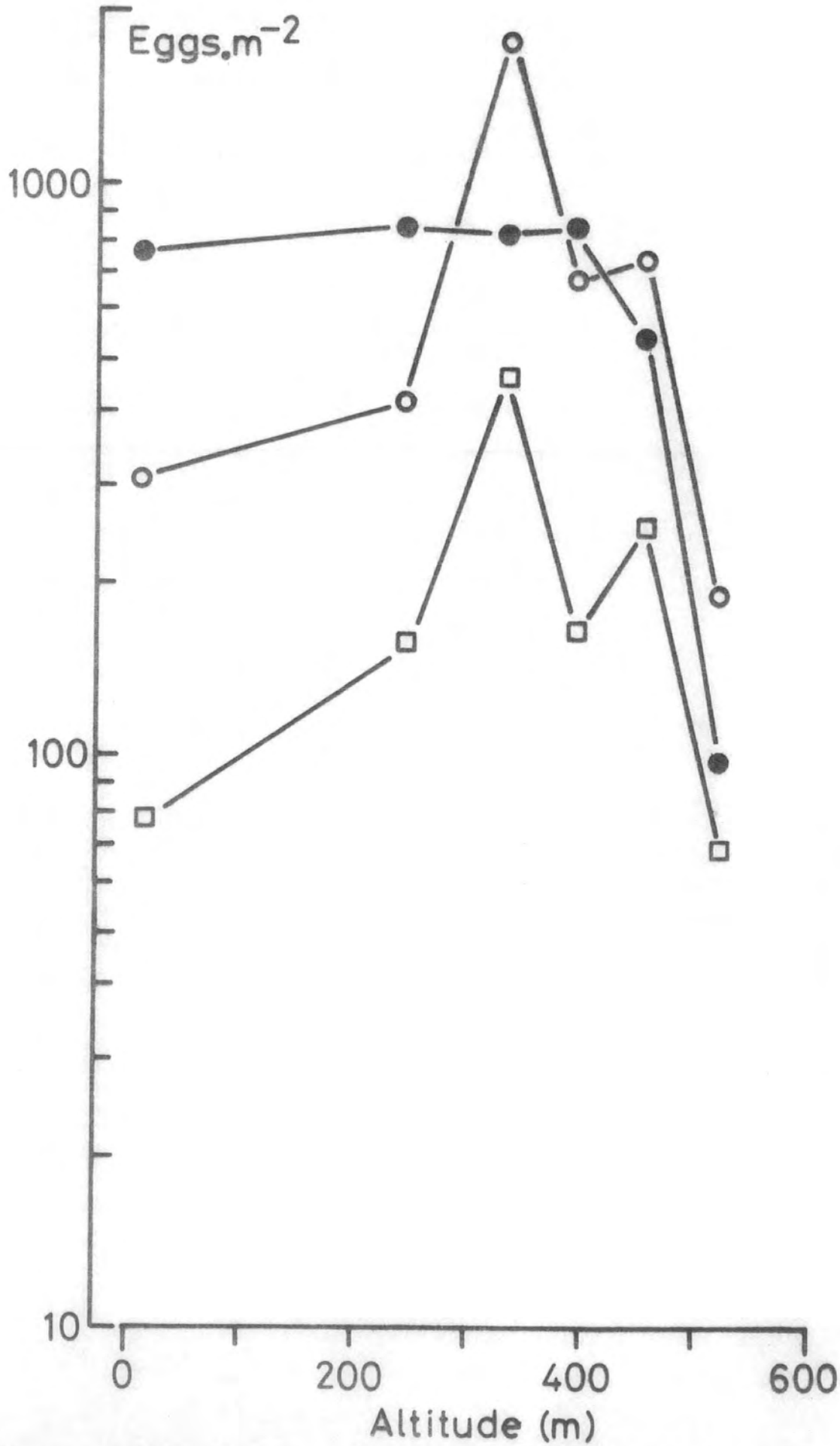
Table 7.2 : *A summary of the mortality factors and the generation mortality, K, at each altitude for the 1977-78 and the 1978-79 generations*

k - factor	Cause
k_o	Seed capsule failure
k_1	First period of grazing
k_2	Parasitoids attacking larvae inside seed capsules
k_3	Other mortality of larvae inside seed capsules
k_4	Parasitoids attacking larvae in cases
k_5	Other mortality of larvae in cases
k_6	Second period of grazing
k_7	Egg shortfall

1977-78	15m	245m	335m	395m	455m	520m
k_0	0.129	0.170	0.222	0.385	0.437	0.324
k_1	0.000	0.070	0.164	0.144	0.114	0.000
k_2	0.087	0.009	0.000	0.000	0.000	0.000
k_3	0.190	0.140	0.183	0.140	0.290	0.301
k_4	0.326	0.111	0.012	0.007	0.000	0.000
k_5	0.035	0.103	0.008	0.033	0.087	0.083
k_6	0.000	0.648	0.034	0.108	0.051	0.325
k_7	1.287	0.707	0.695	0.928	0.533	0.326
K	2.054	1.958	1.318	1.745	1.512	1.359
1978-79						
k_0	0.091	0.162	0.466	0.544	0.761	0.790
k_1	0.007	0.216	0.000	0.038	0.039	0.000
k_2	0.245	0.036	0.000	0.000	0.000	0.000
k_3	0.311	0.270	0.244	0.303	0.396	0.450
k_4	0.464	0.128	0.003	0.000	0.000	0.000
k_5	0.106	0.153	0.004	0.064	0.039	0.196
k_6	0.000	0.162	0.000	0.012	0.115	0.243
k_7	1.022	0.940	1.521	1.302	0.770	0.416
K	2.246	2.067	2.238	2.263	2.120	2.095

Figure 7.1 : The number of *Coleophora alticolella* eggs per square metre plotted on a logarithmic scale against altitude.




Eggs.m^{-2}
1000
100
10
0
200
400
600
Altitude (m)

The density in 1979 was the lowest of the three years at all of the sites. The greatest variation of density during the three year period was at 15 metres; here the density was an order of magnitude less in 1979 than in 1977.

Values for the generation mortality at each site are shown in Figure 7.2. The generation mortality for 1977-78 was more variable between sites than for 1978-79. Values for the first generation were highest at 15 metres and lowest at 335 metres. All of the values for the second generation were over 2.0, which is equivalent to more than 99% mortality at each site.

In the construction of the life-tables it was assumed that the maximum fecundity of females was 90 eggs. From these, two must survive to adulthood the following year for the population to remain at the same density. This is equivalent to a generation mortality of

$$\log 90 - \log 2 = 1.653$$

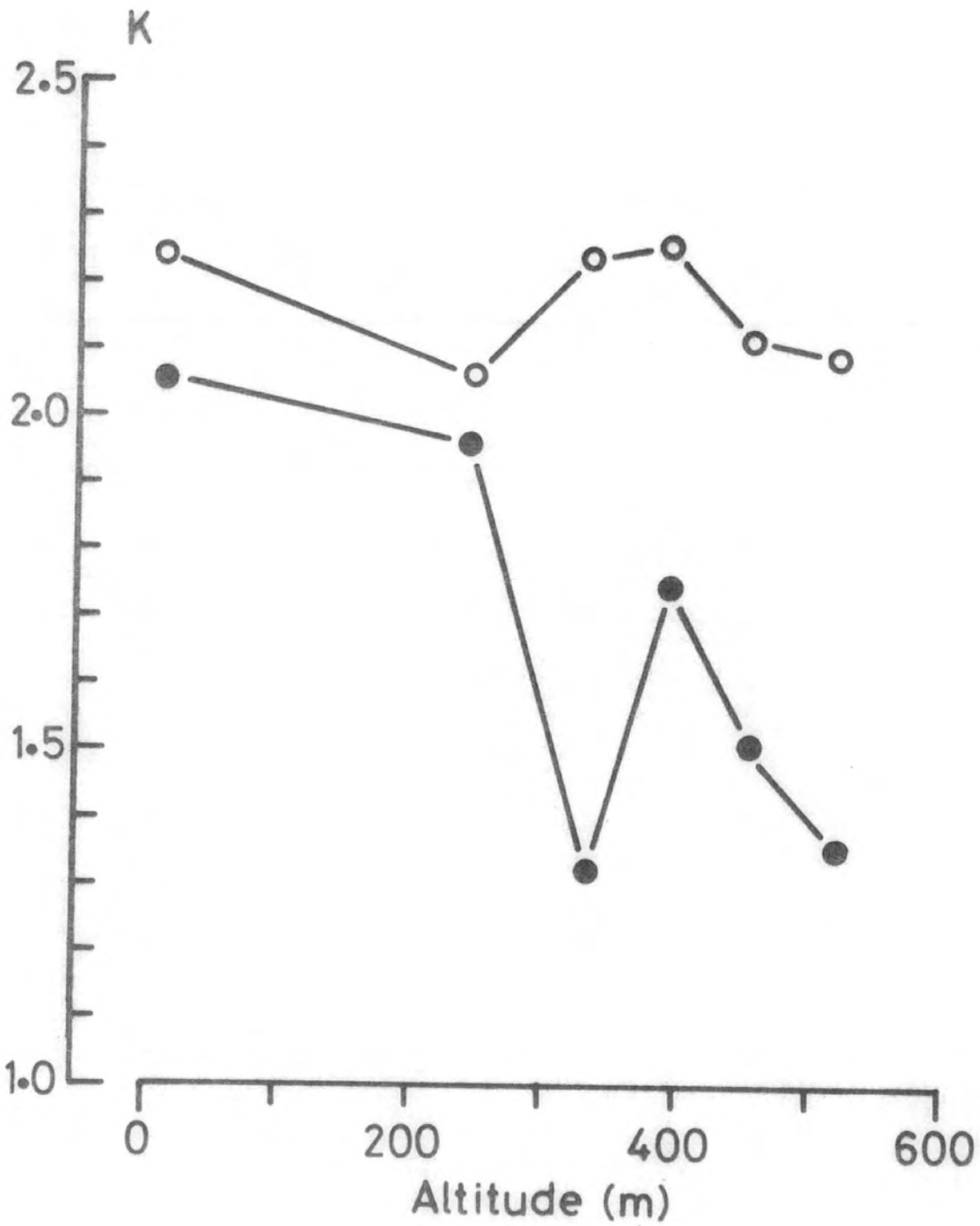
Three sites had values of K less than 1.653 in the 1977-78 generation; 335m, 455m and 520m. These were the only sites where there was an increase in egg density from 1977 to 1978. Generation mortality for 1978-79 was greater than 1.653 at all sites, hence the reduction in density of eggs.

The identification of a key factor responsible for population change can be achieved by the correlation of each k-factor with K for a series of generations (Varley and Gradwell 1960). For *Coleophora alticolella*, however, life-tables are only available for two complete generations which is not sufficient data for this method. As the importance of each mortality factor may change in different locations, the approach used in these analyses is to examine the relationships between each k-factor and altitude. The values for each k-factor

Figure 7.2 : The generation mortality, *K*, of *Coleophora alticolella* plotted against altitude.

○ 1977-78 Generation

O 1978-79 Generation


K
2.5
2.0
1.5
1.0
0
200
400
600
Altitude (m)

are plotted against altitude in Figure 7.3a-h. In doing this, it is possible to judge the relative importance of each factor in determining population change and how each may differ under different environmental conditions. Although the impact of each mortality factor can change along the altitudinal gradient, some may act on the population in similar ways at different sites.

k_0 Seed capsule failure

This factor is responsible for most of the mortality of *Coleophora alticolella* between the egg stage and larval establishment inside the seed capsule. As there is lower seed capsule production at the higher altitudes, k_0 has a greater effect at these sites (Figure 7.3a). The severity of this factor was greater at the higher sites in the 1978-79 generation because here the proportion of florets developing into seed capsules was lower in 1978 than in 1977.

k_1 The first period of grazing

This mortality is due to sheep grazing the *Juncus squarrosus* inflorescences from the time when they were produced until the samples were taken in August. Figure 7.3b shows that there was no relationship between k_1 and altitude.

k_2 Parasitoids attacking larvae inside the seed capsules

There is an inverse relationship between this mortality factor and altitude (Figure 7.3c). Parasitization at this stage was higher in 1978 than in 1977. The value for this k-factor is zero at 335m and above.

Figure 7.3a-d : The k-values of each mortality factor plotted against altitude.

○ 1977-78 Generation

○ 1978-79 Generation

a	k_0	Seed capsule failure
b	k_1	First period of grazing
c	k_2	Parasitoids attacking larvae inside seed capsules
d	k_3	Other mortality of larvae inside seed capsules

Continued.....

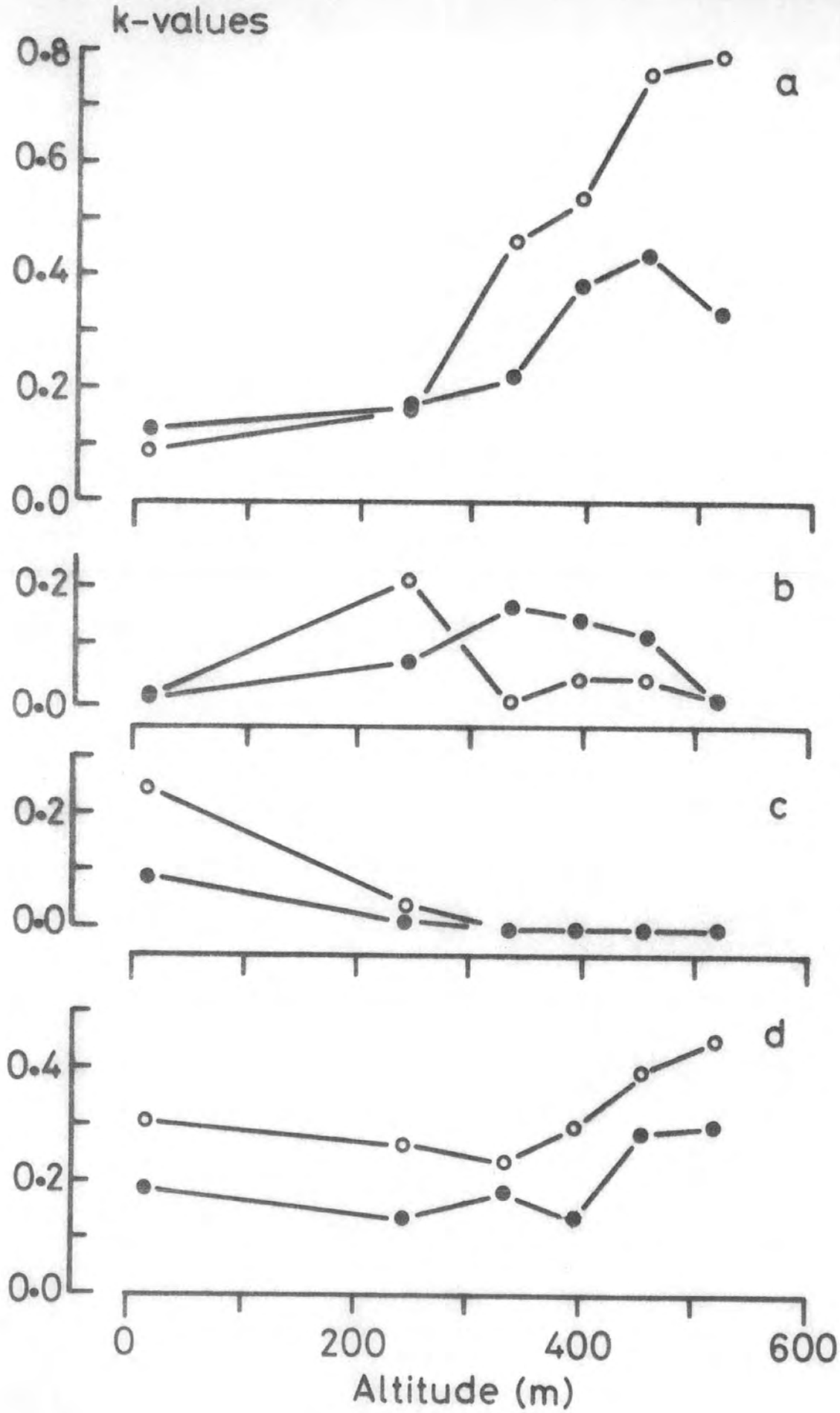

k-values
0.8
0.6
0.4
0.2
0.0
a
0.2
0.0
b
0.2
0.0
c
0.4
0.2
0.0
d
0
200
400
600
Altitude (m)

Figure 7.3e-g : The k-values of each mortality factor plotted against altitude.

○ 1977-78 Generation

○ 1978-79 Generation

e k_4 Parasitoids attacking larvae in cases

f k_5 Other mortality of larvae in cases

g k_6 Second period of grazing

Continued.....

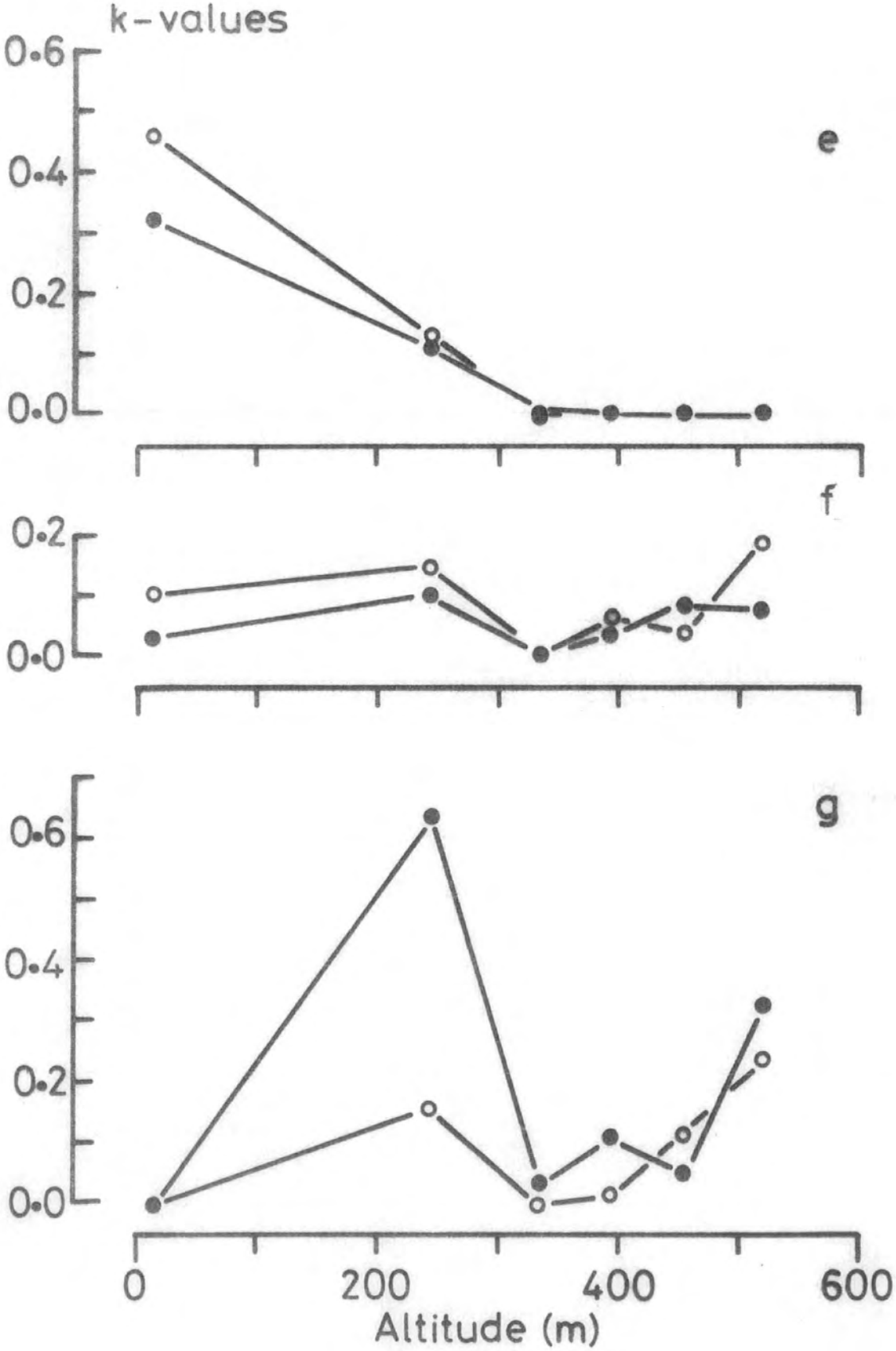
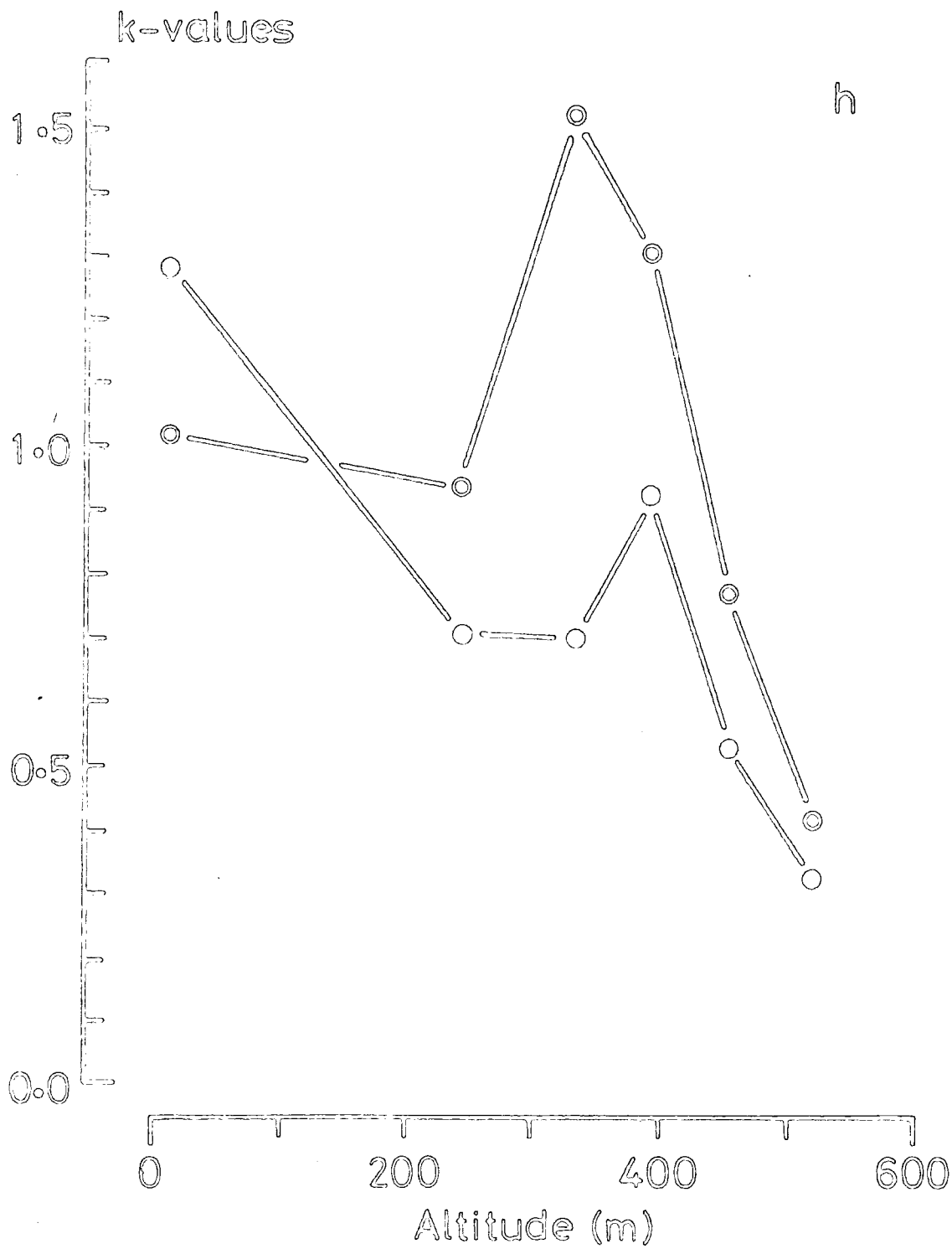

k-values
0·6
0·4
0·2
0·0
e
f
0·2
0·0
g
0·6
0·4
0·2
0·0
0
200
400
600
Altitude (m)

Figure 7.3.h : The values of k_7 (egg shortfall) plotted against altitude.

○ 1977-78 Generation

O 1978-79 Generation


k-values
h
1.5
1.0
0.5
0.0
0
200
400
600
Altitude (m)

k_3 Other mortality of larvae inside seed capsules

This is a residual value which has been calculated to balance the budget, and may consist of several agents causing mortality. There is a direct relationship between this *k*-factor and altitude for the sites above 335m (Figure 7.3d); below this altitude the values are similar within each generation, but vary between generations. The causes of this mortality are unknown. Competition for food between larvae inside the seed capsules can be ruled out; this would result in higher values in the middle region of the transect, where there was a greater proportion of the larvae sharing seed capsules because of the higher larval densities (Chapter 5). It is possible that food quality is reduced at the higher sites, or that the severe climate acts directly on some of the larvae, killing them before they are able to produce their cases.

k_3 at the lowest altitude could have been due to undetected effects of the parasitoids. The Hymenoptera may have killed some of the larvae but failed to oviposit on them. If they oviposited successfully, some of the parasitoid larvae may have failed to develop. These dead *Coleophora alticolella* larvae would not have been classed as parasitized in later samples.

k_4 Parasitoids attacking larvae in cases

This is the first mortality factor to act after the larvae have produced their cases. As with k_2, there is an inverse relationship between the mortality caused by these parasitoids and altitude (Figure 7.3e). *Scambus brevicornis* was recorded from samples taken at 395m in 1977 and at 335m in 1977 and 1978, but parasitization was very low at these sites, so the *k*-values are small. This *k*-factor was greater in the second of the two generations at the two lower sample sites.

k_5 Other mortality of larvae in cases

The values for this k-factor were small; all were less than 0.2 (Figure 7.3f). This mortality was not measured directly but, like k_3, was calculated from the other values; it may consist of several components One component at the low altitudes could be due to more undetected parasitism. Also at these sites, some of the mortality will have been caused by adult female *Scambus brevicornis* feeding on the *Coleophora alticolella* body fluids.

k_6 The second period of grazing

There was no relationship between this k-factor and altitude (Figure 7.3g). The highest values were recorded at 245m and 520m in each generation.

k_7 Egg shortfall

This is another factor which was not measured directly but was calculated from the other values in the life-table. The highest value was recorded at the 335 metre site for the 1978-79 generation, and the lowest values were at 520 metres (Figure 7.3h). k_7 was higher in 1978-79 than in the previous generation at all sites except for 15 metres.

The variation of k_7 with altitude, as shown in Figure 7.3h, suggests that this factor has the greatest effect where the density of the larvae is highest (c.f. Figure 5.1). Density-dependent mortality can be detected by plotting each value of k against the logarithm of the density of the stage on which it acts; a significant positive slope indicates that there is greater rate of mortality at the higher densities. In this case, k_7 has been calculated from the density of larvae per square metre migrating to the leaf litter in each autumn.

Figure 7.4 shows the overall increase of k_7 with increasing density of migrating larvae per square metre. There is a significant correlation between the two values ($r = 0.681$, d.f. = 8, $P < 0.05$). When the data for each site are examined separately, however, this factor is found not to be directly related to density; the lines joining the values for the two generations at each site are independent of each other. Therefore, despite the overall relationship, egg shortfall is not dependent on the density of larvae migrating to the leaf-litter.

If this reduction in natality is due to intraspecific competition for the food supply, then k_7 will be related to the density of larvae with respect to the seed capsules rather than the density per square metre. Therefore, k_7 will not be related to the density of larvae from which it is calculated but will be delayed slightly in its effect.

Larvae are over-dispersed with respect to the food supply at the beginning of the season and, as shown by k_3, there is no density dependent mortality caused by competition for food within the seed capsules. Once the larva has eaten all of the seed in its first capsule and has produced a case, it searches for more food to complete its development. It is at this stage that competition could occur. Therefore, if k_7 is a density-related effect caused by competition for food, it should be directly related to the density of cased larvae per remaining seed capsule (D). These values have been calculated from the data given in the life-tables, by the formula

$$D = \frac{\text{Cases produced.}\ m^{-2}}{\text{Capsules.}\ m^{-2} - \text{Larvae in capsules.}\ m^{-2}}$$

The results of these calculations are given in Table 7.3.

Figure 7.4 : The values of k_7 plotted against $\log_{10}$ of larvae per square metre migrating to leaf-litter at each sample site for the 1977-78 and 1978-79 generations. The two values from each site are joined.

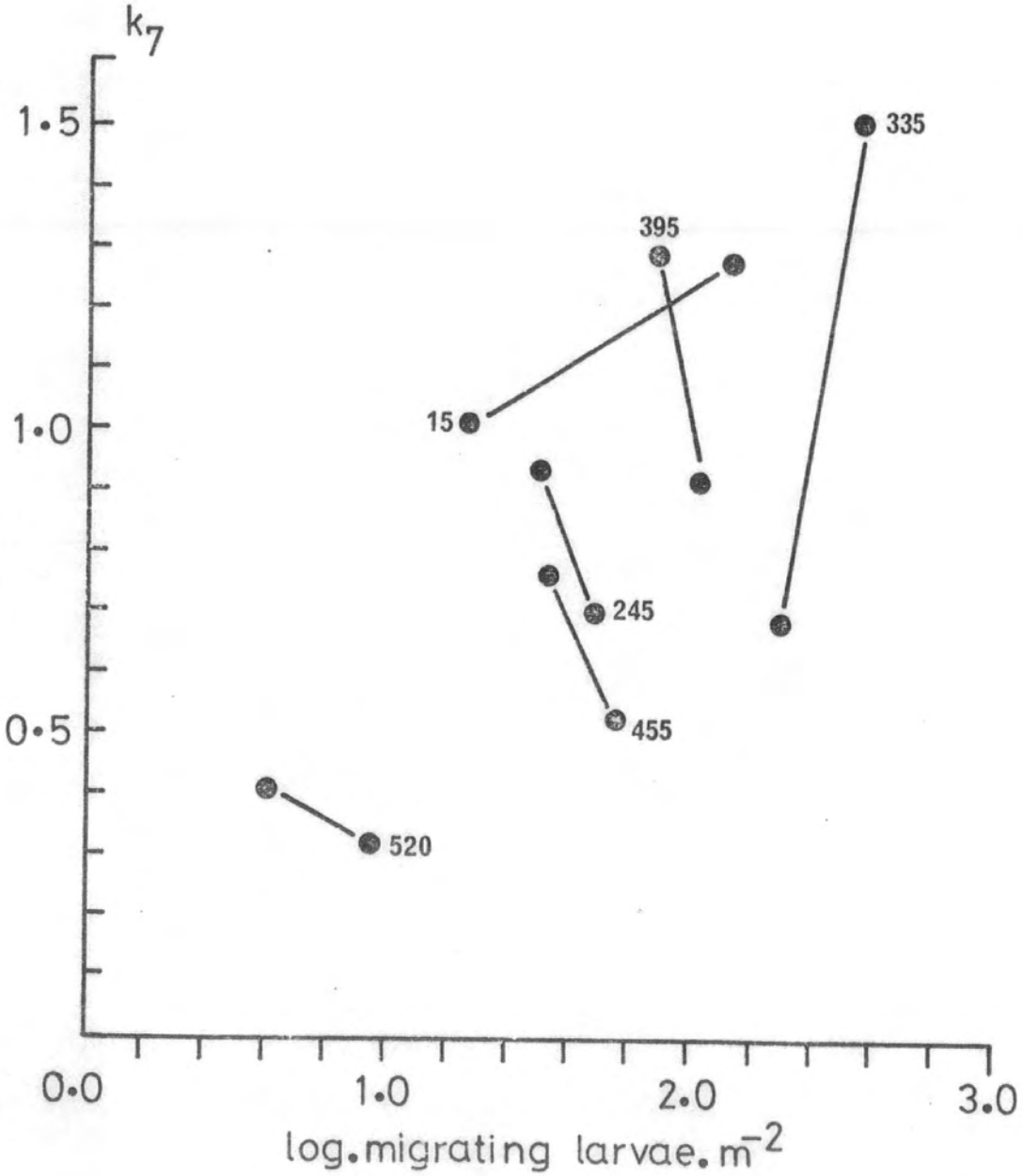

k_7
1·5
1·0
0·5
0·0
1·0
2·0
3·0
log. migrating larvae. m^{-2}
335
395
15
245
455
520

Table 7.3 : *The density of seed capsules, larvae and larval cases produced at the six major sample sites in 1977 and 1978, calculated from the life tables after the first period of grazing. The density of the larval cases with respect to the remaining food supply (D) is shown in the final column. This has been calculated from the formula*

$$D = \frac{\text{Cases produced. } m^{-2}}{\text{Seed capsules. } m^{-2} - \text{larvae. } m^{-2}}$$

Altitude (m)	Seed capsules per m^2 in August	Larvae per m^2 in August	Cases produced per m^2	Density (*D*)
1977				
15	3797	566	299	0.0925
245	752	482	342	1.2667
335	943	335	220	0.3618
395	823	247	179	0.3108
455	820	150	77	0.1149
520	787	46	23	0.0310
1978				
15	869	241	67	0.1067
245	294	174	86	0.7167
335	746	602	343	2.3819
395	245	177	88	1.2941
455	220	117	47	0.4564
520	281	31	11	0.0440

Figure 7.5 shows that, at the four highest sample sites, k_7 was related to the density of cased larvae with respect to the remaining food supply. In spite of the fact that these values have been calculated for a variety of different sample sites, the thin lines in this figure show that there is a direct relationship at all four sites and that the trends at each site are similar to the overall relationship.

The values for the two lowest sample sites do not follow this relationship. At these sites, parasitization of the larvae in the cases will affect their density and, therefore, the amount of competition for the remaining food.

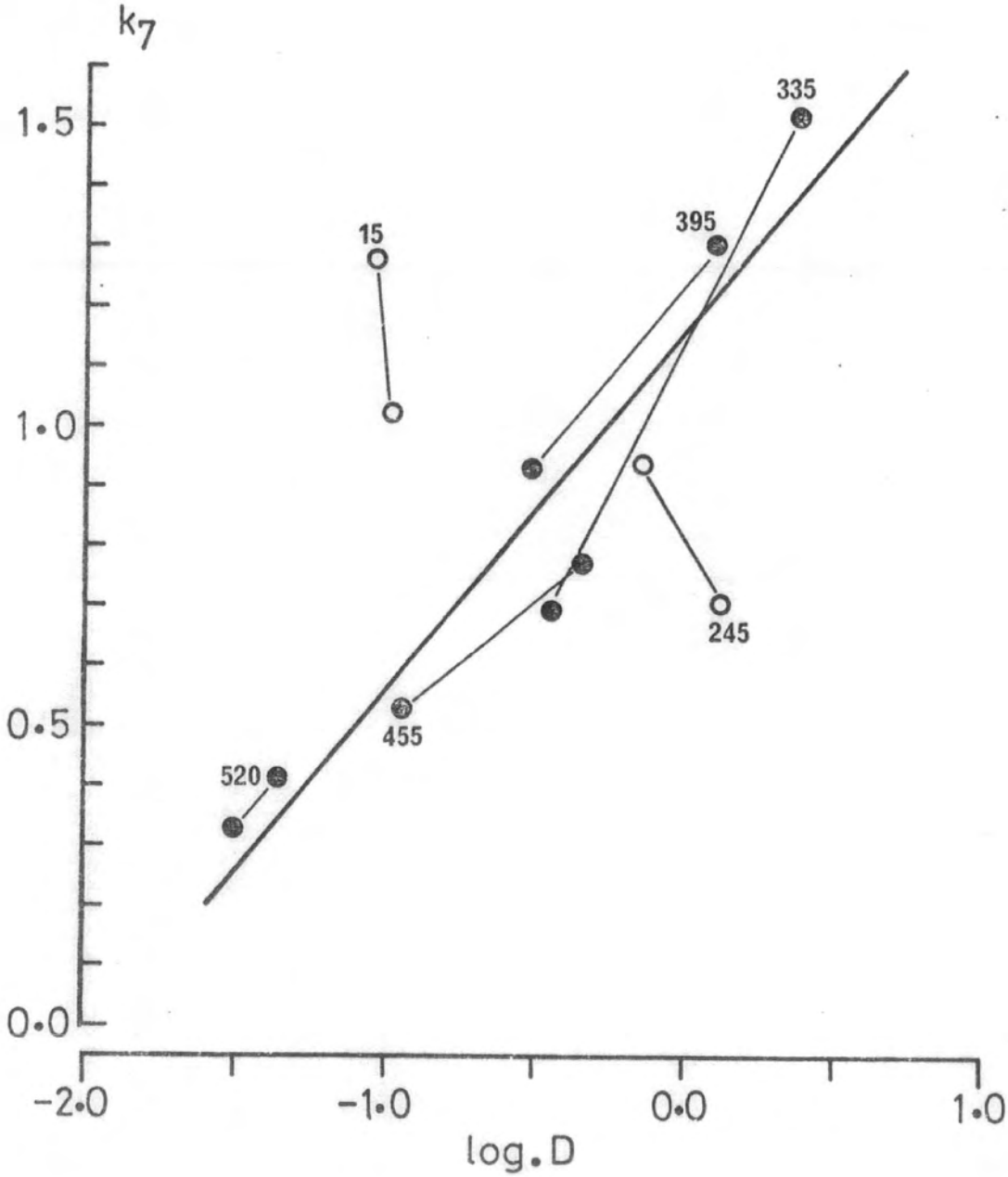
Regression analysis of a *k*-factor on density cannot be taken as proof of a density-dependent relationship because the independent variable may not be free from sampling error, and the two variables may not be independent of each other. To overcome these problems it has been suggested by Varley and Gradwell (1963) that attention should be focused on the relationship between the densities before and after the action of the *k*-factor. If the regression of final density on initial density and initial density on final density both produce slopes that are significantly different from unity, and also that these lines lie on the same side of the slope of unity, then density-dependence has been proved.

In the case of egg shortfall of *Coleophora alticolella*, k_7 is independent of the density used in Figure 7.5, but this density is subject to sampling error. It was not possible to obtain direct measurements of the density of survivors, with the same units as the initial density, because eggs were laid on a different year's growth of inflorescences to those on which the larvae had been feeding in the previous summer. Theoretical values can be calculated, however, from the formula:

Figure 7.5 : The values of k_7 plotted against $\log_{10}D$ (the density of cased larvae per uneaten seed capsule after case production).
The values for the two generations at each altitude are joined by the thin lines.
The thick line is from the regression analysis of the values from 335m and above (○) and has the formula

$$k_7 = 0.606 \log_{10}D + 1.160$$

$r = 0.952$, $n = 8$, S.E. of slope = 0.080, $P < 0.001$


k7
1·5
1·0
0·5
0·0
-2·0
-1·0
0·0
1·0
log. D
335
395
15
245
455
520

$$\log S = \log D - k_7$$

where D is the initial density and S the density of survivors.

The values of log S and log D have been plotted against each other in Figure 7.6 and the regression coefficients calculated. The slopes for log S on log D and log D on log S are both significantly different from, and both on the same side of, a slope of unity.

Thus the reduction in natality at the sites above 245 metres is related to the amount of competition for food between the larvae with cases. However, this density-dependent effect does not exactly compensate for the increase in larval density as the slope of k_7 on log density is less than unity.

Variation in natality could occur in two ways: larvae that obtain insufficient food in the summer may fail to become adults the following year, thus reducing the density of ovipositing females. Alternatively, there could be a reduction in fecundity; at high densities the larvae have a smaller food supply and those that do survive may become smaller adults producing fewer eggs. Reduced fecundity at high larval densities has been recorded in many insect population studies; for example, the cinnabar moth (*Tyria jacobaeae* L.) (Dempster 1971), the pine looper moth (*Bupalus pinarius* L.) (Klomp 1966) and the moorland tipulid *Molophilus ater* (Horobin 1971).

Both of these effects of density on the reduction of natality of *Coleophora alticolella* may occur, but the importance of each could not be separated by using the data available.

The density-related reduction in natality has only been demonstrated for sites above 245 metres. At 15 metres and 245 metres, k_7 was not directly related to the density of larvae with respect to the food supply. It was mentioned previously that mortality due to

Figure 7.6: $\log_{10}S$, the theoretical density of *Coleophora alticolella* larvae surviving the effects of k_7, plotted against $\log_{10}D$, the initial density.

The broken line has a slope of unity.

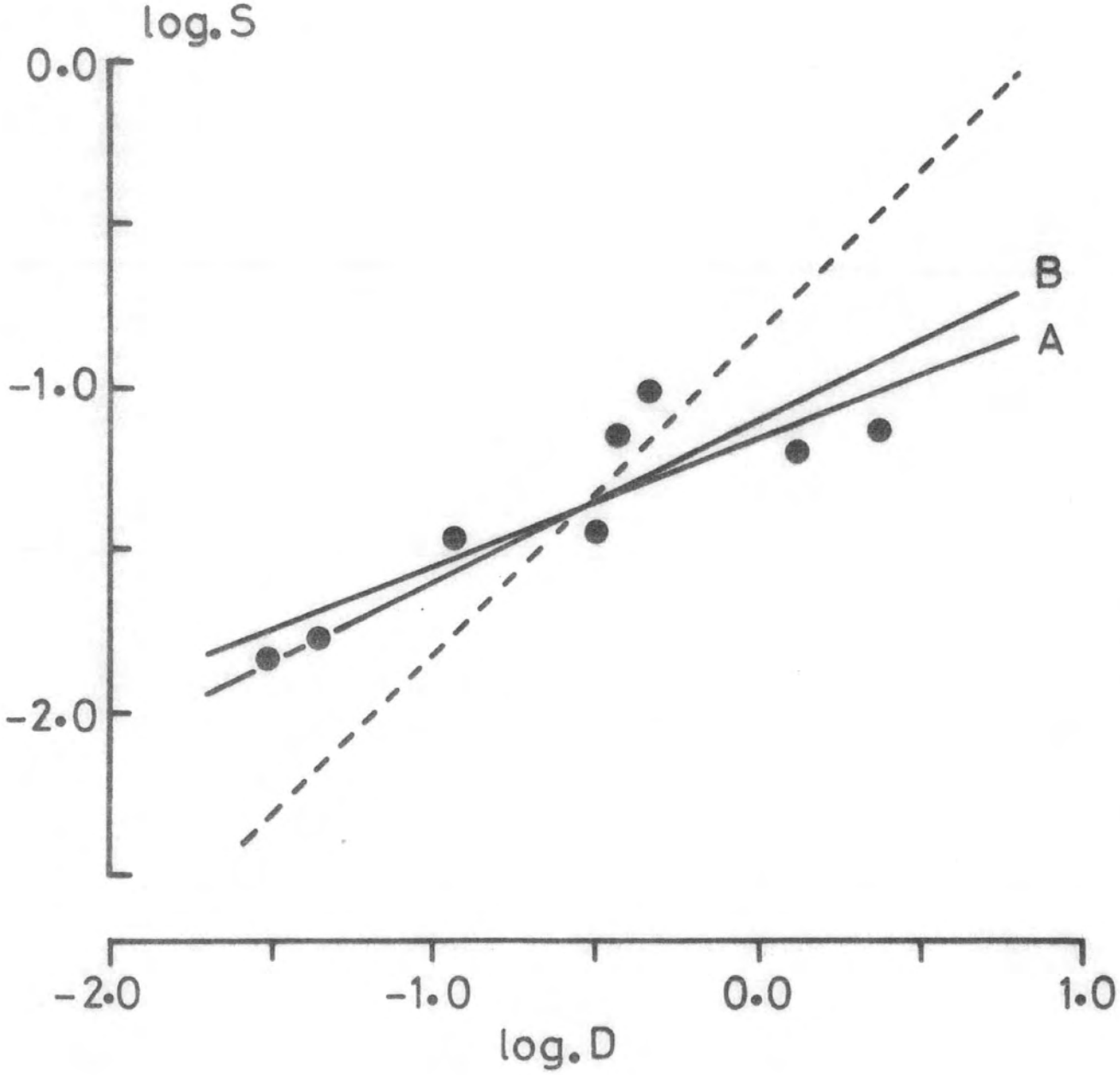
The two solid lines are:

A. $\log_{10}S = 0.395 \log_{10}D - 1.160$

$r = 0.896$; $n = 8$; S.E. of slope = 0.080; $P < 0.01$

B. $\log_{10}D = 2.036 \log_{10}S + 2.248$

$r = 0.896$; $n = 8$; S.E. of slope = 0.412; $P < 0.01$


log. S
0.0
-1.0
-2.0
B
A
-2.0
-1.0
0.0
1.0
log. D

parasitization, which is commonest at these two sites, would reduce the competition for seed capsules. Therefore the effects of density-dependent reduction of natality at these sites would be different from the observed values of k_7.

There may also be other factors contributing to k_7 at the low altitudes. Figure 7.4 showed that k_7 at 15 metres was related to the density of larvae migrating to the leaf-litter. It is possible that parasitization or predation of the overwintering larvae may account for some of this mortality.

i) Parasitization

Parasitoids may have attacked the larvae or pupae in the leaf-litter. This possibility cannot be ruled out as larvae were not removed from the leaf-litter for rearing.

Another possible source of parasitization could have been due to endophagous parasitoids attacking the larvae in the summer, but not killing the hosts until after migration. Such parasitized larvae would have been classed as migrators and alive in the autumn, when in fact they would not contribute to the following generation. Such parasitism was not recorded during this study; Jordan (1958) recorded a few endophagous parasitoids from *Coleophora alticolella*, but he did not identify them.

It is possible that some of the parasitized larvae in cases became dislodged from the inflorescences. If this occurred they would also have been classed as live and migrated. This would lead to an overestimate of the population about to overwinter.

ii) Predation of overwintering larvae

Predation is a difficult factor to measure. Jordan (1962) suggests that predation could be due to sheep, mice or voles. The effect of sheep-grazing is more likely to occur earlier in the season, when the larvae are still feeding, and has been included at an earlier stage of the life-tables. There is no information about the activity of mice or voles in these areas. Common shrews (*Sorex araneus* L.) and pygmy shrews (*S. minutus* L.) both occur in similar areas of *Juncus squarrosus* in northern England but no *Coleophora alticolella* larvae have been found in the guts of these insectivores (Sarah Wanless pers. comm.).

Invertebrate predators (e.g. ants, spiders or carabid beetles) could take *C. alticolella* from the leaf-litter. These predators would also be inactive during the winter months, so their effect on the larval population may not be very great.

Walton (1979) has shown that meadow pipits *(Anthus pratensis* (L.)), common birds of moorlands, eat *Coleophora* larvae. He studied the diets of these birds in Snowdonia and found considerable numbers of larvae with cases among the gut contents of birds that had been feeding on areas of *Juncus squarrosus*. They contributed most to the diet of the pipits in March and April, but were also found in October. There was an average of 13.4 larvae per stomach in March. It was at first thought that these birds may have been feeding on the parasitized larvae, that had not migrated, but had remained on the rush stems. However, my examination of the remains of 235 *Coleophora* larvae from his samples did not reveal any evidence of parasitization. Thus it seems that the meadow pipits were searching through the leaf-litter to find these prey items, and that they will affect the survival of the overwintering larvae. There were

no data available for the density of migrating *Coleophora alticolella* larvae in the areas where the meadow pipits were feeding, so the magnitude of this effect cannot be calculated.

Meadow pipits occurred at all of the sites where *C. alticolella* was studied, but no observations on their feeding behaviour were undertaken.

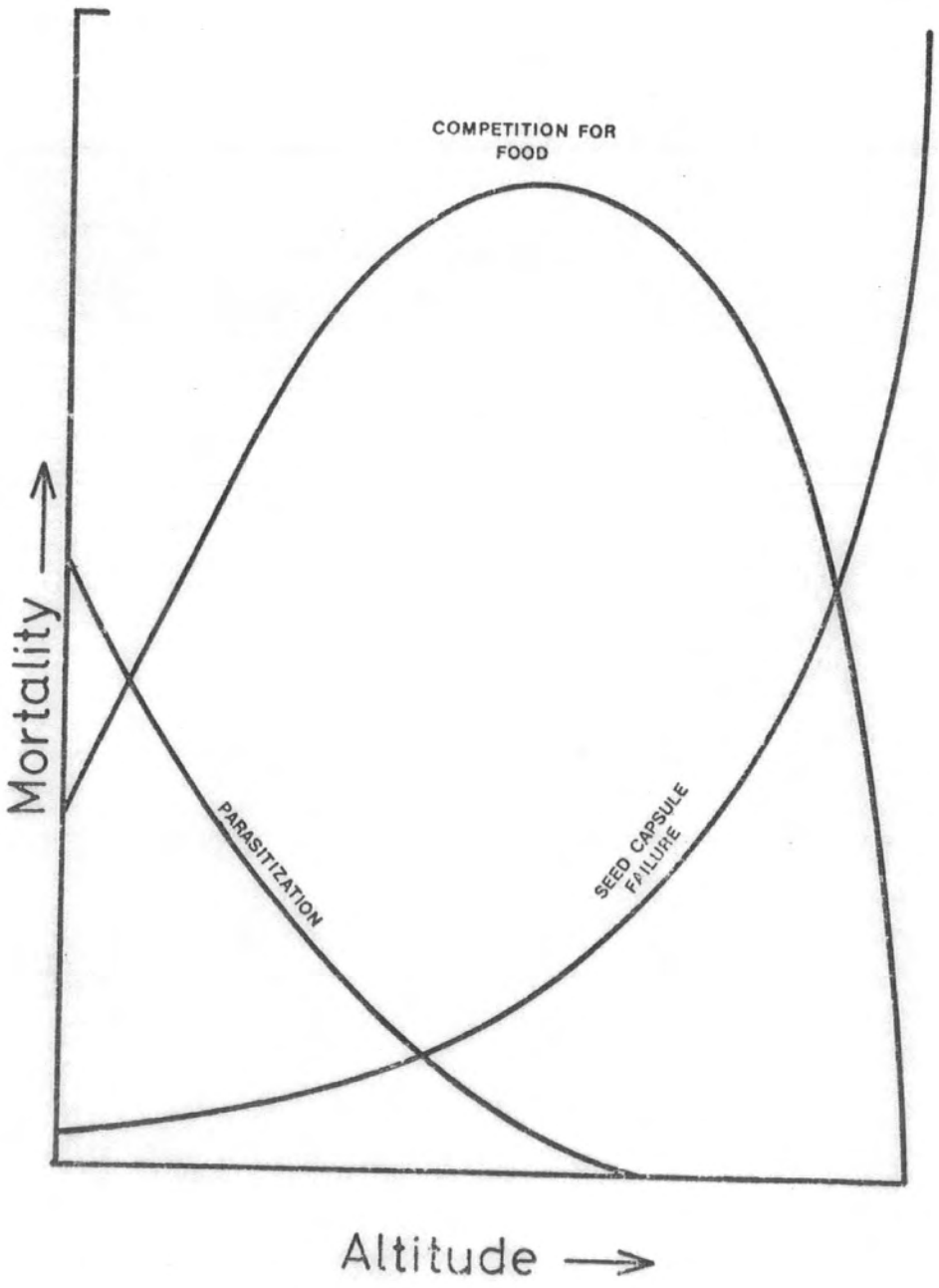
7.4 Changes in the mortality in relation to altitude

There are two main sources of mortality that are related to altitude. The first is starvation of newly hatched larvae and is caused by the failure of seed capsule development by the food plant (k_0). This effect increases in severity with increasing altitude. The other source of mortality, parasitization (k_2 plus k_4), is inversely related to altitude. The changes in the intensity of these two factors with altitude leave a middle region where their combined effect is low. Here the larval density in relation to the food supply is at its highest. This high larval density leads to competition for food and results in a density-dependent reduction in natality (k_7).

The changing intensity of these three factors along with altitudinal gradient is shown diagramatically in Figure 7.7. That part of the curve for competition for food at the low altitude does not correspond to the values for egg shortfall (k_7) but is the trend calculated from the density of larvae at these sites.

Towards the upper altitude limit of *Coleophora alticolella* distribution, competition for food is much reduced and the most important mortality is due to seed capsule failure. At the upper limit, seed capsule failure is responsible for total generation mortality; consequently the values for the other *k*-factors are zero. This will occur when the upper limit of seed-setting is reduced to a level below

Figure 7.7 : A diagramatic representation of the changing intensity of three causes of mortality of *Coleophora alticolella* with increasing altitude.


COMPETITION FOR FOOD
Mortality
PARASITIZATION
SEED CAPSULE FAILURE
Altitude

the previous year's larval distribution, as happened between 520 metres and 610 metres from 1977 to 1978.

At the lowest altitude, parasitization of the larvae on the inflorescences is more important than the reduction of natality caused by competition. Other causes of mortality act on the overwintering population at this sample site; these increase the values for egg shortfall which then masks the general relationship.

7.5 A comparison of the survivorship curves at 15m and 455m

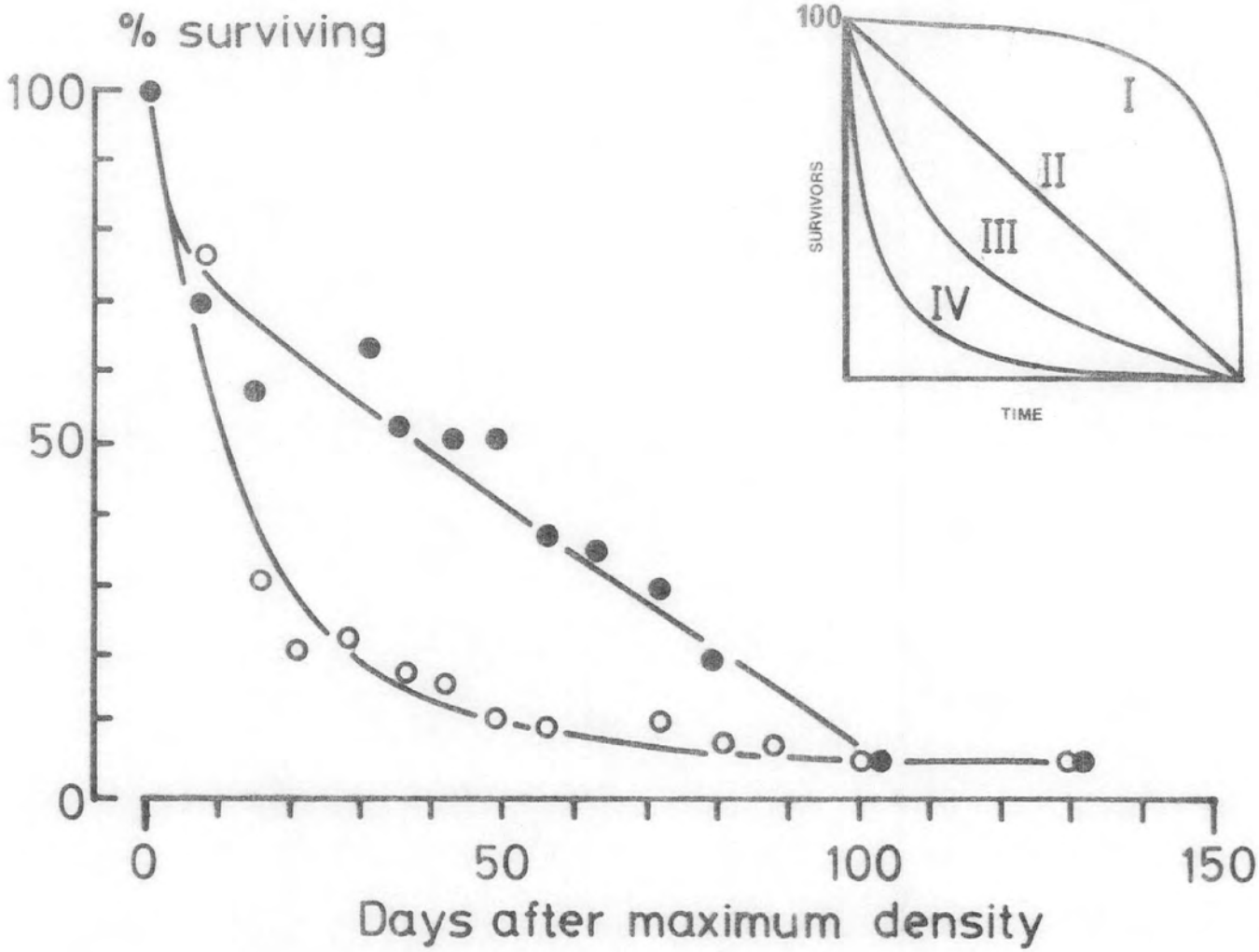
Morris (1965) has pointed out that many mortality factors act contemporaneously or are at least overlapping. The survivorship curve for a generation is really continuous, but in the construction of life-tables the age intervals chosen for population sampling are often too long to show this continuity.

The survivorship curves for *Coleophora alticolella* at 15m and 455min 1978 are shown in Figure 7.8. They have not been separated into age-classes, but have been constructed from the data for the number of eggs and larvae present in the samples of *Juncus squarrosus* (allowances have been made for the larvae migrating). These census data have been plotted against time in days and start with zero as the day when the maximum number of eggs was present. The number surviving has been converted to a percentage of the total eggs for comparing the two sites.

These two survivorship curves are clearly different. At 455m the curve can be classified as type IV under Slobodkin's (1962) terminology (see inset on Figure 7.8); here mortality acts most heavily on the early stages. The curve at 15m is nearer to type III, with a more constant mortality rate.

Figure 7.8 : The survivorship curves for *Coleophora alticolella* at 15 metres (○) and 455 metres (○) in 1978. The number present in each sample is expressed as a percentage of the maximum egg density and is plotted against time in days after the sample date with maximum eggs.

The inset shows the four types of survivorship curves classified by Slobodkin (after Slobodkin 1962).


% surviving
100
50
0
0
50
100
150
Days after maximum density
100
SURVIVORS
TIME
I
II
III
IV

Price (1975) suggests that survivorship curves for insects can be divided into two broad groups which he calls types A and B. Insects with a type A curve show high mortality (usually over 70%) in the early stages of the life-cycle. This is similar to the type IV curve shown in Figure 7.8. Insects of this group live in exposed situations, or have a vulnerable stage during the establishment of the larvae. The insects of group B have high apparent mortality rates in later stages. These are more akin to the type III curve. Type B insects live in protected situations or are defended in colonies.

In view of the data presented in Figure 7.8 it is clear that *Coleophora alticolella* does not fall into one or the other of Price's groups but can occupy either, in different parts of its range. At the higher altitude, most of the mortality occurs in the early stages, during larval establishment; but at 15m *C. alticolella* is in the type B group.

Work by Stark (1959) shows that the survivorship curves for the lodgepole needle miner (*Recurvia starki* Freeman) have different shapes depending on climatic conditions at the time of larval establishment. Cold, wet weather at the time of hatching and the fall of needles with eggs in high winds can be responsible for over 70% mortality; this puts them into type A. In other generations or in other locations, very little mortality occurs at this stage and the survivorship curve appears more like type B.

7.6 Discussion

Animal populations can only be regulated by density-dependent or density related factors. Even when regulated, the population fluctuates around an average density, and the size and direction of these fluctuations

is determined by key factors. The value around which the population fluctuates need not be the same in all parts of the animal's range. Towards the limits of its distribution the population is usually lower; climate can often be implicated in setting the average density level. Different key factors may be responsible for the population changes in different parts of the range. Weather may influence the density fluctuations, but does not regulate the numbers of animals because it cannot act as a density-dependent factor. Weather may, however, determine the number of suitable habitats (Klomp 1962).

Juncus squarrosus is a variable food resource, and its relation to environmental conditions plays an important part in the population dynamics of *Coleophora alticolella*. Changes in the density of the food-plant are often the driving force behind the population changes of the moth. There are two distinct measurements of the production of the food supply. The density of inflorescences produced is responsible for most of the differences between years at any one site. Secondly, the effect of the increasingly severe climate on the development of seed capsules is responsible for the differences between altitudes.

It is important to make a distinction between the two measurements of *C. alticolella* density. The density per square metre shows the changes of the population from one year to the next. The density with respect to the seed capsules gives an indication as to how much competition there will be for the food supply.

At 335 metres a high percentage of the florets develop into seed capsules and parasitization of the larvae is low. It is probable that the key factor responsible for population change in this region is the density-dependent reduction in natality, caused by competition for food in the previous summer. In 1977 there were sufficient seed capsules

for the larvae and so there was an increase in the density in 1978. In 1978 the density of inflorescences was lower than in the previous year and the larvae were at a higher density in relation to the seed capsules; this led to much competition for the seeds, with a consequent reduction in the density per square metre in 1979. If the food supply were constant from year to year the population of *C. alticolella* would be regulated by the density-dependent reduction in natality. The situation is complicated, however, by the widely fluctuating density of inflorescences from one year to the next. Dempster (1975) has shown that the key factors responsible for changes in the population of cinnabar moths (*Tyria jacobaeae*), feeding on ragwort (*Senecio jacobaea* L.) at Weeting Heath in Norfolk, are density-dependent deaths from starvation and the effects of this food shortage on the fecundity of the survivors. However, the number of plants, and therefore the food available, is mainly determined by rainfall (Dempster and Lakhani 1979).

Larval density per seed capsule was low at 520 metres so there was little competition for food. The main factor which determines population changes at the high altitudes is also responsible for setting the upper altitudinal limit of the moth; the low proportion of florets developing into seed capsules. In 1977 seed capsule production rate was high at 520 metres so there was a low mortality rate in the newly hatched larvae. This led to an increase in the density of the moth the following year. Poor seed capsule development in 1978 resulted in a reduced density in 1979. If the weather was mild enough to allow high rates of seed capsule development over a series of years, the population of *Coleophora alticolella* at this site would rise until the effects of competition would form an increasingly important part of the generation mortality.

Regulation of the population density will not normally occur at the high altitudes; the density of successive generations will merely fluctuate according to the intensity of k_0.

At the lowest sample site, seed capsule development was good and there was an excess of food, yet the population of *Coleophora alticolella* declined. The larvae at this site suffered a high rate of parasitization. It was not possible to show any regulation of the population at this low altitude because data were not available for sufficient generations. The fact that parasitization played such an important role as a mortality factor at this site suggests that the population was being held at a low density by these natural enemies. This prevented the *C. alticolella* population from increasing and utilizing all of the food resource. Dempster (1971) found that a natural population of cinnabar moths persisted at low density at Monks Wood, Huntingdon - they never totally defoliated their food plant at this site. The vegetation at Monks Wood supported a large population of arthropod predators which took a higher proportion of the young caterpillars than at Weeting Heath.

The importance of the mortality factors changes gradually from one site to another. Between 335 metres and 520 metres the effects of competition for the seed capsules are reduced and the effects of seed capsule failure increase. The relative strength of these two factors at the intermediate sites will differ between years.

Sheep removed many inflorescences in some years; this was particularly noticeable at 245 metres. Grazing reduces the density of inflorescences but does not affect the density of the larvae in relation to the food supply; therefore it will not affect competition for food among the larvae. The reduced density may, however, affect the response of the parasitoids, and could result in lower rates of parasitization.

The intensity of sheep grazing is not related to the density of *Coleophora alticolella* and cannot regulate the population. They graze the inflorescences without regard to the insect fauna and will not only reduce the density of moths for the following season, but also the density of the parasitoids (particularly those specific to this host). If sheep were prevented from grazing there would be an increase in the density of both moths and parasitoids. The extent to which the parasitoids could restrain the potential population growth under these conditions is not known but it is unlikely that they would be as successful as at the 15 metre site. Competition for food among the *Coleophora alticolella* larvae will form a more important component in the generation mortality at 245 metres than at 15 metres.

CHAPTER 8

THE EFFECT OF *COLEOPHORA ALTICOLELLA* ON THE SURVIVAL OF *JUNCUS SQUARROSUS* SEEDS

8.1 INTRODUCTION

Coleophora alticolella is a major seed predator of *Juncus squarrosus*. The highest densities of larvae, with respect to the seed capsules, were found at the middle altitudes of the transect studied. In some years the larval density in this part of the transect was so high that virtually all of the seed was eaten.

In this chapter the effect of *Coleophora alticolella* on the survival of the seeds at the different altitudes is considered. Survival is the difference between production and the subsequent predation of the seeds by the moth larvae.

In November the larvae had migrated to the leaf-litter and the capsules that had not been attacked had dispersed their seeds. The damaged seed capsules (those with seeds eaten) were easily distinguishable because the pericarp had a characteristic round hole through which the larva had gained access to the seeds (Plate I); also they contained frass, the remains of damaged seeds and parts of the silken galleries constructed by the larvae. Virtually all of the seeds in a damaged seed capsule had been eaten; the few that did escape predation were not included in the analyses as they would not affect the results to any great extent.

Sampling over the whole transect was most comprehensive in 1978; the results from the analyses of these data are presented with comparisons for the other years.

8.2 Seed capsule production in 1978

Seed capsule production by *Juncus squarrosus* in relation to altitude has been discussed in Chapter 3. Values for the density of seeds produced per square metre of *J. squarrosus*-dominated sward in 1978 were given in Table 3.11, assuming a mean number of 80.5 ± 2.1 seeds per capsule. The density of the seed capsules produced at the seven major sites is shown in Table 8.1.

Table 8.1 : *The density of seed capsules produced by* Juncus squarrosus *at different altitudes in 1978. The values have been calculated from data given in Chapter 3 and are shown with 95% confidence limits*

Altitude (m)	Seed capsules produced per m^2 in 1978
15	1085 ± 457
245	523 ± 142
335	777 ± 216
395	295 ± 70
455	179 ± 54
520	78 ± 33
610	17 ± 13

The reduction in seed capsule density with increasing altitude can be described by a linear equation with the formula:

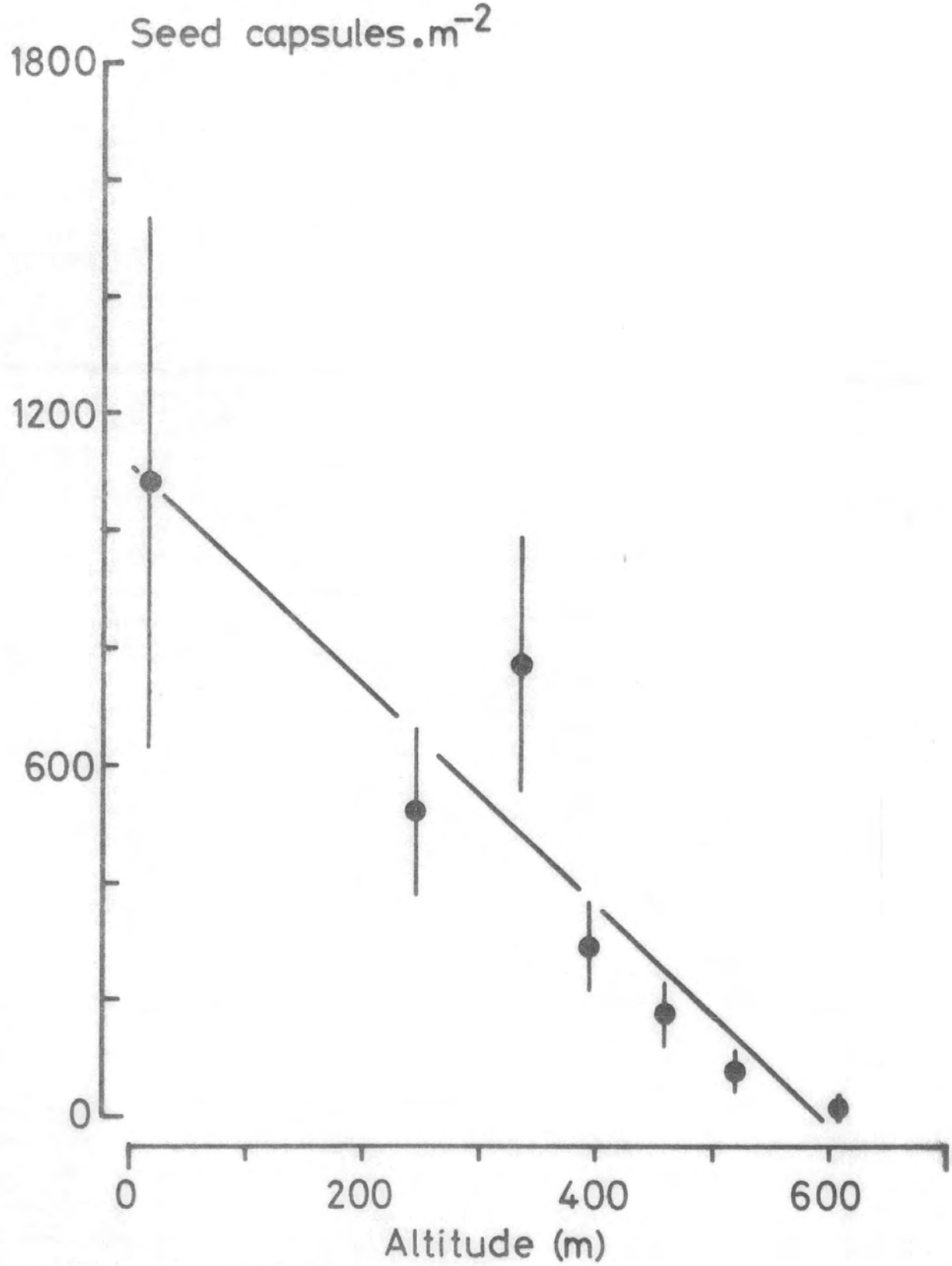
$$C = 1112.2 - 1.876A \qquad (8.1)$$

where C is the density of capsules produced at each altitude A, in metres. This relationship is shown in Figure 8.1.

Figure 8.1 : The relationship between the mean number (± 95% confidence limits) of seed capsules produced (C) per m^2 and altitude (A) in metres in 1978. The regression line has the equation

$$C = 1112.2 - 1.876A$$

$r = -0.933$, $n = 7$, S.E. of slope = 0.418, $P < 0.01$


Seed capsules.m^{-2}
1800
1200
600
0
0
200
400
600
Altitude (m)

8.3 Seed capsule predation in 1978

Table 8.2 shows the total number of seed capsules in samples of *Juncus squarrosus* inflorescences taken in November 1978, and also the number of capsules which had had their seeds eaten by *Coleophora alticolella* larvae. There were high rates of seed capsule predation in the middle region of the transect; the larvae had eaten the seeds from more than 95% of the capsules between 275 metres and 365 metres. There is a peak in the proportion of seed capsules damaged, at 350 metres. The distribution of the proportions at the different altitudes is not symmetrical about this maximum; it reaches zero above 520 metres yet remains around 0.4 at low altitudes.

Fitting a curve to the data for the proportion of seed capsules damaged was achieved by considering them to be of two components. In the lower altitude section there is a logistic increase in the proportion of seed capsules damaged with increasing altitude. In the upper phase there is a sharp reduction in the proportion and this is considered as an exponential decline. Both of these components, in isolation, approach the same asymptote, 1.00; i.e. total seed capsule destruction.

Logan *et al.* (1976) and Wollkind *et al.* (1978) have discussed a method for describing such relationships, where complex phenomena can be considered in two distinct phases, each being described by a separate curve but with matched asymptotes. This method was originally developed to describe temperature-dependent rate phenomena in arthropods but can be used in other situations. Such data can be described more precisely by this technique than by other curves, for example by polynomials (Logan *et al.* 1976).

Table 8.2 : *The total number of seed capsules and the number of seed capsules damaged by* Coleophora alticolella *larvae in samples of* Juncus squarrosus *inflorescences taken at the beginning of November in 1978. The number of damaged seed capsules is also expressed as a proportion of the total*

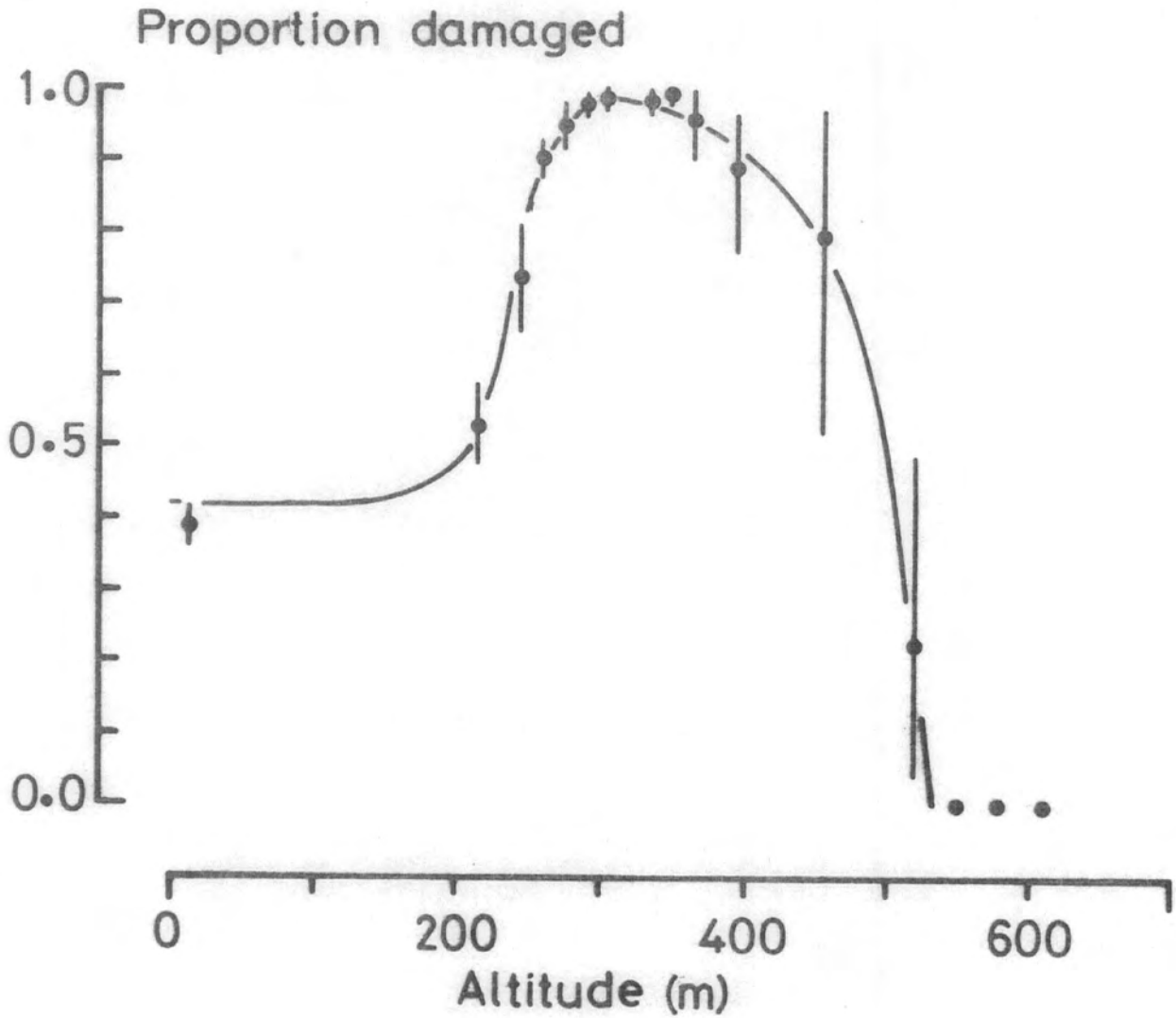
Altitude (m)	Number of inflorescences	Total number of seed capsules	Seed capsules damaged	Proportion damaged
15	50	1136	447	0.394
215	40	513	274	0.534
245	30	324	240	0.741
260	50	625	565	0.904
275	30	378	360	0.952
290	50	770	754	0.979
305	30	337	335	0.994
335	30	298	295	0.990
350	50	439	438	0.998
365	30	209	201	0.962
395	30	117	157	0.887
455	30	93	74	0.796
520	30	98	22	0.226
550	30	14	0	0.000
580	30	8	0	0.000
610	30	1	0	0.000

Figure 8.2 : The proportion of *Juncus squarrosus* seed capsules damaged by *Coleophora alticolella* at different altitudes in 1978. The 95% confidence limits, shown by the vertical lines, have been calculated from the arcsin transformation. The curve has the formula

$$D = \left[0.4248 + \frac{1 - 0.4248}{1+\exp(15.9504 - 0.0666A)}\right] - \exp\left(-\frac{532.735 - A}{52.831}\right)$$

D is the proportion of seed capsules damaged and A is the altitude in metres (see text for explanation).

$$F_{4,8} = 256.1,\ P < 0.001,\ R^2 = 0.988$$


Proportion damaged
1·0
0·5
0·0
0
200
400
600
Altitude (m)

The equation used to describe the curve shown in Figure 8.2 is of the form

$$D = \left[k+(1-k)/1+\exp(a-bA)\right] \cdot \exp\left(-\frac{A_{max} - A}{\Delta A}\right) \quad (8.2a)$$

D is the proportion of seed capsules with their contents eaten by *Coleophora alticolella* at each altitude A in metres. The first part of the expression (in the square brackets) is an equation for a logistic curve with a non-zero asymptote, k, to the left; a and b are the constants of the logistic curve as described in Chapter 2. The second part of the equation is for the exponential decline in the proportion of capsules destroyed, at higher altitudes. A_{max} is the upper altitudinal limit for the seed capsule destruction and ΔA is a small parameter which determines the rate of decline near this upper limit.

The data were fitted to this equation by least squares curvilinear regression and the resulting equation

$$D = \left[0.4248 + \frac{1 - 0.4248}{1+\exp(15.9504 - 0.0666A)}\right] \cdot \exp\left(-\frac{532.753 - A}{52.831}\right) \quad (8.2b)$$

is shown by the curve for $0 \leq A \leq A_{max}$ in Figure 8.2.

This equation predicts that at the lower altitudes, below 210 metres, less than 50% of the seed capsules were damaged by *Coleophora alticolella*; and that the upper altitudinal limit for seed capsule destruction, which is also the upper altitudinal limit of *C. alticolella* distribution, was about 533 metres.

The two phases of this curve are independent of each other and can, by the alteration of the parameters, change their shape and move in relation to each other and to the axes. The lower altitude

phase represents the controlling effect of the larval parasitoids on the ability of *C. alticolella* to utilize all of the available seed. The upper phase represents the increasing effect of climatic harshness on the moth population. The parasitoids had little effect above 300 metres. In the upper altitude region the larvae would have eaten all of the available seed were it not for the climatic effects which played an increasingly important role in the population dynamics of the moth.

8.4 Seed capsule survival in 1978

The proportion of seed capsules surviving predation (S) and thus able to disseminate their seeds is equal to 1 - proportion damaged (D) for values of D within the range $0 \leq A \leq A_{max}$ in equation 8.2. Outside this range D will be zero and therefore S will be 1.

The product of C from equation 8.1, the density of seed capsules produced at each altitude, and S the seed capsule survival rate, gives the expected density of seed capsules surviving attack by the moth larvae. These values are shown by the curve in Figure 8.3, with the density of seed capsules surviving plotted on a log. scale against altitude. There was no relationship between the number of seeds per seed capsule and altitude, the mean being 80.5 ± 2.1. The ordinate on the right hand side of this graph shows the equivalent density of surviving seeds. The points on this graph are the observed results, calculated from the differences between the number of seed capsules per inflorescence and the number that had had their seeds eaten, multiplied by the density of inflorescences at the end of the season (Appendix 2).

There is good agreement between the observed values and those predicted from the equations, over most of the range. Deviations occur at the three lowest sites on Little Dun Fell, where sheep grazing caused large reductions from the expected altitudinal trend of seed capsule production.

Figure 8.3 : The density of seed capsules and seeds surviving predation by the *Coleophora alticolella* larvae in relation to altitude in 1978. The points have been calculated from the samples taken in November and are plotted on a log scale. The curve is for the expected values.

Altitude (m)
0
200
400
600
Seeds.m⁻²
80.5
805
8050
80500
Capsules.m⁻²
1
10
100
1000

The expected density of surviving seed capsules at 245m is $149.9m^{-2}$ and the observed value was $51.5m^{-2}$. This latter value was calculated using the density of inflorescences at the end of the season, after the effects of sheep grazing. The sheep reduced the density of inflorescences here from $49.2m^{-2}$ to $18.4m^{-2}$, which is a loss of 62.6%. Correcting the observed density of seed capsules surviving for this loss gives a value of $137.7m^{-2}$, which is very close to that predicted.

This graph (Figure 8.3) can be considered in three sections. At the highest altitudes, above A_{max}, there is no predation of the seed by *Coleophora alticolella*. Consequently, the reduction in the density of seed capsules surviving to disseminate their seed is solely due to their reduced production by the plant. This is caused by the climatic effects upon both floret production and subsequent seed capsule development.

The increase in seed survival in the middle phase, from about 320 metres to A_{max}, is a result of the reduced impact of the seed predators under the influence of the increasingly severe climatic conditions.

Very low densities of seed survived around 320 metres, but at sites below this altitude there was an increasing density left after the larvae had finished feeding. It is in this low altitude section that the larvae are attacked by parasitoids. The parasitization of *C. alticolella* larvae not only reduces the moth population for the following season, but also reduces the effects of the larvae on seed capsule survival in the same year that the parasitization occurs. Each *C. alticolella* larva consumes the contents of more than two seed capsules during its complete development but, because some of the parasitoids kill their hosts while still on their initial seed capsule,

they are often prevented from eating their full complement of seeds. At progressively higher altitudes in this zone, parasitization decreases and the larvae are able to utilize an increasing proportion of the seed produced.

The final result of the changes in the density of seed produced, and the effects of the seed predators and their parasites, is a region where seed capsule development rate is high and parasitization of the seed predators is low. Here the high density of *C. alticolella*. causes almost total destruction of the seed capsules, leaving only about ten per square metre to disseminate their seeds. At altitudes higher and lower than this region, the survival of seed is such that below 250 metres and around 525 metres there were over one hundred seed capsules per m^2 remaining after the larvae had finished feeding. This is despite the density of seed capsules produced at 525 metres being less than 20% of the density at 250 metres.

8.5 Seed survival in other years

The highest densities of larvae per seed capsule in 1977 and 1979 were also in the middle region of the transect (Chapter 5). Samples were taken in November 1977 at a more limited range of sites than in November 1978; sampling was not carried out in November 1979. The proportion of capsules that had had their contents eaten by the larvae in 1977 reflects the larval densities, and follows a similar pattern with increasing altitude to the values in 1978 (Table 8.3). All of the seeds were eaten at the 305m site, 67.5% of the capsules were damaged at 455m and only 30.2% at the lowest site.

Table 8.3 : *The total number of seed capsules and the number of seed capsules damaged by* Coleophora alticolella *larvae in samples of* Juncus squarrosus *inflorescences taken at the beginning of November in 1977. The number of damaged seed capsules is also expressed as a proportion of the total*

Altitude (m)	Number of inflorescences	Total number of seed capsules	Seed capsules damaged	Proportion damaged
15	30	698	211	0.302
245	30	290	247	0.851
275	30	367	356	0.970
305	30	323	323	1.000
335	30	276	234	0.848
365	30	200	155	0.775
395	30	242	167	0.690
455	30	157	106	0.675

Table 8.4 gives values for the density of seeds surviving predation by *Coleophora alticolella* at comparable sites in 1977 and 1978. There was a similar pattern of seed survival in relation to altitude in the two years, with the lowest densities at the middle altitudes. There were, however, variations between years at some of the sites. These were due to differences in the density of seeds produced by the plants, which was caused by variation in the inflorescence density.

Samples were not taken in November of 1979, but larval density per seed capsule was greatest at the 275 metre site and so the highest seed predation would have been around this altitude. The larval densities in 1979 were comparatively low, however, and it is unlikely that there would have been as few seeds surviving as in the two preceding years.

Table 8.4 : *The density of* Juncus squarrosus *seeds surviving predation by the larvae of* Coleophora alticolella *at different altitudes in 1977 and 1978. The values are given with 95% confidence limits*

Altitude (m)	Number of seeds surviving x 10^{-3} per square metre	
	1977	1978
15	236.7 ± 62.0	52.9 ± 22.4
245	12.1 ± 3.7	10.9 ± 3.0
305	0.0 ± 0.0	0.3 ± 0.08
335	17.9 ± 4.1	0.6 ± 0.02
395	27.3 ± 7.7	2.7 ± 0.6
455	23.7 ± 8.3	2.9 ± 0.9

8.6 Discussion

Seed production by *Juncus squarrosus* is adversely affected by the severe climate at high altitudes. Climate also affects the density of the seed predators and at some altitudes all of the seed is eaten.

Total destruction of *J. squarrosus* seed by *Coleophora alticolella* has been noted by previous workers (Jordan 1962; Reay 1964). The results from the summer of 1953, given by Jordan (*loc. cit.*), show that total seed destruction occurred over a limited altitudinal range on the Little Dun Fell transect, similar to that found in the present study. Reay (1964) found that all of the *Juncus squarrosus* seed capsules were destroyed on a transect on the eastern side of the Pennines in 1956, but this was due to very low inflorescence densities.

Unfortunately, the data given by these previous authors is not detailed enough to allow the type of analysis used in this Chapter.

Welch (1966b) suggested that *Coleophora alticolella* would do no more than balance the increased production of seed capsules at the lower altitudes. Clearly this is not the case for all sites, as larval density is not directly related to seed capsule production. However, the density of seed surviving at the lowest site on Little Dun Fell was similar to the density near the upper altitudinal limit of *C. alticolella*.

Such drastic reductions in the reproductive capacity of *Juncus squarrosus*, as occurred around 320 metres in 1978, could have serious consequences on its population were it not for its ability to reproduce vegetatively. The seed is essential for the colonization of new and disturbed habitats (Welch 1966a). If this high level of predation were repeated over many years it would reduce the contribution of *J. squarrosus* to the seed bank and lower its competitive ability.

CHAPTER 9

GENERAL DISCUSSION

Whittaker (1971) studied the spittle-bug *Neophilaenus lineatus* in a favourable habitat, a low altitude grassland in southern England, and in a 'hazardous' environment in the northern Pennines, where the population was at the edge of its range. He found that the lowland population showed evidence of being regulated by density-dependent mortality. Parasitism by the dipteran *Verrallia aucta* (Fallén) contributed to this regulation. The high altitude population did not appear to be regulated. Local extinctions were common in this part of the bug's range.

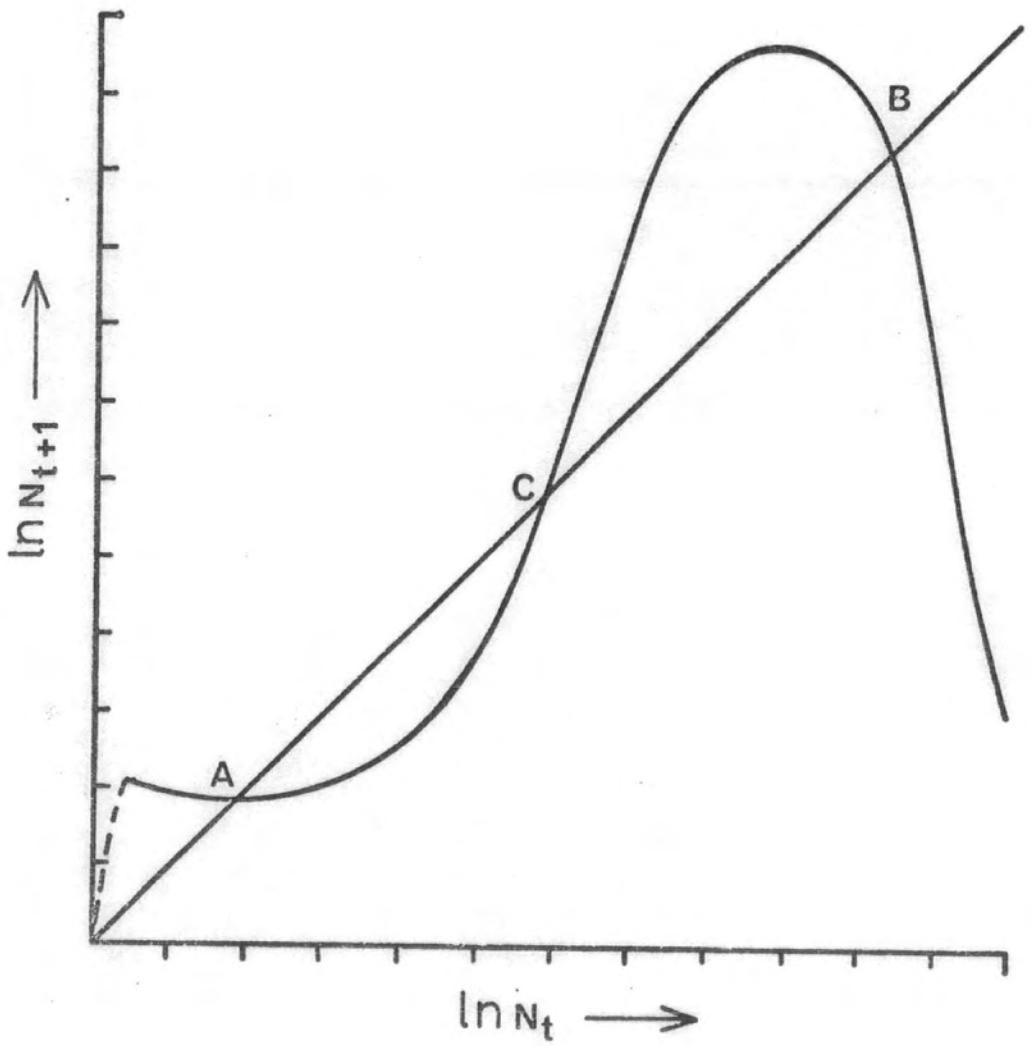
In contrast to Whittaker's work at two sites, the present study has been an investigation into the ecology of an insect along a gradient of increasing environmental harshness. This research has discerned three main regions in the altitudinal distribution of *Coleophora alticolella*. At the low altitude site at Drigg, there was high larval mortality due to hymenopterous parasitoids. This mortality was reduced with increasing altitude and the natural enemies were absent from the higher sites on Little Dun Fell. At the highest altitudes, towards the edge of its range, the population was at the mercy of the harsh climate and its adverse effects on the larval food, the seeds of *Juncus squarrosus*. Between these two extremes, *Coleophora alticolella* was free from the effects of parasitoids and failed seed-setting. This enabled the population to increase to a level at which it exploited all of the available food. At these higher population densities, density-dependent reduction of natality caused by competition for food was the major factor limiting population growth.

One way of expressing population growth is by the Ricker-type curve (Holling 1973; Southwood 1975; May 1977). The population in one generation is expressed as a function of the population in the previous generation. When the curve crosses the line with a slope of unity an equilibrium is possible. Sinuous curves (Figure 9.1) may result from the combined effects of fecundity, predation and interspecific competition, at different population densities; these can have a number of equilibria, some stable, some transient (Holling 1973). The properties and implications of this type of curve have been described by May (1977). In the curve shown in Figure 9.1 there are two attracting equilibrium points (A and B) and one repelling point (C). When the population is controlled by predators the population fluctuates around the lower endemic level, A. If the fluctuations carry the population above the release point, C, the population will 'explode' to point B. Extreme competition at the high density is then often responsible for a population crash, bringing the level back to the equilibrium at A.

Outbreaks of phytophagous insects, many of them pest species, which occur in simple habitats, such as crop monocultures and arctic environments, may be due to a lack of control by natural enemies (Pimentel 1961; Nuoroteva 1963; Price and Waldbauer 1975). Evidence for this has been given by Smith and Whittaker (1980), in their study of the chrysomelid beetle *Gastrophysa viridula* Degeer, which feeds on the broad-leaved dock (*Rumex obtusifolius* L.). They found that in plots with diverse vegetation, typical of communities well advanced in succession, predation prevented the beetle from successfully exploiting the dock. They concluded that "*Gastrophysa viridula* is probably confined to young communities by the influence of predation".

Southwood (1977a) has discussed the role of the environment in the evolution of the bionomic strategies of animals and has particularly

Figure 9.1 : An example of a Ricker-type population growth curve, with the population in generation $t+1$ as a function of the population in the preceding generation. Two stable (A and B) and one unstable (C) equilibria occur where the curve crosses the slope of unity (after May 1977).


ln N t+1
ln N t
A
B
C

related this to the *r*- and *K*-selection continuum. Habitat stability, or the position along this continuum, is one of the three axes used by Southwood and Comins (1976) in producing the landscape of their synoptic population model. The other two axes are population density and population growth. The surface of this model extends from extreme *r*-selected animals to those with *K*-selected characteristics. Natural enemies do not play a significant role at the two ends of this spectrum. Populations in these positions have only one stable equilibrium, determined by competition. In the intermediate region, predator effects are more significant in population regulation. Here there is a valley in the surface; this is called the 'natural enemy ravine' and a lower predator-maintained equilibrium point occurs if the ravine dips below the zero growth contour. The population growth curve in this region is as that shown by Figure 9.1.

Southwood and Comins (*loc. cit.*) illustrate their model, and the effects of the natural enemy ravine on population growth, by using the example of I.R. Clark's work on the eucalyptus psyllid, *Cardiaspina albitextura* Taylor. During the endemic phases of this insect, the population is regulated by density-dependent mortality and predation caused by a range of predators, mainly birds, and parasitoids. Occasionally, weather conditions are such that mortality from the parasitoids is reduced and the bird predators are not able to respond to the increasing prey density. The population then moves past the release point and the adult density rises dramatically to epidemic levels. The high population levels cause extreme 'scramble-competition' and consequent larval starvation, with an eventual return to the endemic level.

Habitat stability may be measured as the degree of its permanence and predictability (Southwood 1975). Southwood *et al.* (1974) claim that

the instability - stability spectrum of the habitat gives rise to the *r* - *K* selection continuum. However, although a species is confined to a particular type of habitat (temporary pools, one plant species etc), there will be some variation in the relative stability of habitats within its range. Habitat stability is reduced in harsh climates (Whittaker 1975; Southwood 1977a). Thus for any species there will be limited movement along the *r* - *K* continuum, depending on the degree of this stability throughout its range. The altitudinal distribution of *Coleophora alticolella* can be regarded as movement along the stability - instability axis of the synoptic model. Theoretically, the model would suggest that with increasing altitude the system travels along to the r-end of the landscape and the natural enemy ravine is gradually filled in. This removes the lower predator-maintained equilibrium point and leaves only the upper one. This upper point is near to the carrying capacity of the food-supply (May 1977) and the population should be regulated by density-dependent mortality, due to competition for *Juncus squarrosus* seed capsules. At the highest altitudes, this process is 'short-circuited' by the severe climate which reduces the population by density-independent mortality.

Southwood and Comins (1976) emphasise that stochastic elements, such as weather, will complicate the conclusions generated from their deterministic model. As with most natural systems, there is a great deal of 'noise' associated with the relationships between *Coleophora alticolella* and *Juncus squarrosus*. This is due to the large variation in the density of inflorescences produced from one year to the next. These theoretical studies cannot mimic the observed behaviour of the *Coleophora alticolella* population because of this variation in the food-supply.

The formulation of population models, such as those described here, can help in the implementation of appropriate control programmes against pests with different ecological strategies (Southwood 1977a). Native *r*-pests, such as malarial mosquitoes (*Anopheles* spp.) cannot be successfully controlled by natural enemies alone. Insecticides, which can act quickly to prevent population increase, are more likely to contain such pests. *K*-pests can be controlled by pesticides, but also by sterile mating techniques and changes in agricultural practice. This approach has been used to control the tsetse fly (*Glossina* spp.) in parts of Africa. Biological control has better chances of succeeding against intermediate-pests (Conway 1976; Southwood 1977b). In fact, the use of insecticides against such species may be counter-productive since it can lead to an eradication of the natural enemies and hence any potential endemic equilibrium point (Price and Waldbauer 1975; Conway 1976).

Intermediate-pests may become *r*-pests if they are introduced into new environments without their natural enemies (May 1976). Indeed, a high proportion of serious insect pests are exotic species (Simmonds and Greathead 1977). It is against such pests that 'classical' biological control programmes (the importation of parasitoids and predators) are aimed.

The theories of biological control have been covered in numerous texts (e.g. DeBach 1964; Huffaker 1971). Commonly, these measures are aimed at controlling introduced pests by the introduction of natural enemies, usually parasitoids, from their native home, with the hope that they will quickly become established and reduce the pest to a lower equilibrium level. Force (1972, 1974) has suggested that parasitoids which could be classed as *r*-strategists should be used, since their tolerance of a wide range of environmental conditions and high rate of increase allows them to colonise the new area quickly and dramatically reduce

their host's density. The major problems with this approach, as Force has pointed out, is that in the pest's native country the *r*-parasitoids are usually scarce and could be overlooked, because of the better competitive abilities of the *K*-species in the parasitoid complex. These ideas can be illustrated by the relationship between the winter moth (*Operophtera brumata* (L.)) and one of its parasitoids, the tachinid fly *Cyzenis albicans* (Fallén). The fecundity of *C. albicans* is potentially very high, being about 2000 eggs per female (Varley, Gradwell and Hassell 1973) and, although it has very little impact on its host population in Wytham Woods, England, it is a very effective controlling agent of the pest in Newfoundland (Hassell 1980). *C. albicans* is ineffective in Wytham because its puparia are exposed to predators for a long period, and it is attacked by an ichneumonid hyperparasitoid *Phygadeuon dumetorum* Gravenhorst (Varley and Gradwell 1968).

The use of several species of parasitoids to control a pest has its dangers because of the chance of inadvertently introducing hyperparasitoids. The presence of hyperparasitoids can seriously impair the controlling influence of the primary parasitoid on its host. Hassell (1979) has shown, theoretically, that the introduction of a hyperparasitoid into a host-parasitoid equilibrium can produce a locally stable three-species equilibrium with the host density raised to a level higher than before the introduction of the hyperparasitoid.

During the present study, *Tetrastichus endemus*, the parasitoid of *Elachertus olivaceus*, was only found on *Coleophora alticolella* at the site with the mildest climate. It would be interesting to find out whether the density of *C. alticolella* is raised by the effects of this secondary parasitism. This could be the reason why the proportion of *Juncus squarrosus* seed capsules destroyed by the larvae at 15m was similar to that at 215m.

The damage done by phytophagous insects can be put to good use if the plant which they attack is a weed. An insect intended for weed control is introduced without its natural enemies; in their absence the population increases and destroys the food-plant. Such an interaction should eventually reduce both the plant and insect to low levels. This was the result of introducing the chrysomelid beetle *Chrysolina quadrigemina* (Suffrian) into California to control the St John's wort *Hypericum perforatum* L. (the Klamath weed) (Wilson 1964).

Seed predators, such as *Coleophora alticolella*, are unlikely to be efficient control agents of perennial weeds because the host persists and vegetative reproduction is common. However, they may be useful in preventing the weed from colonizing new habitats. Seed-eaters are more effective against annuals (Wilson *loc. cit.*).

Climatic conditions can severely reduce the ability of a parasite to control its host. One important study into the effects of climate on a pest control programme is that of DeBach (1965). He studied the parasitoids of the California red scale, *Aonidiella aurantii* (Maskell), particularly *Aphytis lignanensis* Compere. His research showed that weather does not impose upper limits to the host population increase but, in areas with favourable weather, parasitoids could regulate the host's population at low densities. These favourable conditions only occur on the Californian coast. The climate is harsher inland and, although the parasitoid can survive here, it cannot control its host's density.

DeBach (*loc. cit.*) used the following words to describe the relationships between the California red scale, its parasite *Aphytis lignanensis* and climate. They also apply to the relationships between *Coleophora alticolella*, its larval parasitoids and altitude:

> "Effective parasites regulate their own average population densities at low levels by regulating their host population densities at low levels. Thus we may find a host insect and its parasite rare in a climatic zone optimum for both if the parasite is intrinsically effective ..... On the other hand, in a climatic zone suboptimum for the host but even more so for an intrinsically effective parasite, the host may be unregulated and become abundant, ... Here we have the anomaly of scarcity being associated with ideal weather conditions."

Marginal areas, where a population may not be under the control of natural enemies, can act as reservoirs for pest species. The population density in these areas may rise to a very high level and result in migration into nearby crops (Way 1977). Pests are often ignored in these areas or while they are feeding on alternative host-plants of no economic importance (Southwood 1977b).

Coleophora alticolella is not a pest species, although other members of this genus damage crops. The larch-casebearer, *C. laricella*, is a serious forestry pest of the European larch, *Larix decidua* Miller, (Thorpe 1933). This insect is now a major pest of the western larch, *L. occidentalis*, and is responsible for much damage in plantations throughout the north and west of the U.S.A. and much of Canada (Quednau 1967; Brown and Kulhavy 1978b). The birch-casebearer, *Coleophora serratella*, was accidentally introduced into North America in about 1920 and is now a common pest in the eastern part of that Continent. Although it attacks several hardwood species, its principal host-plant in these areas is the white birch, *Betula papyrifera* Marsh (Bryant and Raske 1975).

This research on *Coleophora alticolella* has shown that the climatic conditions in different parts of its altitudinal range have profound effects on the mortality factors acting during its life-cycle. Pest species will be affected in a similar manner. Consequently, serious consideration must be given to the prevailing climate of an area before deciding on the most appropriate method of pest control.

SUMMARY

1. Aspects of the ecology of the moth *Coleophora alticolella* were studied in relation to altitude, during the period 1977 to 1979.

2. Study sites were located in two regions:
   i) a low-altitude site, 15m above sea-level, at Drigg on the Cumbrian coast.
   ii) along a transect from 215m to 610m on the western escarpment of Little Dun Fell in the northern Pennines.

3. The larvae eat the seeds of several species of *Juncus*; the main food-plant in the study areas was *J. squarrosus*.

4. Seed production by *J. squarrosus* at different altitudes was measured by using four parameters:
   i) the density of inflorescences produced.
   ii) the number of florets per inflorescence.
   iii) the proportion of florets developing into seed capsules.
   iv) the number of seeds per capsule.

5. There was no significant variation in the density of inflorescences produced between different altitudes in any one year, but there was significant variation between years. The mean densities were highest in 1977 and lowest in 1978. It is suggested that variation between years may be due to the amount of rainfall during the inflorescence growth period and also during the period of bud formation for the following year's growth.

6. There was a reduction of 1.99 florets per inflorescence per 100m increase in altitude between 15m and 455m in 1978. The mean number of florets is reduced in dry soil conditions.

7. There was a reduction of 3.7 seed capsules per inflorescence per 100m increase in altitude between 15m and 455m in 1978. The change in the proportion of florets developing into seed capsules with increasing altitude has been described by a logistic curve for each sample date. The point of inflexion of these curves, which is the altitude at which half of the maximum development is realized, was highest in August 1979 (459m) and lowest in August 1978 (364m); the 1977 value was 414m. These values are related to the mean daily temperature during June and July, the period of seed capsule maturation.

8. There was no relationship between the mean number of seeds per capsule and altitude. The overall mean value (with 95% confidence limits) is 80.5 ± 2.1 seeds per capsule.

9. The variation in the density of seeds produced per m^2 at each site in different years was mainly due to variations in the density of inflorescences. The reduction in the proportion of florets developing into seed capsules with increasing altitude was the most important factor contributing to the lower density of seeds produced at higher sites.

10. Sheep graze the inflorescences mainly at the lower altitudes during the first part of the year. The greater part of the grazing at the high altitudes occurs after August. Sheep grazed over 50% of the inflorescences below 325m. Grazing was negligible at Drigg.

11. The eggs of *Coleophora alticolella* are 0.398mm long and 0.200mm along the other two axes. During embryonic development they change colour from white through yellow to orange. It takes approximately two weeks for an egg to turn orange.

12. The number of oviposition sites on an inflorescence is determined by the number of florets but, because an oviposition site can contain more than one egg, the relationship between the number of eggs and the number of florets is more variable.

13. The highest density of eggs was recorded at 335m, where there were 1.120 eggs per floret in 1978. Only 0.102 eggs per floret were found at 520m. The egg density was also reduced at low altitudes, with 0.287 eggs per floret at 15m.

14. There was little difference in the rate of egg-laying at each altitude. Between 3% and 4% of the total eggs were laid each day, during the 1978 oviposition period, at sites below 500m.

15. The median date of oviposition was delayed by 3.7 days per 100m increase in altitude in 1978.

16. The mean number of eggs per oviposition site increased with the increase in the density of eggs per floret, during the first part of the oviposition period. This relationship did not hold for the latter part of the oviposition period because the increase in the structural complexity of the inflorescence during their development makes more oviposition sites available. At the end of the oviposition period, there were sufficient sites for all of the eggs to be laid singly.

17. The effect of heterogeneity in the density of inflorescences within a *Juncus squarrosus* sward on oviposition behaviour was investigated. The number of eggs per floret was inversely related to the expected average distance between nearest neighbouring inflorescences in different density plots. It is argued that at high densities of inflorescences, less time must be spent travelling from one inflorescence to another and more time will be available for ovipositing on each inflorescence. This results in higher numbers of eggs per floret in areas with relatively higher densities of inflorescences.

18. The highest larval densities (over 0.8 per seed capsule in 1978) were recorded at the middle altitudes of the transect. The larval density fell to zero above 520m in 1978 and 1979, but in 1977 there were 0.019 larvae per seed capsule at 610m. Larval densities were also reduced at low altitudes, but never to extinction. Generally, densities at each site were highest in 1978 and lowest in 1979.

19. The larvae were significantly overdispersed with respect to the seed capsules, but the percentage of larvae sharing capsules at each site was related to the larval density.

20. The major mortality factor acting between the egg stage and larval establishment inside the seed capsules was starvation caused by failed seed capsule development. This factor was very important at the highest altitudes and resulted in over 80% mortality of this stage, above 500m in 1978.

21. The lowering of the upper altitudinal limit of larval distribution is a result of the lowering of the upper limit of seed production. This upper limit is not a sudden cut-off, but is a result of the gradual decline in survival at the larval establishment stage, caused by the decline in the proportion of florets developing into seed capsules with increasing altitude.

22. The duration of the egg stage was 25 days at 15m and 31 days at 455m. The first larval instar took 10 and 13 days at these two sites and the second instar 15 and 16 days respectively. The median date of the oviposition period was 15 days later at 455m than at 15m. Equivalent mean instars were achieved about three weeks later at 455m, during the first half of larval development. The Q_{10} for egg development, based on a temperature difference of $3^{o}C$ between the two sites, was 2.10. Temperature had much less effect on the development rate of the early larval instars, the Q_{10} being only 1.30.

23. The mean date of larval case production was delayed by 5.7 days per 100m increase in altitude in 1977. The mean date was later at each site in 1978 than in 1977. There was no significant relationship between the mean date of case production and altitude in 1978.

24. There was an indirect relationship between the standard deviation of the case production date and the density of larvae per seed capsule at each site, apart from 15m. Although larvae tend to produce their cases at the end of the third or beginning of the fourth instar, this can be modified if the food-supply in their first seed capsule is exhausted. A significantly greater proportion of larvae that were sharing seed capsules had started to produce their cases than those in capsules by themselves at 335m on 1 September 1978.

25. The mean date of larval migration to overwinter in the leaf-litter was delayed by 11.4 days per 100m increase in altitude in 1977. There was no significant relationship between mean migration date and altitude in 1978.

26. When there was adequate food available to the larvae after they had produced their cases, the time between the mean date of case production and the mean date of larval migration increased with increasing altitude.

27. Six species of primary parasitoid and one hyperparasitoid were recorded from *C. alticolella* larvae. They were all Hymenoptera. The primary parasitoids were: *Scambus brevicornis, Gonotypus melanostoma, Gelis* sp., *Elachertus olivaceus, Euderus viridis* and *Pteromalus semotus*.

28. The hyperparasitoid was *Tetrastichus endemus* and was reared from *Elachertus olivaceus* pupae.

29. There were two generations of *E. olivaceus* on each host generation. The first mainly attacks host larvae inside the seed capsules and the second attacks those with cases.

30. The larger hosts can support up to five *E. olivaceus* but the smaller hosts can only support two. Pupal size was reduced with increasing brood size and those from 245m were smaller than their counterparts at 15m. Pupae in equivalent sized broods were smaller on the younger of the two host categories at 245m. There was over a four-fold difference between the maximum and minimum pupal volumes, calculated from the mean pupal lengths on different categories of host and brood sizes.

31. Significant deviations from a 1:1 sex-ratio were found for three of the primary parasitoids; the numbers of females as percentages of the totals reared were: *Elachertus olivaceus* 99.4%, *Euderus viridis* 60.5% and *Scambus brevicornis* 3.2%.

32. The female *S. brevicornis* that were caught whilst ovipositing on *Coleophora alticolella* had significantly longer wings and ovipositors than their counterparts bred from this host. The alternative host, on which the majority of the females developed, was not identified.

33. The date of first attack by *Elachertus olivaceus* was not delayed with increasing altitude. *Euderus viridis* attacked earlier at 15m than at 245m. *Scambus brevicornis* only attacked *Coleophora alticolella* larvae after they had produced their cases. The first attack by *Scambus brevicornis* was 3 weeks later at 245m than at 15m; it was also 3 weeks later in 1978 than in 1977 at both sites.

34. The percentage of *Coleophora alticolella* larvae parasitized was reduced with increasing altitude. 46.1% of the larvae at 15m were parasitized in 1977 and 61.1% in 1978. Parasitism at 335m was only 1.8% in 1977 and 0.3% in 1978.

35. The number of different species of parasitoids recorded was reduced from 6 primary and one secondary at 15m, to only one species, *Scambus brevicornis*, at 335m and above. No parasitoids were recorded above 395m in 1977 and 365m in 1978. *Tetrastichus endemus* and *Gonotypus melanostoma* were only recorded at 15m.

36. Life-tables have been constructed for *Coleophora alticolella* at 15m, 245m, 335m, 395m, 455m and 520m. They cover the period from eggs in 1977 to larvae established inside seed capsules in 1979, a little over two generations.

37. The major factor influencing population change at the highest altitude was starvation of the larvae between hatching and establishment inside the seed capsules. Parasitization was most important at the lowest altitude. Competition for food, between larvae after they have produced their cases, resulted in a density-dependent reduction in natality in the following spring. This was detected at sites above 245m and was most important in the population dynamics of *C. alticolella* in the middle region of the transect, around 335m.

38. The survivorship curves for *C. alticolella* at 15m and 455m were compared for the 1978 generation. At 15m, the curve was similar to a 'Slobodkin type III' curve (Price type B), whereas at 455m it was more like a 'Slobodkin type IV' curve (Price type A). These differences are due to variations in the mortality during larval establishment.

39. Predation of the *Juncus squarrosus* seed capsules by *Coleophora alticolella* larvae was greatest around 335m. In some years, almost all of the seed is eaten in this region.

40. In 1978, over 100 seed capsules per m^2 survived predation by *C. alticolella* at sites below 250m and around 525m, but only 10 per m^2 survived at 320m.

41. The results from this study have been discussed in relation to current population models and to theories on the biological control of insect pests and weeds.

REFERENCES

Andrewartha, H.G. and Birch, L.C. (1954) The Distribution and Abundance of Animals. University of Chicago Press, Chicago.

Anscombe, F.J. and Tukey, J.W. (1963) The examination and analysis of residuals. Technometrics, 5, 141-160.

Arthur, A.P. and Wylie, H.G. (1959) Effects of host size on sex ratio, development time and size of *Pimpla turionella* (L.) (Hymenoptera: Ichneumonoidea). Entomophaga, 4, 297-301.

Askew, R.R. (1964) On the biology and taxonomy of some European species of the genus *Elachertus* Spinola (Hymenoptera, Eulophidae). Bull. ent. Res., 55, 53-58.

Askew, R.R. (1968) Chalcidoidea - Elasmidae and Eulophidae (Elachertinae, Eulophinae and Euderinae). Handbk. Ident. Br. Insects, VII (2b), 1-39. Royal Entomological Society, London.

Askew, R.R. (1971) Parasitic Insects. Heinemann, London.

Aubert, J-F. (1969) Les Ichneumonides Ouest-paleartiques et leurs Hôtes. Vol. 1 (Pimplinae, Xoridinae, Acaeitinae). pp 1-302. Quatre-Feuilles, Paris.

Bailey, N.T.J. (1959) Statistical Methods in Biology. The English Universities Press, London.

Barbosa, P. (1977) *r* and *K* strategies in some larval and pupal parasitoids of the gypsy moth. Oecologia, Berlin, 29, 311-327.

Beck, S.D. (1968) Insect Photoperiodism. Academic Press, New York.

Beddington, J.R., Hassell, M.P. and Lawton, J.H. (1976) The components of arthropod predation. II. The predator rate of increase. J. Anim. Ecol., 45, 165-185.

Birch, L.C. (1945) The influence of temperature on the development of the different stages of *Calandra oryzae* L. and *Rhizopertha dominica* Fab. (Coleoptera). Aust. J. exp. Biol. med. Sci., 23, 29-35.

Bliss, C.I. (Ed.) (1970) Statistics in Biology: Statistical Methods for Research in the Natural Sciences. McGraw-Hill, New York.

Boldt, P.E. (1974) Temperature, humidity and host: effect on rate of search of *Trichogramma evanescens* and *T. minutum* auctt. (not Riley, 1871). Ann. ent. Soc. Am., 67, 706-708.

Boucek, Z. and Askew, R.R. (1968) Index of entomophagous insects: 3. Palearctic Eulophidae (excl. Tetrastichinae) (Hym., Chalcidoidea). Le François, Paris.

Bradley, J.D. (1955) The result of a re-examination of the type material of *Coleophora caespititiella* Zeller, 1839, *C. alticolella* Zeller, 1849 and *C. agramella* Wood, 1892. (Lep.: Coleophoridae). Entomologist, 88, 273-277.

Brantjes, N.B.M. (1976) Riddles around the pollination of *Melandrium album* (Mill.) Garcke (Caryophyllaceae) during the oviposition by *Hadena bicruris* Hufn. (Noctuidae, Lepidoptera); I. Proc. K. ned. Akad. Wet. C, 79, 1-12.

Brower, L.P. (1961) Experimental analyses of egg cannibalism in the monarch and queen butterflies *Danaus plexippus* and *D. gilippus* berenice. Physiol. Zool., 34, 287-296.

Brown, M.W. and Kulhavy, D.L. (1978a) Egg dispersion in the larch casebearer, *Coleophora laricella* (Lepidoptera: Coleophoridae), in northern Idaho. J. Entomol. Soc. Brit. Columbia, 75, 27-28.

Brown, M.W. and Kulhavy, D.L. (1978b) Pre-wintering mortality in the larch casebearer, *Coleophora laricella* (Lepidoptera: Coleophoridae), on western larch in northern Idaho. J. Entomol. Soc. Brit. Columbia, 75, 29-33.

Bryant, D.G. and Raske, A.G. (1975) Defoliation of white birch by the birch casebearer, *Coleophora fuscedinella* (Lepidoptera: Coleophoridae). Can. Ent., 107, 217-223.

Burnett, T. (1951) Effects of temperature and host density on the rate of increase of an insect parasite. Am. Nat., 85, 337-352.

Burnett, T. (1954) Influences of natural temperatures and controlled host densities on oviposition of an insect parasite. Physiol. Zool., 27, 239-248.

Burnett, T. (1956) Effects of natural temperatures on oviposition of various numbers of an insect parasite (Hymenoptera, Chalcididae, Tenthredinidae). Ann. ent. Soc. Am., 49, 55-59.

Butterfield, J. (1976) The response of development rate to temperature in the univoltine cranefly, *Tipula subnodicornis* Zetterstedt. Oecologia, Berlin, 25, 89-100.

Cameron, P. (1903) Monograph of the Phytophagous Hymenoptera. 4, pp 1-248. Ray Society, London.

Chewyruev, Iv. (1913) Le rôle des femelles dans la détermination du sexe de leur descendance dans le groupe des Ichneumonides. C. r. Séanc. Soc. Biol. (Paris), 74, 695-699.

Clarke, P.J. and Evans, F.C. (1954) Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology, 35, 445-453.

Clausen, C.P. (1939) The effect of host size upon the sex ratio of Hymenopterous parasites and its relation to methods of rearing and colonization. Jl. N.Y. ent. Soc., 47, 1-9.

Conway, G.R. (1976) Man versus pests. Theoretical Ecology: Principles and Applications. (Ed. by R.M. May), pp 257-281. Blackwell Scientific Publications, Oxford.

Coshan, P.F. (1974) The biology of *Coleophora serratella* (L.) (Lepidoptera: Coleophoridae). Trans. R. ent. Soc. Lond., 126, 169-188.

Coulson, J.C. (1962) The biology of *Tipula subnodicornis* Zetterstedt with comparative observations on *Tipula paludosa* Meigen. J. Anim. Ecol., 31, 1-21.

Coulson, J.C., Horobin, J.C., Butterfield, J. and Smith, G.R.J. (1976) The maintenance of annual life-cycles in two species of Tipulidae (Diptera); a field study relating development, temperature and altitude. J. Anim. Ecol., 45, 215-233.

Coulson, J.C. and Whittaker, J.B. (1978) Ecology of moorland animals. Production Ecology of British Moors and Montane Grasslands. (Ed. by O.W. Heal and D.F. Perkins), pp 52-93. Springer, Berlin.

Cragg, J.B. (1961) Some aspects of the ecology of moorland animals. J. Ecol., 49, 477-506.

Danilevskii, A.S. (1965) Photoperiodism and Seasonal Development of Insects. Oliver and Boyd, Edinburgh.

Davidson, J. (1942) On the speed of development of insect eggs at constant temperatures. Aust. J. exp. Biol. med. Sci., 20, 233-239.

Davidson, J. (1944) On the relationship between temperature and the rate of development of insects at constant temperatures. J. Anim. Ecol., 13, 26-38.

DeBach, P. (Ed.) (1964) Biological Control of Insect Pests and Weeds. Chapman and Hall, London.

DeBach, P. (1965) Weather and the success of parasites in population regulation. Can. Ent., 97, 848-863.

Delucchi, V. and Verbeke, J. (1953) *Habrocytus milleri* n. sp., ectoparasite de *Coleophora frischella* L. Bull. Inst. r. Sci. nat. Belg., 29, 1-14.

Dempster, J.P. (1971) The population ecology of the Cinnabar Moth, *Tyria jacobaeae* L. (Lepidoptera, Arctiidae). Oecologia, Berlin, 7, 26-67.

Dempster, J.P. (1975) Animal Population Ecology. Academic Press, London.

Dempster, J.P. and Lakhani, K.H. (1979) A population model for cinnabar moth and its food plant, ragwort. J. Anim. Ecol., 48, 143-163.

Dixon, W.J. (1975) Biomedical Computer Programs. University of California Press, London.

Eddy, A., Welch, D. and Rawes, M. (1969) The vegetation of the Moorhouse National Nature Reserve in the northern Pennines. Vegetatio, 16, 239-284.

Fitton, M.G., Graham, M.W.R. de V., Bouček, Z.R.J., Fergusson, N.D.M., Huddleston, T., Quinlan, J. and Richards, O.W. (1978) Kloet and Hincks: A Check List of British Insects (2nd edition). Part 4: Hymenoptera. Handbk. Ident. Br. Insects, XI (4), 1-159. Royal Entomological Society, London.

Flanders, S.E. (1939) Environmental control of sex in hymenopterous insects. Ann. ent. Soc. Am., 32, 11-26.

Flanders, S.E. (1945) The bisexuality of uniparental Hymenoptera, a function of the environment. Am. Nat., 79, 122-141.

Flanders, S.E. (1962) The parasitic Hymenoptera: Specialists in population regulation. Can. Ent., 94, 1133-1147.

Force, D.C. (1970) Competition among four hymenopterous parasites of an endemic insect host. Ann. ent. Soc. Am., 63, 1675-1688.

Force, D.C. (1972) *r*- and *K*-strategists in endemic host-parasitoid communities. Bull. ent. Soc. Am., 18, 135-137.

Force, D.C. (1974) Ecology of insect host-parasitoid communities. Science, 184, 624-632.

Force, D.C. (1975) Succession of *r* and *K* strategists in parasitoids. Evolutionary Strategies of Parasitic Insects and Mites. (Ed. by P.W. Price), pp 112-129. Plenum, New York.

Ford, E.B. (1972) Moths. 3rd edition, Collins, London.

Fox, L.R. (1975) Cannibalism in natural populations. A. Rev. Ecol. Syst., 6, 87-106.

Francis, P.E. (1978) The climate of upland Britain. The Future of Upland Britain. (Ed. by R.B. Tranter). Symposia of the Centre for Agricultural Strategy, 2, 387-396.

Gepp, J. (1975) Zum Parasitenkomplex von *Coleophora fuscedinella* Z. (Lep., Coleophoridae) in Ostösterreich. Z. angew, Ent., 79, 76-96.

Geyspits, K.F. and Zarankina, A.I. (1963) Some features of the photoperiodic reaction of *Dasychira pudibunda* L. (Lepidoptera, Orgyidae). Ent. Rev., Wash., 42, 14-19.

Graham, M.W.R. de V. (1969) The Pteromalidae of North-Western Europe (Hymenoptera: Chalcidoidea). Bull. Br. Mus. nat. Hist. (Ent.) Suppl., 16, 1-908.

Grieg-Smith, P. (1957) Quantitative Plant Ecology. Butterworths, London.

Hadley, M. (1971) Aspects of the larval ecology and population dynamics of *Molophilus ater* Meigen (Diptera: Tipulidae) on Pennine moorland. J. Anim. Ecol., 40, 445-466.

Hågvar, S. (1975) Studies on the ecology of *Melasoma collaris* L. (Col., Chrysomelidae) in alpine habitats at Finse, south Norway. Norw. J. Ent., 22, 31-47.

Hågvar, S. (1976) Altitudinal zonation of the invertebrate fauna on branches of birch (*Betula pubescens* Ehrh.). Norw. J. Ent., 23, 61-74.

Hassell, M.P. (1976) The Dynamics of Competition and Predation. Edward Arnold, London.

Hassell, M.P. (1978) The Dynamics of Arthropod Predator-Prey Systems. Princeton University Press, Princeton.

Hassell, M.P. (1979) The dynamics of predator-prey interactions: polyphagous predators, competing predators and hyperparasitoids. Population Dynamics. (Ed. by R.M. Anderson, B.D. Turner and L.R. Taylor), pp 283-306. Blackwell Scientific Publications, Oxford.

Hassell, M.P. (1980) Foraging strategies, population models and biological control: a case study. J. Anim. Ecol., 49, 603-628.

Hassell, M.P. and May, R.M. (1974) Aggregation of predators and insect parasites and its effect on stability. J. Anim. Ecol., 43, 567-594.

Hedwig, K. (1943) Verzeichnis der bisher in Schlesien aufgefunden Hymenopteren, V. Ichneumonoidea. Z. Ent., Breslau, 19, 3.

Henty, C.J. (1979) Foraging activity of snow buntings wintering in Scotland. Bird Study, 26, 192-194.

Hodkinson, I.D. (1973) The biology of *Strophingia ericae* (Curtis) (Homoptera, Psylloidea) with notes on its primary parasite *Tetrastichus actis* (Walker) (Hym., Eulophidae). Norsk. ent. Tidsskr., 20, 237-243.

Holling, C.S. (1973) Resiliance and stability of ecological systems. A. Rev. Ecol. Syst., 4, 1-23.

Horobin, J.C. (1971) Studies on the biology of moorland Tipulidae with particular reference to *Molophilus ater* Meigen. Ph.D. Thesis, University of Durham.

Houston, W.W.K. (1970) Ecological studies on moorland ground beetles. Ph.D. Thesis, University of Durham.

Huffaker, C.B. (1958) The concept of balance in nature. Proc. 10th int. Congr. Ent., 2, 625-636.

Huffaker, C.B. (Ed.) (1971) Biological Control. Plenum, New York.

Humpesch, U.H. and Elliott, J.M. (1980) Effect of temperature on the hatching time of eggs of three *Rhithrogena* spp. (Ephemeroptera) from Austrian streams and an English stream and river. J. Anim. Ecol., 49, 643-661.

Johnson, G.A.L. and Dunham, K.C. (1963) The geology of Moorhouse. Monograph of the Nature Conservancy, H.M.S.O. 182pp.

Jordan, A.M. (1955) Studies on *Coleophora caespititiella* Zell. (Lep.) associated with *Juncus squarrosus* L. Ph.D. Thesis, University of Durham.

Jordan, A.M. (1958) The life history and behaviour of *Coleophora alticolella* Zell. (Lep.) Trans. Soc. Br. Ent., 13, 1-16.

Jordan, A.M. (1962) *Coleophora alticolella* Zell. (Lepidoptera) and its food plant *Juncus squarrosus* in the northern Pennines. J. Anim. Ecol., 31, 293-304.

Juillet, J.A. (1960) Some factors influencing the flight activity of Hymenopterous parasites. Can. J. Zool., 38, 1057-1061.

Juillet, J.A. (1964) Influence of weather on flight activity of parasitic Hymenoptera. Can. J. Zool., 42, 1133-1141.

Kershaw, K.A. and Tallis, J.H. (1958) Pattern in a high-level *Juncus squarrosus* community. J. Ecol., 46, 739-748.

Klomp, H. (1962) The influence of climate and weather on the mean density level, fluctuations and the regulation of animal populations Arch. néerl. Zool., 15, 68-109.

Klomp, H. (1966) The dynamics of a field population of the pine looper, *Bupalus pinarius* L. Adv. Ecol. Res., 3, 207-305.

Laughlin, R. (1963) Biology and ecology of the garden chafer *Phyllopertha horticola* (L.). VIII. -temperature and larval growth. Bull. ent. Res., 54, 745-759.

Lawton, J.H. (1978) Host-plant influences on insect diversity: the effects of space and time. Insect Diversity. (Ed. by L.A. Mound and N. Waloff), Symp. Roy. ent. Soc. Lond., 9, 105-125. Blackwell Scientific Publications, Oxford.

Lipscomb, W. (1886) Grouse and their food. A letter to the editor of 'The Field, The Country Gentleman's Newspaper' 16 October 1886.

Logan, J.A., Wollkind, D.J., Hoyt, S.C. and Tanigoshi, L.K. (1976) An analytical model for description of temperature-dependent rate phenomena in arthropods. Environ. Entomol., 6, 1133-1140.

MacArthur, R.H. and Wilson, E.O. (1967) The Theory of Island Biogeography. Princeton University Press, Princeton.

Manley, G. (1936) The climate of the northern Pennines: The coldest part of England. Q. Jl. R. met. Soc., 62, 103-115.

Manley, G. (1943) Further climatological averages for the northern Pennines, with a note on topographical effects. Q. Jl. R. met. Soc., 69, 251-261.

Manley, G. (1952) Climate and the British Scene. Collins, London.

May, R.M. (1976) Coexistence with insect pests. Nature, London, 264, 211-212.

May, R.M. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature, London, 269, 471-477.

Morley, C. (1908) Ichneumonologia britannica. 3: Pimplinae. J.H. Keys, Plymouth.

Morley, C. and Rait-Smith, W. (1933) The Hymenopterous parasites of British Lepidoptera. Trans. Roy. ent. Soc. Lond., 81, 133-183.

Morris, R.F. (1965) Contemporaneous mortality factors in population dynamics. Can. Ent., 97, 1173-1184.

Murdoch, W.W. and Oaten, A. (1975) Predation and population stability. Adv. Ecol. Res., 9, 1-131.

Newell, R.C. (1966) Effect of temperature on the metabolism of poikilotherms. Nature, London, 212, 426-428.

Newell, R.C. (1970) Biology of Intertidal Animals. Logos Press, London.

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. and Bent, D.H. (1975) Statistical Package for the Social Sciences, 2nd edition. McGraw-Hill, New York.

Nielsen, E.T. and Evans, D.G. (1960) Duration of the pupal stage of *Aedes taeniorhynchus* with a discussion of the velocity of development as a function of temperature. Oikos, 11, 200-222.

Nuoroteva, P. (1963) The influence of *Oporinia autumnata* (Bkh.) (Lep:Geometridae) on the timber-line in subarctic conditions. Ann. Ent. Fenn., 29, 270-277.

Oaten, A. (1977) Transit time and density-dependent predation on a patchily distributed prey. Am. Nat., 111, 1061-1075.

Parkin, J. (1977) Birds of the Moorhouse National Nature Reserve. Aspects of the Ecology of the Northern Pennines: Occasional Papers, No. 10.

Pearl, R. and Reed, L.J. (1920) On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc. Nat. Acad. Sci. U.S.A., 6, 275-288.

Pearsall, W.H. (1950) Mountains and Moorlands. Collins, London.

Pianka, E.R. (1970) On *r*- and *K*-selection. Am. Nat., 104, 592-597.

Pimentel, D. (1961) Species diversity and insect population outbreaks. Ann. ent. Soc. Am., 54, 76-86.

Price, P.W. (1970) Characteristics permitting coexistence among parasitoids of a sawfly in Quebec. Ecology, 51, 445-454.

Price, P.W. (1971) Niche breadth and dominance of parasitic insects sharing the same host species. Ecology, 52, 587-596.

Price, P.W. (1973) Parasitoid strategies and community organisation. Environ. Entomol., 2, 623-626.

Price, P.W. (1975) Evolutionary strategies of parasitoids. Evolutionary Strategies of Parasitic Insects and Mites. (Ed. by P.W. Price), pp 87-111. Plenum, New York.

Price, P.W. and Waldbauer, G.P. (1975) Ecological aspects of pest management. Introduction to Insect Pest Management. (Ed. by R.L. Metcalfe and W.H. Luckman), pp 36-73. Wiley, New York.

Quednau, F.W. (1967) Notes on mating, oviposition, adult longevity, and incubation period of eggs of the larch casebearer, *Coleophora laricella* (Lepidoptera: Coleophoridae), in the laboratory. Can. Ent., 99, 397-401.

Randall, M.G.M. (1976) Sheep census. Unpublished report for the Moorhouse National Nature Reserve.

Ranwell, D.S. and Ratcliffe, D.A. (1977) Coastlands. A Nature Conservation Review. (Ed. by D.A. Ratcliffe), pp 25-68. Cambridge University Press, Cambridge.

Rathcke, B.J. (1976) Competition and coexistence within a guild of herbivorous insects. Ecology, 57, 76-87.

Rawes, M. and Welch, D. (1964) Studies on sheep grazing in the northern Pennines. J. Br. Grassld. Soc., 19, 403-411.

Rawes, M. and Welch, D. (1969) Upland productivity of vegetation and sheep at Moorhouse National Nature Reserve, Westmorland, England. Oikos, supplement II, 72pp.

Reay, R.C. (1959) A Population Study on *Coleophora alticolella* Zell. (Lep.). Ph.D. Thesis, University of Durham.

Reay, R.C. (1964) The numbers of eggs and larvae of *Coleophora alticolella* Zell. (Lep.). J. Anim. Ecol., 33, 117-127.

Richards, P.W. and Clapham, A.R. (1941) Biological Flora of the British Isles: *Juncus* L. J. Ecol., 29, 362-368.

Root, R.B. (1967) The niche exploitation pattern of the blue-grey gnat-catcher. Ecol. Monogr., 37, 317-350.

Schmidt-Nielsen, K. (1979) Animal Physiology: Adaptation and Environment. Cambridge University Press, Cambridge.

Sich, A. (1923) Observations on the family Coleophorides - The case. Entomologist's Record, 35, 105-113.

Simmonds, F.J. and Greathead, D.J. (1977) Introductions and pest and weed problems. Origins of Pest, Parasite, Disease and Weed Problems. (Ed. by J.M. Cherrett and G.R. Sagar), pp 109-124. Blackwell Scientific Publications, Oxford.

Slobodkin, L.B. (1962) Growth and Regulation of Animal Populations. Holt, Rinehart and Winston, New York.

Smith, R.W. and Whittaker, J.B. (1980) Factors affecting *Gastrophysa viridula* populations (Coleoptera: Chrysomelidae) in different habitats. J. Anim. Ecol., 49, 537-548.

Snedecor, G.W. and Cochran, W.G. (1967) Statistical Methods. 6th edition. The Iowa State University Press, Iowa.

Southwood, T.R.E. (1966) Ecological methods with particular reference to the study of insect populations. Methuen, London.

Southwood, T.R.E. (1975) The dynamics of insect populations. Insects, Science and Society. (Ed. by D. Pimentel), pp 151-199. Academic Press, New York.

Southwood, T.R.E. (1977a) Habitat, the templet for ecological strategies? J. Anim. Ecol., 46, 337-365.

Southwood, T.R.E. (1977b) The relevance of population dynamic theory to pest status. Origins of Pest, Parasite, Disease and Weed Problems. (Ed. by J.M. Cherrett and G.R. Sagar), pp 35-54. Blackwell Scientific Publications, Oxford.

Southwood, T.R.E. and Comins, H.N. (1976) A synoptic population model. J. Anim. Ecol., 45, 949-965.

Southwood, T.R.E., May, R.M., Hassell, M.P. and Conway, G.R. (1974) Ecological strategies and population parameters. Am. Nat., 108, 791-804.

Stark, R.W. (1959) Population dynamics of the lodgepole needle miner *Recurvaria starki* Freeman, in Canadian Rocky Mountain Parks. Can. J. Zool., 37, 917-943.

Stuart, A.M. (1957) *Ephialtes brevicornis* (Grav.) as an external parasite of the Diamond-back Moth, *Plutella maculipennis* (Curt.). Bull. ent. Res., 48, 477-488.

Tauber, M.J. and Tauber, C.A. (1976) Insect seasonality: Diapause maintenance, termination and post diapause development. A. Rev. Ent., 21, 81-107.

Taylor, J.A. (1967) Growing season as affected by land aspect and soil texture. Weather and Agriculture. (Ed. by J.A. Taylor), pp 15-36. Pergamon Press, Oxford.

Taylor, J.A. (1976) Upland climates. The Climate of the British Isles. (Ed. by T.J. Chandler and S. Gregory), pp 265-287. Longman, London.

Thompson, W.R. (1945) A catalog of the parasites and predators of insect pests. Section 1, part 6. Imperial Parasite Service, Belville, Ontario.

Thorpe, W.H. (1930) Observations on the parasites of the Pine-shoot Moth, *Rhyacionia buoliana*, Schiff. Bull. ent. Res., 21, 387-412.

Thorpe, W.H. (1933) Notes on the natural control of *Coleophora laricella*, the larch case-bearer. Bull. ent. Res., 24, 271-291.

Varley, G.C. and Gradwell, G.R. (1960) Key factors in population studies. J. Anim. Ecol., 29, 399-401.

Varley, G.C. and Gradwell, G.R. (1963) Predatory insects as density dependent mortality factors. Proc. 16th Int. Congr. Zool., 1, 240.

Varley, G.C. and Gradwell, G.R. (1968) Population models for the winter moth. Insect abundance. (Ed. by T.R.E. Southwood), Symp. Roy. ent. Soc. Lond., 4, 132-142. Blackwell Scientific Publications, Oxford.

Varley, G.C., Gradwell, G.R. and Hassell, M.P. (1973) Insect Population Ecology. Blackwell Scientific Publications, Oxford.

Verhulst, P.F. (1838) Notice sur le loi que la population suit dans son accroissement. Corresp. Math. Phys., 10, 113-121.

Waloff, N. (1968) Studies on the insect fauna on Scotch broom *Sarothamnus scoparius* (L.) Wimmer. Adv. Ecol. Res., 5, 87-208.

Walton, K.C. (1979) Diet of meadow pipits *Anthus pratensis* on mountain grassland in Snowdonia. Ibis, 121, 325-329.

Way, M.J. (1977) Pest and disease status in mixed stands vs. monocultures; the relevance of ecosystem stability. Origins of Pest, Parasite, Disease and Weed Problems. (Ed. by J.M. Cherrett and G.R. Sagar), pp 127-138. Blackwell Scientific Publications, Oxford.

Welch, D. (1964) Studies in the autecology of *Juncus squarrosus* L. M.Sc. Thesis, University of Durham.

Welch, D. (1965) A change in the upper altitudinal limit of *Coleophora alticolella* Zell. (Lep.). J. Anim. Ecol., 34, 725-729.

Welch, D. (1966a) Biological flora of the British Isles: *Juncus squarrosus* L. J. Ecol., 54, 535-548.

Welch, D. (1966b) The reproductive capacity of *Juncus squarrosus*. New Phytol., 65, 77-86.

Welch, D. (1967a) Communities containing *Juncus squarrosus* in upper Teesdale, England. Vegetatio, 14, 229-240.

Welch, D. (1967b) Germination and establishment of *Juncus squarrosus*. New Phytol., 66, 89-98.

White, M.J.D. (1977) Animal Cytology and Evolution, 3rd edition. Cambridge University Press, Cambridge.

Whittaker, J.B. (1965) The distribution and population dynamics of *Neophilaenus lineatus* (L.) and *N. exclamationis* (Thun.) Homoptera, Cercopidae) on Pennine moorland. J. Anim. Ecol., 34, 277-297.

Whittaker, J.B. (1971) Population changes in *Neophilaenus lineatus* (L.) Homoptera:Cercopidae) in different parts of its range. J. Anim. Ecol., 40, 425-443.

Whittaker, R.H. (1975) The design and stability of some plant communities. Unifying Concepts in Ecology. (Ed. by W.H. van Dobben and R.H. Lowe-McConnell), pp 169-181. Junk, The Hague.

Wigglesworth, V.B. (1965) The Principles of Insect Physiology. Methuen, London.

Wilson, E.A. and Leslie, A.S. (1911) Food of the red grouse. The Grouse in Health and Disease. (Ed. by Lord Lovat), pp 67-92. Smith, Elder and Company, London.

Wilson, F. (1964) The biological control of weeds. A. Rev. Ent., 9, 225-244.

Wilson, F. (1968) Insect abundance: prospect. Insect abundance. (Ed. by T.R.E. Southwood), Symp. Roy. ent. Soc. Lond., 4, 143-158. Blackwell Scientific Publications, Oxford.

Wollkind, D.J., Logan, J.A. and Berryman, A.A. (1978) Asymptotic methods for modeling biological processes. Res. Popul. Ecol., 20, 79-90.

Wood, J.H. (1891) On oviposition, and the ovipositor, in certain Lepidoptera. Ent. mon. Mag., 27, 175-185.

Zwart, K.W.R. (1978) Intraspecific variation in some *Gelis* species, induced by the host (Hym., Ichneumonidae). First European Congress of Entomology (Abstracts) (Reading, 1978), p 23.

Zwölfer, H. (1970) The structure and effect of parasite complexes attacking phytophagous host insects. Dynamics of Populations. (Ed. by P.J. den Boer and G.R. Gradwell), Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970), pp 405-418.

Appendix 1 : A list of the statistical symbols and abbreviations used in the text

χ^2	Chi-squared
d.f.	Degrees of freedom
e	Base of natural logarithms
F	Variance ratio
n	Sample size
N.S.	Not significant
P	Probability
r	Correlation coefficient
R^2	Coefficient of determination
s	Standard deviation
s^2	Variance
S.E.	Standard error
t	Student's 't' statistic
$\bar{x}$	Mean of a sample

Appendix 2a : The mean density of ungrazed *Juncus squarrosus* inflorescences $^{1}/_{4m}{}^{-2}$ in 1977

15m site

Date	*n*	Mean	Standard error
26 July	16	39.2 ✡	3.6
24 August	16	32.5	4.1
31 August	16	40.1	3.9
7 September	16	39.1	3.7
15 September	16	39.3	3.9
20 September	12	40.8	3.9
28 September	8	38.6	4.8

245m site

10 June	16	22.1	1.6
1 July	16	23.8 ✡	3.3
8 July	16	14.4	1.1
28 July	16	5.9	0.8
11 August	16	5.3	0.7
19 August	16	5.3	0.6
26 August	16	5.0	0.7
2 September	16	4.4	0.6

335m site

17 June	16	37.4 ✡	3.0
24 June	16	36.5	2.5
30 June	16	29.9	2.3
8 July	16	27.8	1.8
19 August	16	25.6	1.9
26 August	16	20.4	2.0
3 September	16	19.0	1.7
16 September	16	19.9	1.9
21 September	8	22.0	2.9

395m site

17 June	16	35.5 ✡	3.9
18 August	16	25.5	2.8
26 August	16	20.4	3.1
2 September	16	21.6	2.6
8 September	16	22.1	2.7
16 September	16	19.8	2.4

✡ denotes the values used as the total density produced at each site

/continued

Appendix 2a (continued)

Date	*n*	Mean	Standard error
455m site			
17 June	12	56.6 *	3.5
23 June	16	51.0	2.9
30 June	16	47.1	3.3
9 July	16	44.8	3.4
14 July	16	46.4	3.8
22 July	16	45.3	3.1
10 August	16	39.2	2.1
25 August	16	39.3	3.1
1 September	16	38.5	2.2
16 September	16	34.9	2.4
21 September	8	32.9	2.4
29 September	8	31.1	2.5
520m site			
16 June	16	31.8	2.3
23 June	16	39.0	2.7
30 June	16	44.2 *	3.3
9 July	16	46.2	3.0
22 July	16	44.6	3.2
10 August	16	33.9	2.3
25 August	16	19.3	2.1
1 September	16	13.6	1.0
8 September	16	16.8	2.1
16 September	16	15.5	1.1
610m site			
16 June	16	15.3	1.5
23 June	16	30.1	3.0
30 June	16	37.1	3.6
9 July	16	41.7 *	3.7
14 July	16	41.9	4.1
18 August	16	37.0	3.9
16 September	16	26.9	3.5

* denotes the values used as the total density produced at each site

The data are from permanent quadrats at each altitude.

Appendix 2b : The mean density of ungrazed *Juncus squarrosus* inflorescences $^{1}/_{4m}{}^{-2}$ in 1978

Date	*n*	Mean	Standard error
15m site			
21 June	16	11.4*	2.4
28 June	16	9.7	1.0
29 July	16	10.8	1.0
2 August	16	10.4	1.1
10 August	16	9.4	0.7
16 August	16	8.5	0.5
23 August	16	9.0	0.9
30 August	16	9.9	1.0
15 September	16	9.3	0.9
24 September	16	9.6	1.2
245m site			
22 June	16	11.4	1.0
29 June	16	11.2 *	1.2
6 July	16	12.3	1.6
14 July	16	10.3	1.1
22 July	16	9.4	1.1
3 August	16	7.1	1.1
11 August	16	6.8	0.9
24 August	16	9.6	1.6
1 September	16	8.8	0.7
9 September	16	8.7	1.6
16 September	16	5.1	1.1
25 September	16	4.6	1.1
335m site			
22 June	16	17.0 *	2.2
29 June	16	18.4	2.4
6 July	16	14.8	1.5
14 July	16	14.8	1.5
22 July	16	15.5	2.3
3 August	16	13.1	1.6
11 August	16	15.1	1.2
17 August	16	17.6	1.3
24 August	16	18.4	1.9
1 September	16	16.0	1.5
9 September	16	16.5	1.9
16 September	16	17.1	2.4
25 September	16	17.3	2.0
7 November	30	18.8	1.1

* denotes the value used as the total density produced at each site.

/continued...

Appendix 2b (continued)

Date	n	Mean	Standard error
395m site			
22 June	16	13.1 *	1.4
29 June	16	11.3	1.2
6 July	16	10.8	0.9
14 July	16	9.7	1.0
22 July	16	9.3	1.1
3 August	16	10.9	0.9
11 August	16	10.4	1.0
17 August	16	11.8	1.1
24 August	16	9.6	1.2
1 September	16	8.5	1.2
9 September	16	9.3	1.0
16 September	16	8.8	1.3
25 September	16	8.3	1.0
7 November	30	10.1	0.7
455m site			
22 June	16	17.9	2.2
29 June	16	19.5 *	1.8
6 July	16	12.4	1.2
14 July	16	15.1	2.2
22 July	16	16.6	2.5
3 August	16	13.9	1.5
11 August	16	17.8	1.5
17 August	16	13.1	1.1
24 August	16	11.3	2.0
1 September	16	11.0	1.7
9 September	16	11.4	1.5
16 September	16	12.3	1.7
25 September	16	11.9	1.5
7 November	30	13.8	1.5
520m site			
22 June	16	11.8	1.7
29 June	16	18.9 *	2.3
6 July	16	20.0	1.8
14 July	16	15.1	2.2
3 August	16	25.2	3.0
11 August	16	21.5	1.6
17 August	16	17.9	1.4
16 September	16	22.9	1.7
7 November	30	12.4	0.9
610m site			
29 June	16	20.2 *	2.9
14 July	16	18.2	2.2
11 August	16	19.4	2.3
7 November	30	19.4	1.3

* denotes the value used as the total density produced at each site.

/continued.....

Appendix 2b (continued)

The mean *Juncus squarrosus* inflorescence density $^{1}/_{4m}{}^{-2}$

on 11 August 1978

Altitude (m)	*n*	Mean	Standard error
215	16	5.4	0.6
260	16	4.6	0.5
275	16	12.9	1.5
290	16	9.1	0.8
305	16	14.6	1.5
350	16	12.1	1.9
365	16	19.3	2.2
550	16	13.3	1.1
580	16	15.8	1.5

Appendix 2c : Mean *Juncus squarrosus* inflorescence density $^{1}/_{4m}{}^{-2}$ in 1979

i. Density of ungrazed inflorescences

Altitude (m)	*n*	Mean	Standard error
15	16	24.7	2.0
215	-	-	-
245	16	7.2	0.9
260	16	4.5	0.9
275	16	8.3	1.5
290	16	10.0	1.6
305	16	8.0	1.0
335	16	18.1	2.0
350	16	12.7	1.7
365	16	17.2	1.9
395	16	12.7	1.8
455	16	17.4	2.0
520	16	25.4	2.1
550	16	26.1	2.1
580	16	22.9	1.7
610	16	24.4	2.0

ii. Density of inflorescences produced (ungrazed + grazed)

Altitude (m)	*n*	Mean	Standard error
15	16	24.7	2.0
215	-	-	-
245	16	23.4	2.5
260	16	17.6	2.6
275	16	23.2	2.2
290	16	20.4	1.7
305	16	19.5	1.8
335	16	25.8	2.1
350	16	20.9	1.7
365	16	23.5	2.1
395	16	24.7	2.3
455	16	24.5	1.9
520	16	27.1	1.9
550	16	26.8	2.3
580	16	23.1	1.7
610	16	24.7	2.0

Data were collected on 23 August 1979 at 15m and on 24 August on the Little Dun Fell transect. Only isolated individuals were found at 215m.

Appendix 3a : The mean number of florets and seed capsules per inflorescence of *Juncus squarrosus* in 1977

Altitude (m)		Florets		Seed capsules	
	n	Mean	S.E.	Mean	S.E.
15	30	26.63	1.01	24.70	1.01
245	30	15.87	0.79	13.30	0.81
335	30	16.19	1.01	12.13	1.10
395	30	18.63	1.00	9.65	0.60
455	30	15.17	0.64	6.93	0.57
520	30	11.75	0.80	8.70	0.71
610	30	12.30	1.02	5.25	0.80

Samples taken in August: 395m, 455m, 520m, 610m - 10 August
245m, 335m - 11 August
15m - 24 August

Altitude (m)		Florets		Seed capsules	
	n	Mean	S.E.	Mean	S.E.
15	30	25.76	1.43	24.14	1.38
245	30	11.63	0.62	9.67	0.54
275	30	13.87	0.83	12.23	0.86
305	30	14.03	0.79	10.77	0.68
335	30	14.23	0.88	9.20	0.66
365	30	13.33	0.77	6.67	0.52
395	30	13.88	0.71	8.07	0.45
455	30	13.10	0.58	5.23	0.40

Samples taken in November: 15m - 5 November
Little Dun Fell - 6 November

Appendix 3b :

i. The mean number of florets and seed capsules per inflorescence of *Juncus squarrosus* in August 1978 (15m - 10 August, Little Dun Fell - 11 August)

Altitude (m)		Florets		Seed capsules	
	n	Mean	S.E.	Mean	S.E.
15	30	17.23	0.90	14.75	0.81
215	30	15.47	0.69	14.20	0.65
245	30	13.97	0.61	12.00	0.54
260	30	12.77	0.60	10.07	0.50
275	30	14.07	0.72	11.67	0.68
290	30	14.03	0.73	10.67	0.59
305	30	15.03	0.66	9.53	0.61
335	30	16.03	0.81	7.60	0.60
350	30	16.33	0.64	8.03	0.60
365	30	14.20	0.75	6.03	0.46
395	30	13.87	0.67	4.93	0.48
455	30	12.80	0.49	3.33	0.54
520	30	11.97	0.48	1.80	0.36
550	0	-	-	-	-
580	0	-	-	-	-
610	30	11.30	0.51	0.10	0.10
685	20	10.00	0.52	0.00	0.00
760	20	9.75	0.52	0.00	0.00
830	20	9.50	0.57	0.00	0.00

ii. The mean number of florets and seed capsules per inflorescence of *Juncus squarrosus* in November 1978 (15m - 8 November, Little Dun Fell - 7 November)

Altitude (m)		Florets		Seed capsules	
	n	Mean	S.E.	Mean	S.E.
15	50	24.54	0.77	22.72	0.72
215	40	14.10	0.57	12.83	0.55
245	30	12.27	0.55	10.80	0.52
260	50	14.24	0.48	12.50	0.44
275	30	14.87	0.82	12.60	0.75
290	50	19.10	0.59	15.40	0.51
305	30	16.07	0.76	11.23	0.54
335	30	16.73	0.85	9.93	0.76
350	50	15.62	0.50	8.78	0.50
365	30	15.00	0.75	6.97	0.75
395	30	14.23	0.47	5.90	0.61
455	30	12.00	0.57	3.10	0.51
520	30	12.63	0.62	3.27	0.62
550	30	12.33	0.59	0.47	0.16
580	30	10.80	0.34	0.27	0.10
610	30	11.23	0.53	0.03	0.03
685	0	-	-	-	-
760	0	-	-	-	-
830	0	-	-	-	-

Appendix 3c : The mean number of florets and seed capsules per inflorescence of *Juncus squarrosus* at two sites during 1978

Drigg 15m

Date		Florets		Seed capsules	
	n	Mean	S.E.	Mean	S.E.
30 May	30	19.37	0.67	0.00	0.00
6 June	30	18.30	0.75	0.00	0.00
14 June	20	19.25	0.90	0.00	0.00
21 June	20	22.10	1.39	3.30	0.97
28 June	20	21.45	1.60	12.05	1.34
5 July	20	23.80	1.26	20.50	0.90
13 July	20	21.10	0.92	18.10	0.86
29 July	20	21.70	0.95	18.80	1.07
2 August	20	21.70	1.23	17.15	1.24
10 August	30	17.23	0.90	14.75	0.81
16 August	20	21.35	1.17	18.65	0.99
23 August	20	21.15	1.05	17.85	0.95
30 August	20	21.25	1.02	17.95	1.00
8 September	20	21.50	0.91	18.90	0.90
15 September	20	21.25	1.03	18.75	1.00
24 September	20	22.80	1.18	19.20	1.20
11 October	20	22.30	1.02	19.90	1.06
8 November	50	24.54	0.77	22.72	0.72

Little Dun Fell 455m

Date		Florets		Seed capsules	
	n	Mean	S.E.	Mean	S.E.
9 June	30	12.33	0.57	0.00	0.00
15 June	30	12.48	0.75	0.00	0.00
18 June	30	10.73	0.59	0.00	0.00
22 June	30	11.40	0.76	0.00	0.00
29 June	20	11.95	0.54	0.60	0.22
6 July	20	12.65	0.76	1.15	0.42
14 July	20	12.75	0.56	1.10	0.37
22 July	20	15.20	0.71	2.35	0.54
27 July	20	13.25	0.75	2.25	0.54
3 August	20	11.75	0.84	2.85	0.63
11 August	30	12.80	0.49	3.33	0.54
17 August	20	13.25	0.85	2.65	0.38
24 August	20	13.75	0.73	2.30	0.32
1 September	20	11.90	0.74	2.45	0.56
16 September	20	12.65	0.70	2.90	0.59
25 September	20	12.70	0.56	2.45	0.53
12 October	20	12.80	0.83	2.10	0.39
7 November	30	12.00	0.57	3.10	0.51

Appendix 3d : The mean number of florets and seed capsules per inflorescence of *Juncus squarrosus* in August 1979 (15m - 23 August; Little Dun Fell - 24 August)

Altitude (m)		Florets		Seed capsules	
	n	Mean	S.E.	Mean	S.E.
15	20	25.85	1.23	21.65	1.12
215	20	15.85	0.95	14.75	0.93
245	20	15.20	0.80	14.45	0.80
275	20	16.70	1.15	14.55	1.14
305	20	17.35	0.80	14.60	0.68
335	20	15.96	0.93	13.70	0.71
365	20	15.95	0.85	10.90	0.89
395	20	14.00	0.75	11.05	0.68
455	20	15.85	0.63	6.95	0.66
520	20	16.95	1.01	4.40	0.85
550	20	15.45	0.87	1.05	0.30
580	20	16.50	0.96	0.80	0.30
610	20	15.05	0.71	0.35	0.22

Appendix 4 : The mean number of florets per inflorescence, and the mean number of eggs and larvae per inflorescence, at different altitudes during the oviposition period in 1978

Date	Florets per inflorescence			Eggs and larvae per inflorescence		Total larvae present
	n	$\bar{x}$	S.E.	$\bar{x}$	S.E.	
15m sample site						
30 May	30	19.37	0.67	0.30	0.16	0
6 June	30	18.30	0.75	2.83	0.56	0
14 June	20	19.25	0.90	4.80	0.89	0
21 June	20	22.10	1.39	5.80	1.02	2
28 June	20	21.45	1.60	6.15	0.98	13
5 July	20	23.80	1.26	4.30	0.90	64
245m sample site						
7 June	30	15.80	0.64	1.33	0.46	0
15 June	30	15.43	0.66	4.43	0.54	0
18 June	30	15.63	1.02	6.03	0.76	0
22 June	30	12.07	0.70	4.77	0.51	0
29 June	30	11.93	0.77	8.77	0.88	12
335m sample site						
7 June	30	16.50	0.68	1.80	0.35	0
9 June	30	15.67	0.87	1.73	0.53	0
15 June	30	14.10	0.79	3.90	0.64	0
18 June	30	16.80	0.69	7.60	0.76	0
22 June	30	14.10	0.76	9.57	0.91	0
29 June	30	15.83	0.78	13.70	0.86	1
6 July	30	14.20	0.59	15.90	1.20	10
395m sample site						
9 June	30	14.17	0.62	1.20	0.32	0
15 June	30	14.10	0.62	3.20	0.36	0
18 June	30	14.93	0.66	5.00	0.50	0
22 June	30	14.20	0.81	7.53	0.62	0
29 June	30	12.37	0.58	8.77	0.97	0
6 July	20	14.35	0.65	12.90	1.40	0

/continued

Appendix 4 (continued)

Date	Florets per inflorescence			Eggs and larvae per inflorescence		Total larvae present
	n	$\bar{x}$	S.E.	$\bar{x}$	S.E.	
455m sample site						
9 June	30	12.33	0.57	1.07	0.27	0
15 June	30	12.48	0.75	1.70	0.30	0
18 June	30	10.73	0.59	1.93	0.35	0
22 June	30	11.40	0.76	4.17	0.74	0
29 June	20	11.95	0.54	6.45	0.76	0
6 July	20	12.65	0.76	10.05	0.98	0
14 July	20	12.75	0.56	7.60	1.04	6
22 July	20	15.20	0.71	3.10	0.59	28
520m sample site						
9 June	30	10.73	0.67	0.00	0.00	0
15 June	30	11.23	0.44	0.00	0.00	0
22 June	30	12.07	0.67	0.17	0.08	0
29 June	30	12.37	0.58	0.50	0.16	0
6 July	30	14.03	0.53	1.43	0.23	0
14 July	30	12.80	0.62	0.90	0.24	0
22 July	20	13.45	0.69	0.55	0.20	0
610m sample site						
29 June	30	10.60	0.64	0.00	0.00	0
14 July	30	12.57	0.50	0.00	0.00	0

29 June 1978

Sample site	Florets per inflorescence			Eggs and larvae per inflorescence		Total larvae present
	n	$\bar{x}$	S.E.	$\bar{x}$	S.E.	
275m	30	15.87	0.71	16.47	1.45	6
305m	20	15.55	0.97	14.45	1.75	3

Appendix 5a : The mean number of *Coleophora alticolella* larvae per inflorescence, floret and seed capsule of *Juncus squarrosus* in 1977. Samples were taken on 9 August at 15m; 10 August at 395m, 455m, 520m and 610m; and 11 August at 245m and 335m. These values include dead and parasitized larvae

Altitude (m)	Larvae per inflorescence $\bar{x}$	S.E.	(n)	Larvae per floret $\bar{x}$	S.E.	(n)	Larvae per seed capsule $\bar{x}$	S.E.	(n)
15	2.70	0.48	(20)	0.138	0.018	(390)	0.149	0.019	(263)
245	8.17	0.67	(30)	0.515	0.025	(476)	0.614	0.027	(399)
335	4.31	0.63	(16)	0.266	0.028	(259)	0.356	0.035	(194)
395	2.90	0.35	(20)	0.155	0.019	(374)	0.301	0.035	(193)
455	1.27	0.24	(30)	0.084	0.013	(455)	0.183	0.027	(208)
520	0.50	0.12	(20)	0.043	0.013	(235)	0.058	0.018	(174)
610	0.10	0.10	(20)	0.008	0.006	(246)	0.019	0.013	(105)

Appendix 5b : The mean number of *Coleophora alticolella* larvae per inflorescence, floret and seed capsule of *Juncus squarrosus* in 1978. All samples taken on 11 August, except for those from 15m, which were taken on 10 August. These values include dead and parasitized larvae

Altitude (m)	Larvae per inflorescence $\bar{x}$	(n)	S.E.	Larvae per floret $\bar{x}$	(n)	S.E.	Larvae per seed capsule $\bar{x}$	(n)	S.E.
15	4.00	(30)	0.59	0.232	(517)	0.019	0.278	(432)	0.023
215	2.87	(30)	0.36	0.185	(464)	0.018	0.202	(426)	0.020
245	7.10	(30)	0.49	0.508	(419)	0.028	0.592	(360)	0.030
260	6.53	(30)	0.52	0.512	(383)	0.028	0.590	(332)	0.031
275	9.67	(30)	0.64	0.687	(422)	0.030	0.829	(350)	0.032
290	8.00	(30)	0.66	0.570	(421)	0.029	0.750	(320)	0.033
305	8.00	(30)	0.60	0.532	(451)	0.029	0.839	(286)	0.035
335	6.13	(30)	0.53	0.383	(481)	0.027	0.807	(228)	0.043
350	6.57	(30)	0.65	0.402	(490)	0.029	0.817	(241)	0.043
365	4.13	(30)	0.34	0.291	(426)	0.026	0.685	(181)	0.047
395	3.57	(30)	0.40	0.257	(416)	0.025	0.723	(148)	0.055
455	1.77	(30)	0.35	0.138	(384)	0.019	0.530	(100)	0.059
520	0.20	(30)	0.09	0.017	(359)	0.007	0.111	(54)	0.043
610	0.00	(30)	0.00	0.000	(339)	0.000	0.000	(3)	0.000

Appendix 5c : The mean number of *Coleophora alticolella* larvae per inflorescence, floret and seed capsule of *Juncus squarros* in 1979. All of the samples were taken on 24 August, except for those at 15m, which were taken on 23 August. These values include dead and parasitized larvae

Altitude (m)	Larvae per inflorescence $\bar{x}$	(n)	S.E.	Larvae per floret $\bar{x}$	(n)	S.E.	Larvae per seed capsule $\bar{x}$	(n)	S.E.
15	0.50	(20)	0.18	0.019	(517)	0.006	0.023	(433)	0.007
215	0.95	(20)	0.12	0.060	(317)	0.013	0.064	(295)	0.014
245	1.30	(20)	0.25	0.086	(304)	0.016	0.092	(289)	0.017
275	5.25	(20)	0.58	0.314	(334)	0.026	0.361	(291)	0.029
305	3.05	(20)	0.47	0.176	(347)	0.020	0.209	(292)	0.024
335	3.05	(20)	0.33	0.191	(319)	0.027	0.223	(274)	0.026
365	2.00	(20)	0.36	0.125	(319)	0.019	0.184	(218)	0.026
395	1.05	(20)	0.26	0.075	(280)	0.016	0.095	(221)	0.020
455	0.90	(20)	0.27	0.057	(317)	0.014	0.129	(139)	0.030
520	0.40	(20)	0.18	0.024	(339)	0.008	0.091	(88)	0.031
550	0.00	(20)	0.00	0.000	(309)	0.000	0.000	(21)	0.000
580	0.00	(20)	0.00	0.000	(330)	0.000	0.000	(16)	0.000
610	0.00	(20)	0.00	0.000	(301)	0.000	0.000	(7)	0.000

Appendix 6a : The number of *Coleophora alticolella* eggs and live larvae of each instar, per inflorescence of *Juncus squarrosus*, from samples taken at the 15m site during 1978. (The blanks are zero values).

Date	STADIUM Eggs	I	II	III	IV	Total per inflorescence	Total in sample	Number of inflorescences
30 May	0.30					0.30	9	30
6 June	2.83					2.83	85	30
14 June	4.80					4.80	96	20
21 June	5.80					5.80	116	20
28 June	5.50	0.65				6.15	123	20
5 July	1.10	2.25	0.95			4.30	86	20
13 July		1.65	1.55	0.40		3.60	72	20
29 July		0.15	1.70	1.80	0.30	3.95	79	20
2 Aug		0.15	1.30	1.55	0.25	3.25	65	20
10 Aug			0.60	1.80	0.73	3.13	94	30
16 Aug			0.25	1.85	1.05	3.15	63	20
23 Aug			0.10	1.15	1.05	2.30	46	20
30 Aug				1.05	0.95	2.00	40	20
8 Sept				0.65	1.20	1.85	37	20
15 Sept				0.10	1.15	1.25	25	20
24 Sept				0.05	0.40	0.45	9	20
11 Oct					0.25	0.25	5	20
8 Nov					0.06	0.06	3	50

Appendix 6b : The number of *Coleophora alticolella* eggs and live larvae of each instar, per inflorescence of *Juncus squarrosus*, from samples taken at the 455m site during 1978. (The blanks are zero values)

Date	STADIUM					Total per inflorescence	Total in each sample	Number of inflorescences
	Eggs	I	II	III	IV			
9 June	1.07					1.07	32	30
15 June	1.70					1.70	51	30
18 June	1.93					0.93	58	30
22 June	4.17					4.17	125	30
29 June	6.45					6.45	129	20
6 July	10.05					10.05	201	20
14 July	7.60	0.30				7.90	158	20
22 July	1.70	1.30	0.10			3.10	62	20
27 July	0.60	1.55	0.15			2.30	46	20
3 Aug	0.05	1.20	1.10			2.35	47	20
11 Aug		0.53	1.10	0.13		1.76	53	30
17 Aug		0.20	1.15	0.25		1.60	32	20
24 Aug			0.35	0.75	0.05	1.15	23	20
1 Sept			0.05	0.85	0.10	1.00	20	20
16 Sept			0.05	0.80	0.30	1.15	23	20
25 Sept				0.20	0.65	0.85	17	20
12 Oct						0.00	0	20
7 Nov						0.00	0	30

Appendix 7a : *Coleophora alticolella* larval case production and migration to the leaf-litter in 1977. Numbers per inflorescence of *Juncus squarrosus*

Date	No. marked on each sample date	Total produced (cumulative)	Number present	Number migrated
15m				
23 July	0.000	0.000	0.000	0.000
26 July	0.170	0.170	0.170	0.000
3 Aug	0.234	0.404	0.332	0.072
9 Aug	0.175	0.579	0.429	0.150
17 Aug	0.306	0.885	0.660	0.225
24 Aug	0.219	1.104	0.813	0.291
31 Aug	0.174	1.278	0.860	0.418
7 Sept	0.101	1.379	0.868	0.511
15 Sept	0.058	1.437	0.859	0.578
20 Sept	0.014	1.451	0.847	0.604
28 Sept	0.017	1.468	0.839	0.629
9 Oct	0.010	1.478	0.837	0.641
5 Nov	0.000	1.478	0.837	0.641
Total number of cases marked, 918. Total number of cases migrated, 398.				
18.77 seed capsules per inflorescence in November				
245m				
4 Aug	0.000	0.000	0.000	0.000
11 Aug	0.043	0.043	0.043	0.000
19 Aug	1.086	1.129	1.129	0.000
26 Aug	1.187	2.316	1.960	0.356
2 Sept	0.822	3.138	2.412	0.726
9 Sept	0.662	3.800	2.809	0.991
17 Sept	0.275	4.075	2.464	1.611
21 Sept	0.058	4.133	2.058	2.075
30 Sept	0.044	4.177	1.899	2.278
10 Oct	0.029	4.206	1.638	2.568
6 Nov	0.000	4.206	1.638	2.568
Total number of cases marked, 327. Total number of larvae migrated, 199.				
9.24 seed capsules per inflorescence in November				

Continued.....

Appendix 7a : continued

Date	No. marked on each sample date	Total produced (cumulative)	Number present	Number migrated
335m				
11 Aug	0.000	0.000	0.000	0.000
19 Aug	0.129	0.129	0.129	0.000
26 Aug	0.373	0.502	0.480	0.022
3 Sept	0.523	1.025	0.984	0.041
9 Sept	0.502	1.527	1.385	0.142
17 Sept	0.339	1.866	1.381	0.485
21 Sept	0.028	1.894	1.176	0.718
13 Oct	0.014	1.908	0.131	1.777
6 Nov	0.000	1.908	0.085	1.823
Total number of cases marked, 555. Total number of larvae migrated, 530. 8.17 seed capsules per inflorescence in November.				
395m				
11 Aug	0.000	0.000	0.000	0.000
18 Aug	0.034	0.034	0.034	0.000
26 Aug	0.241	0.275	0.264	0.011
2 Sept	0.323	0.598	0.566	0.032
8 Sept	0.412	1.010	0.897	0.113
16 Sept	0.261	1.271	1.080	0.191
29 Sept	0.108	1.379	0.868	0.511
13 Oct	0.025	1.404	0.593	0.811
6 Nov	0.000	1.404	0.123	1.281
Total number of cases marked, 429. Total number of larvae migrated, 391. 6.47 seed capsules per inflorescence in November.				
455m				
18 Aug	0.000	0.000	0.000	0.000
25 Aug	0.055	0.055	0.055	0.000
1 Sept	0.096	0.151	0.146	0.005
8 Sept	0.121	0.272	0.234	0.038
16 Sept	0.125	0.397	0.341	0.056
21 Sept	0.057	0.454	0.362	0.092
29 Sept	0.052	0.506	0.357	0.149
13 Oct	0.008	0.514	0.281	0.233
6 Nov	0.000	0.514	0.091	0.423
Total number of cases marked, 220. Total number of larvae migrated, 181. 5.47 seed capsules per inflorescence in November.				

Appendix 7b : *Coleophora alticolella* larval case production and migration to the leaf-litter in 1978. Numbers per inflorescence on *Juncus squarrosus*

Date	No. marked on each sample date	Total produced (cumulative)	Number present	Number migrated
15m				
21 July	0.000	0.000	0.000	0.000
29 July	0.041	0.041	0.041	0.000
2 Aug	0.042	0.083	0.078	0.005
10 Aug	0.060	0.143	0.120	0.023
16 Aug	0.052	0.195	0.162	0.033
23 Aug	0.111	0.306	0.257	0.049
30 Aug	0.132	0.438	0.358	0.080
8 Sept	0.193	0.631	0.537	0.094
15 Sept	0.128	0.759	0.638	0.121
24 Sept	0.078	0.837	0.618	0.219
11 Oct	0.000	0.837	0.614	0.223
8 Nov	0.000	0.837	0.614	0.223

Total number of cases marked, 127. Total number migrated, 34.

10.80 seed capsules per inflorescence in November.

245m				
17 Aug	0.000	0.000	0.000	0.000
24 Aug	0.124	0.124	0.124	0.000
1 Sept	0.121	0.245	0.241	0.004
9 Sept	0.482	0.727	0.712	0.015
16 Sept	0.463	1.190	1.122	0.068
25 Sept	0.338	1.528	1.176	0.352
12 Oct	0.039	1.567	0.745	0.822
7 Nov	0.000	1.567	0.745	0.822

Total number of cases marked, 169. Total number migrated, 89.

5.37 seed capsules per inflorescence in November.

Continued.....

Appendix 7b : continued

Date	No. marked on each sample date	Total produced (cumulative)	Number present	Number migrated
335m				
17 Aug	0.000	0.000	0.000	0.000
24 Aug	0.192	0.192	0.192	0.000
1 Sept	0.629	0.821	0.801	0.020
9 Sept	1.462	2.283	2.159	0.124
16 Sept	0.533	2.816	1.832	0.984
25 Sept	0.239	3.055	0.688	2.367
12 Oct	0.029	3.084	0.279	2.805
7 Nov	0.000	3.084	0.072	3.012
Total number of cases marked, 508. Total number migrated, 496. 6.64 seed capsules per inflorescence in November.				
395m				
17 Aug	0.000	0.000	0.000	0.000
24 Aug	0.065	0.065	0.065	0.000
1 Sept	0.110	0.175	0.169	0.006
9 Sept	0.524	0.699	0.651	0.048
16 Sept	0.521	1.220	1.093	0.127
25 Sept	0.496	1.716	1.000	0.716
12 Oct	0.040	1.756	0.238	1.518
7 Nov	0.000	1.756	0.089	1.667
Total number of cases marked, 246. Total number migrated, 213. 4.88 seed capsules per inflorescence in November.				
455m				
24 Aug	0.000	0.000	0.000	0.000
1 Sept	0.034	0.034	0.034	0.000
9 Sept	0.153	0.187	0.186	0.001
16 Sept	0.096	0.283	0.183	0.100
25 Sept	0.067	0.350	0.168	0.182
12 Oct	0.022	0.372	0.065	0.307
7 Nov	0.000	0.372	0.032	0.340
Total number of cases marked, 69. Total number migrated, 63. 1.74 seed capsules per inflorescence in November.				

Appendix 8 : Examples of logistic curves fitted to the data for larval case production (○) and larval migration (○). In the formulae, y is the number of larval cases produced and z the number of larvae migrating, per inflorescence, in relation to time (x) measured in days with 1 = 1 June

a. 15m in 1977

larval case production

$$y = \frac{1.4734}{1 + \exp\ (8.1901 - 0.1102x)}$$

$F_{2,10} = 1251.3$ $\quad P < 0.001$ $\quad R^2 = 0.995$

larval migration

$$z = \frac{0.6481}{1 + \exp(8.2582 - 0.0965x)}$$

$F_{2,10} = 1055.5$ $\quad P < 0.001$ $\quad R^2 = 0.994$

b. 455m in 1978

larval case production

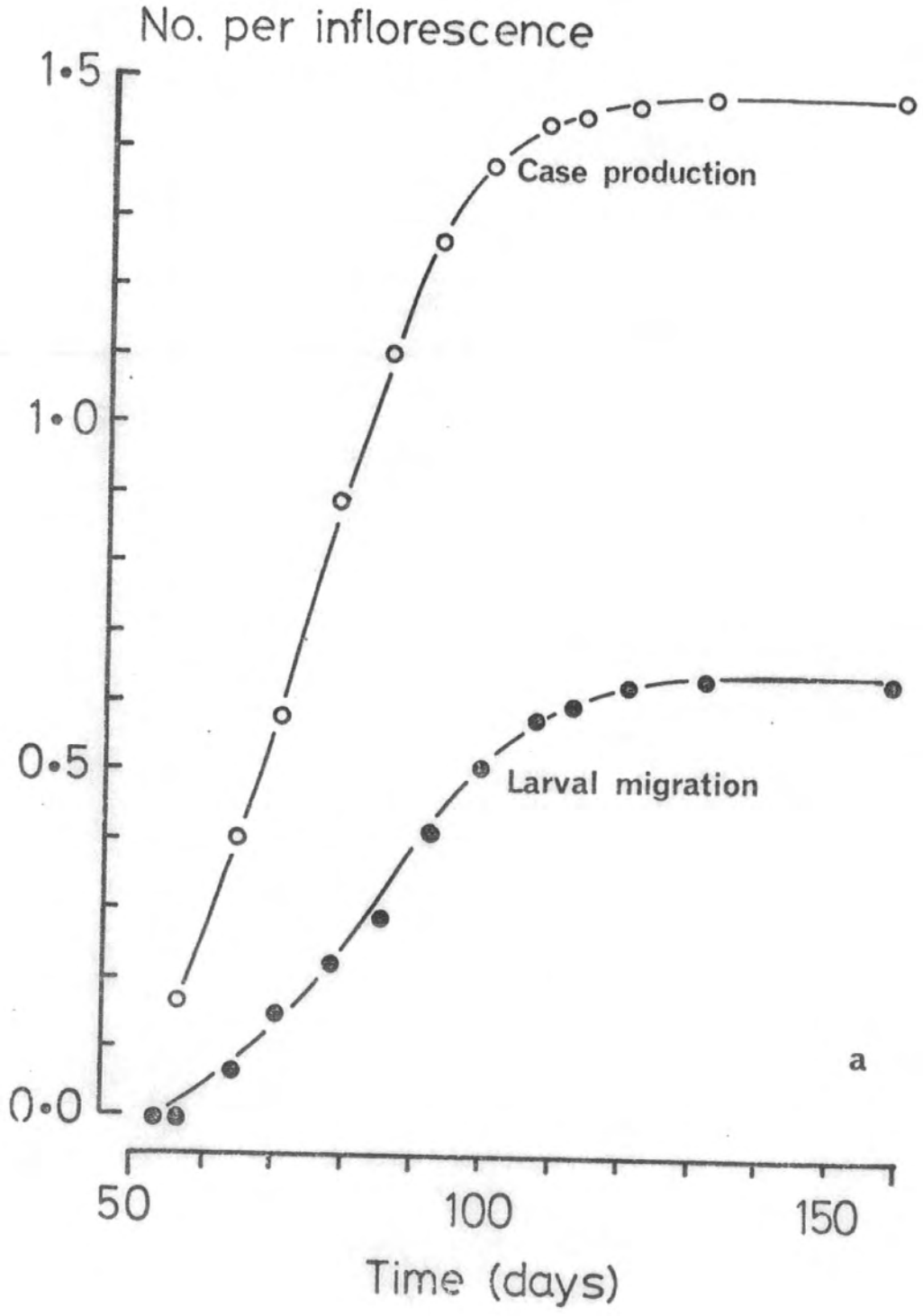
$$y = \frac{0.3672}{1 + \exp(22.4258 - 0.2207x)}$$

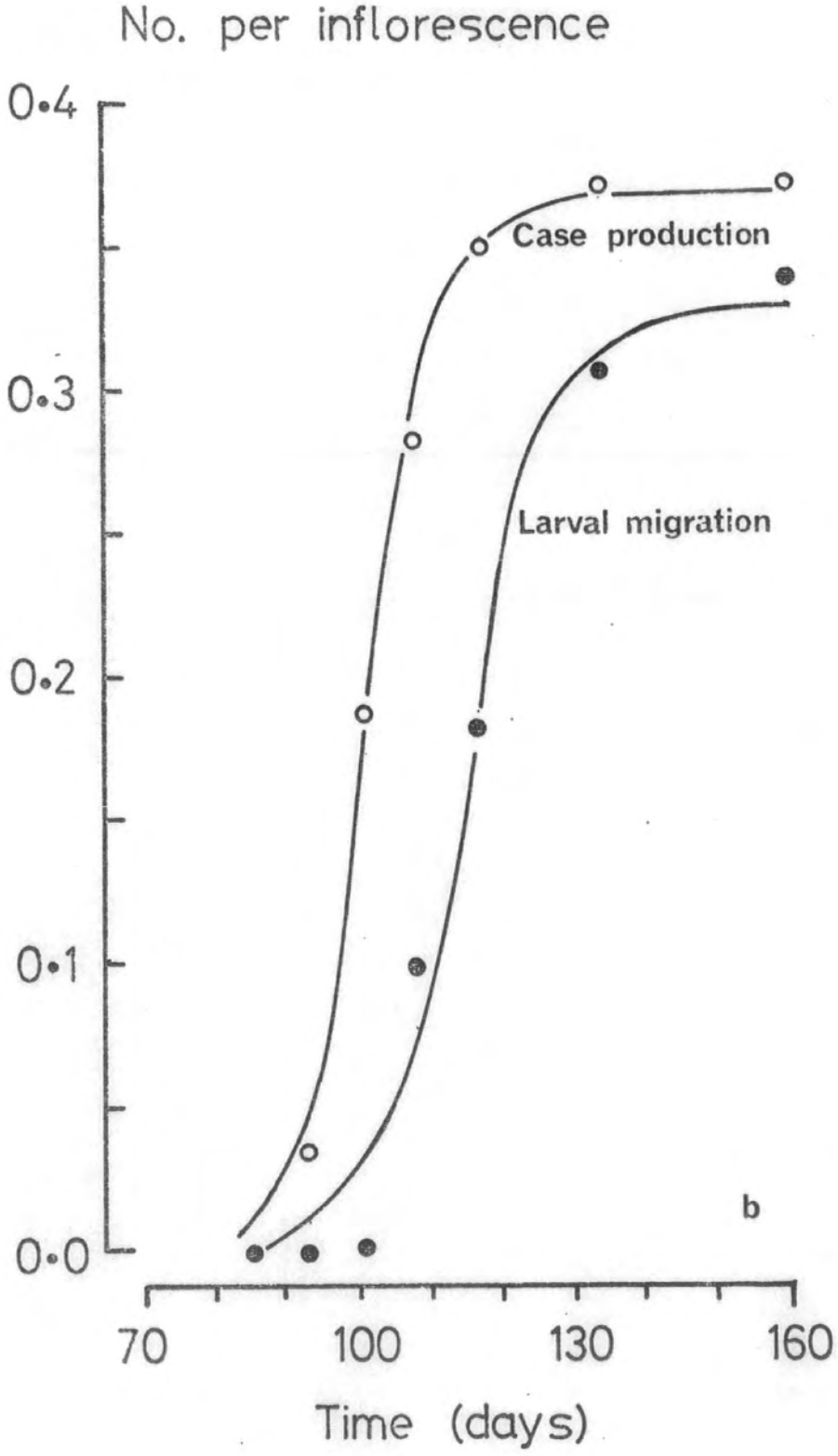
$F_{2,4} = 424.9$ $\quad P < 0.001$ $\quad R^2 = 0.993$

larval migration

$$z = \frac{0.3319}{1 + \exp(18.5413 - 0.1606x)}$$

$F_{2,4} = 159.7$ $\quad P < 0.001$ $\quad R^2 = 0.981$


No. per inflorescence
1·5
1·0
0·5
0·0
Case production
Larval migration
a
50
100
150
Time (days)



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