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HOME RANGE AND TERRITORY OF WOODLAND WRENS (*TROGLODYTES TROGLODYTES TROGLODYTES* Linn.) IN SPRING AND SUMMER.

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A dissertation submitted as part of the requirements
for the M.Sc. Advanced Ecology course at Durham
University.

September 1976

Plate 1.

Male Wren (m7) at song post.

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INTRODUCTION

Introduction

In this dissertation I shall describe a study of some aspects of territoriality in the Wren (Troglodytes troglodytes troglodytes Linn.) and the efficiency of song as a means of ensuring exclusive use of a specific site. To aid understanding of the functions of territoriality in this species, feeding and song behaviour have been investigated, as also have possible mechanisms to reduce competition within the species and between the sexes. Information on breeding biology was also collected to attempt to relate this to territory size.

The British population of the Wren has been steadily increasing since the severe winter of 1962-63 when abnormally cold conditions drastically reduced numbers. Indeed the Wren is now considered as one of the more common resident birds (Batten 1973; Batten and Marchant 1975;1976). In the last 5-6 years maintenance of high populations of smaller birds, such as the Goldcrest (Regulus regulus Linn.) and the Wren has been associated with a series of mild winters. It would appear from this that the winter climate exerts a strong, though probably indirect, influence upon the number of Wrens. The milder conditions have not led to such marked increases in numbers of larger birds such as the Blackbird (Turdus merula Linn.). It is thought that the territorial behaviour is the limiting factor to the maximum breeding density (Batten and Marchant 1976). However, the male Wren is claimed to be strongly territorial and to defend a specific site by song (Armstrong 1955). Although Wrens have been known to sing at all times of the year song output increases during the breeding season (Colquhoun 1940; Armstrong 1944; Cox 1944; Clark 1949).

The function of song in birds has been reviewed by Thorpe (1961); Armstrong (1963) and Hinde (1969). In the Wren it is claimed to repel other males and attract females (Armstrong 1955). Only the males sings, with a volume remarkable for a bird of such a small size (Witherby et al 1945). The song produced could delimit a selected site by the 'song distance' between individuals (Altrum 1868); the song distance being the site defended by song around a song post into which a neighbouring individual will not trespass.

The concept of exclusion from a specific topographical area was noted as early as 300 B.C. by Aristotle.

> ' The fact is that a pair of eagles demand an extensive space for its maintenance and consequently cannot allow other birds to quarter themselves in close neighbourhood'. (D'Arcy Wentworth Thompson's translation of 'Historia Animalium ' 1910)

More recently the subject has been reviewed many times, e.g. by Dewar (1920); Jourdain (1921); Alexander (1921); Lack and Lack (1933); Lack (1934); Nicholson (1934); Nice (1941); Armstrong (1953b)and Hinde (1956). Several authors who have written of territory have presented their own definitions of the term (Mayr 1935; Tinbergen 1939; Crawford 1939) but Noble's (1939) description of ' any defended area' is the simplest and most applicable (Nice 1941).

Many functions have been attributed to the 'defended area'. These have been reviewed most recently by Hinde (1956). To assimilate the mass of information concerning territoriality, classificatory systems have been developed (Nice 1941) whereby bird species can be grouped according to their territorial activities. The Wren was said to defend an area for 'mating, nesting and the feeding of the young' (Nice 1941). In Holland an area was defended throughout the year by song and posturing except during the moulting season (August) and in severe winter conditions (Kluijver _et al_ 1940).

Selection and maintenance of an area by male Wrens will set upper and lower limits to the breeding population density if the territories have both minimum and maximum size. Less than the minimum area would provide insufficient resources for the occupants to breed successfully. Too great an area would require too great an allocation of time to its defence and would reduce the time available for other activities. Huxley (1934) discussed the elasticity of territorial boundaries, their ability to expand or contract and the fact that the 'rubber disc' apparently cannot be compressed indefinitely. The division of habitat into 'defended areas' provides a mechanism for dispersion, and results in a limit to the breeding population density. The concept was first presented by Moffat (1903).

> '....the battles of the male birds each claiming a territory resulting in such a parcelling out of the land as must limit the numbers of breeding pairs to a constant figure and prevent indefinite increase in the case of a species-at the same time condemning the less powerful individuals to unproductiveness rather than death'.

However, many animals do not restrict themselves solely to use a defended site but establish a larger home range. This has been documented more often for mammals than birds (Burt 1943), perhaps because the mechanisms of defence are easier to identify in the latter. Home range can be considered as the total area that an animal utilises. Wynne-Edwards (1962) postulated that there are four different types of home range; solitary and exclusive; solitary and overlapping; gregarious and exclusive, and gregarious and overlapping. If defence creates exclusion the exclusive home ranges can be considered as territories.

Defence does not necessarily require overt aggression. Song is a non-contact mechanism of defence which alleviates any chance of harm to the individuals and yet can lead to exclusive use of areas by mutual avoidance. Thus song can be as effective a mechanism of defence and dispersion as methods involving physical contact.

THE STUDY AREA

The Study Area

The sites selected for study were the mixed deciduous Hollinside Wood (NZ 276405) and the Durham University Zoological Field Station (NZ274405). Both of these sites were approximately 2 km. south of the Durham city centre.

The limits to the site were established by the movements of the Wren population under investigation and not by any physical or vegetational features. The area is shown in Fig.1.

Topographically (Fig.2) the area is divided by a ridge along which runs an unmetalled road. To the east the ground slopes down steeply through Hollinside Wood, and to the west less steeply through the Field Station. The floor of the wood is undulating and the depressions form a series of "valley-like" features opening to the east.

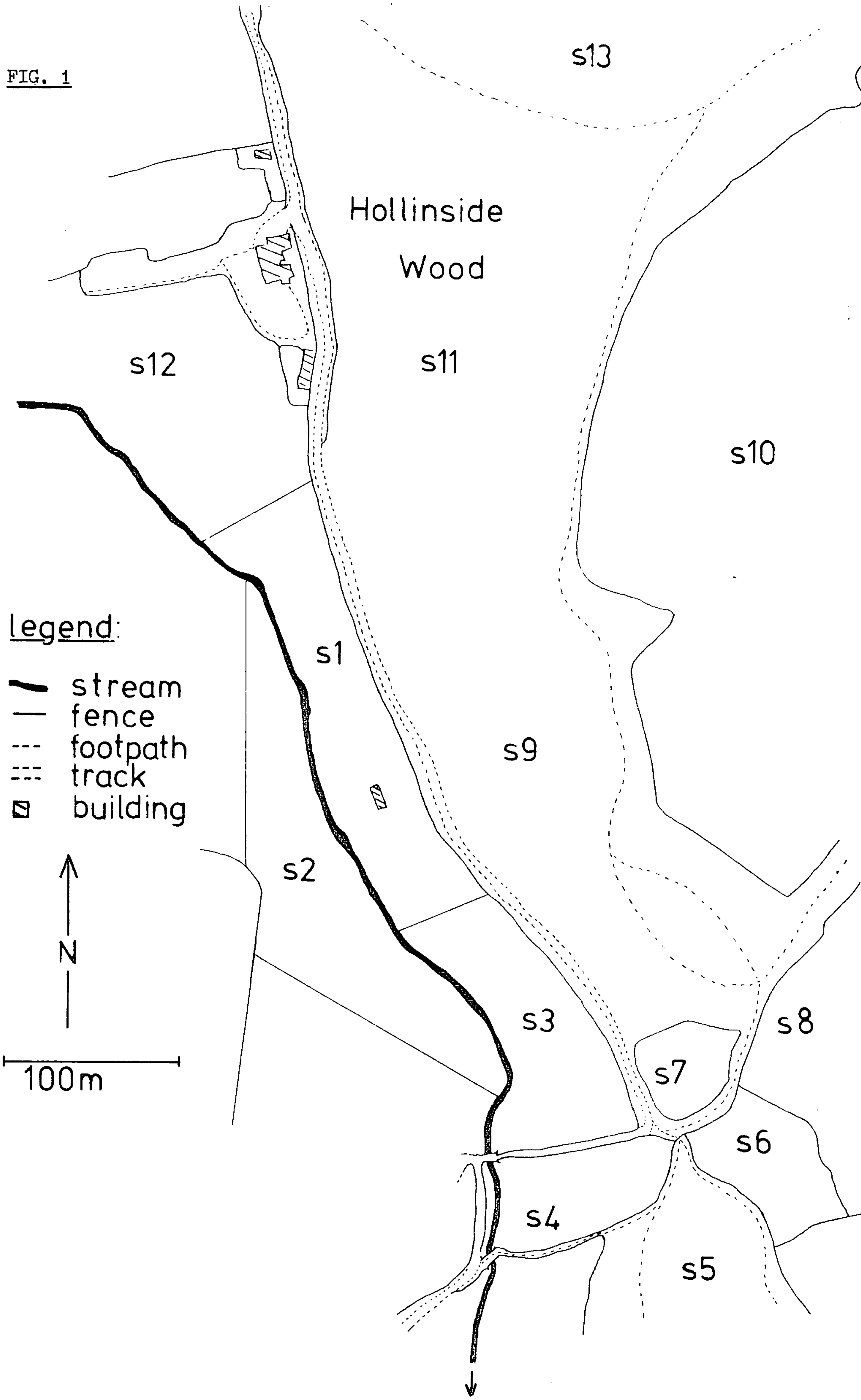
Flowing from north to south through the Field Station a small stream carries water run-off from adjacent woods and fields. The stream underwent dramatic changes in depth related to the rainfall.

Hollinside Wood contained a wide variety of trees although sycamore (Acer pseudoplatanus Linn.) and beech (Fagus sylvatica Linn.) were dominant throughout. Ground cover was provided mainly by bramble (Rubus fruticosus Linn.), distribution in Fig.4; and bracken (Pteridium spp.), distribution.(Fig 3.)

Mature larch (Larix decidua Linn.) plantations, which had less ground cover, were found in areas s4; s6 and s7 (see Fig. 1). Reduced ground cover was also found under dense beech canopy. (see Plate 6)

The Field Station contains chiefly mature oaks (Quercus robur Linn.) and a ground cover of grasses (see Plate 4). The stream was bordered by a dense hedge of hawthorn (Crataegus monogyna Linn.)

FIG. 1


s13
Hollinside
Wood
s12
s11
s10
legend:
stream
fence
footpath
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building
s1
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100m
s7
s6
s4
s5

FIG. 2

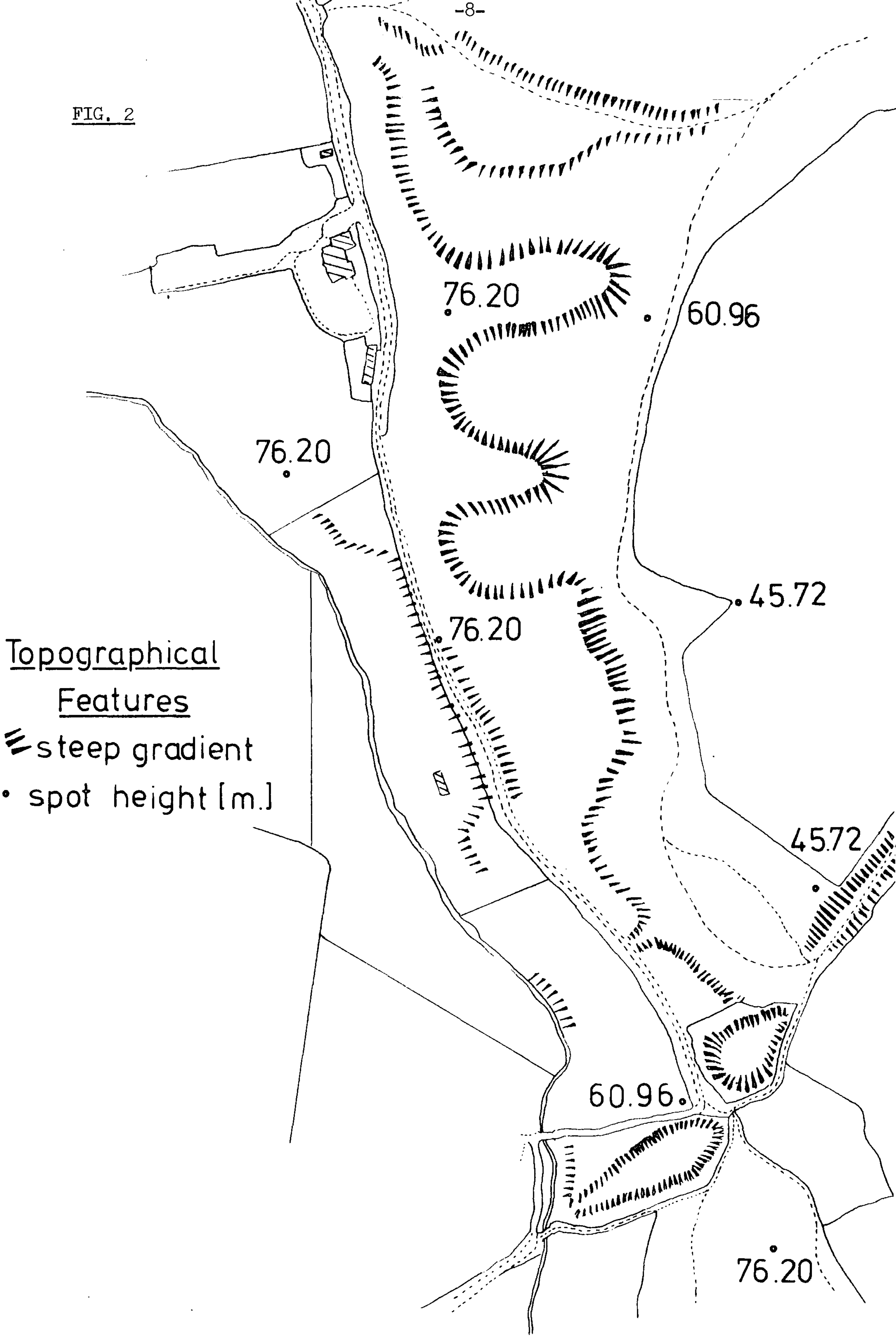

76.20
60.96
76.20
76.20
45.72
45.72
60.96
76.20
Topographical Features
steep gradient
spot height [m.]

FIG. 3

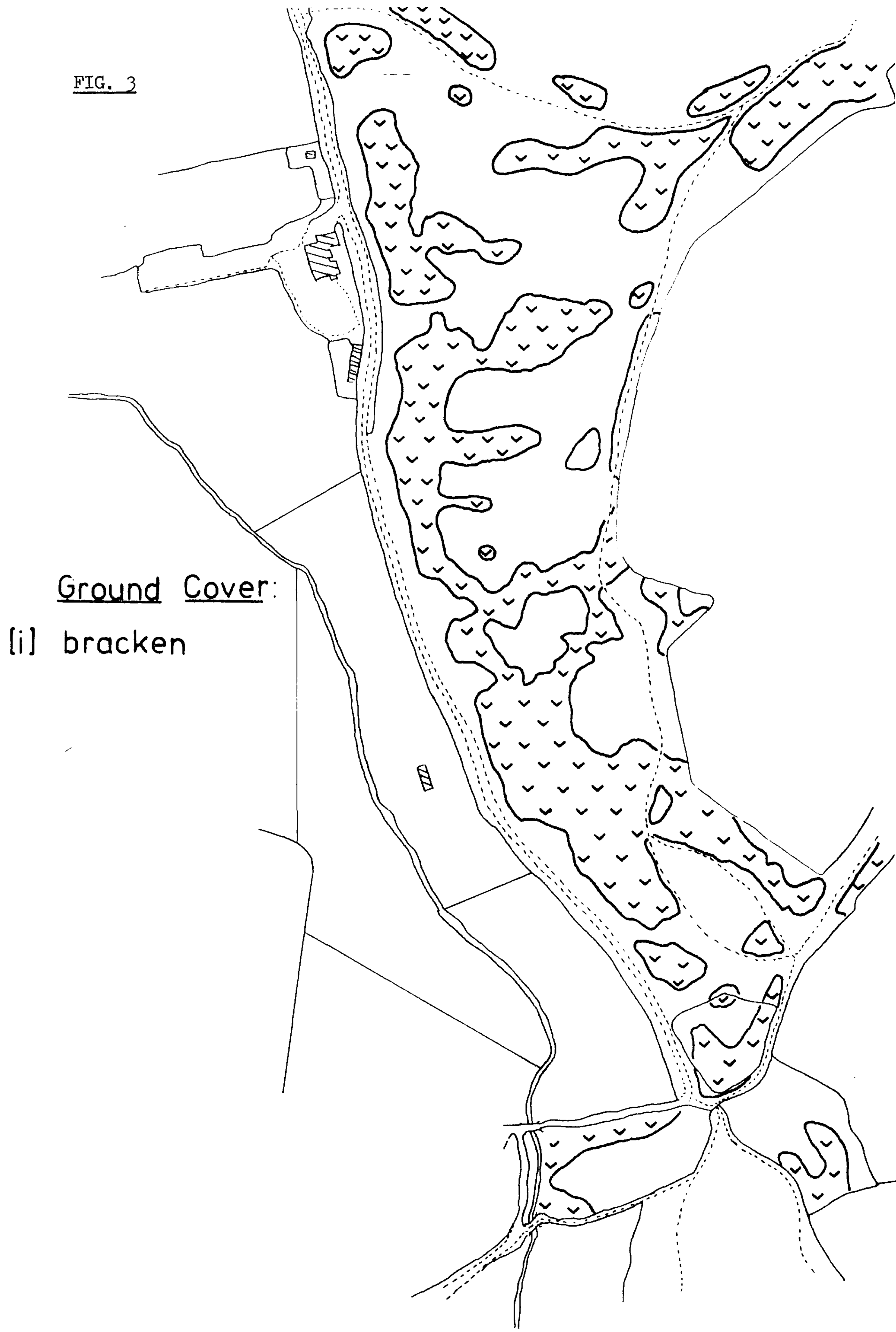


FIG. 4

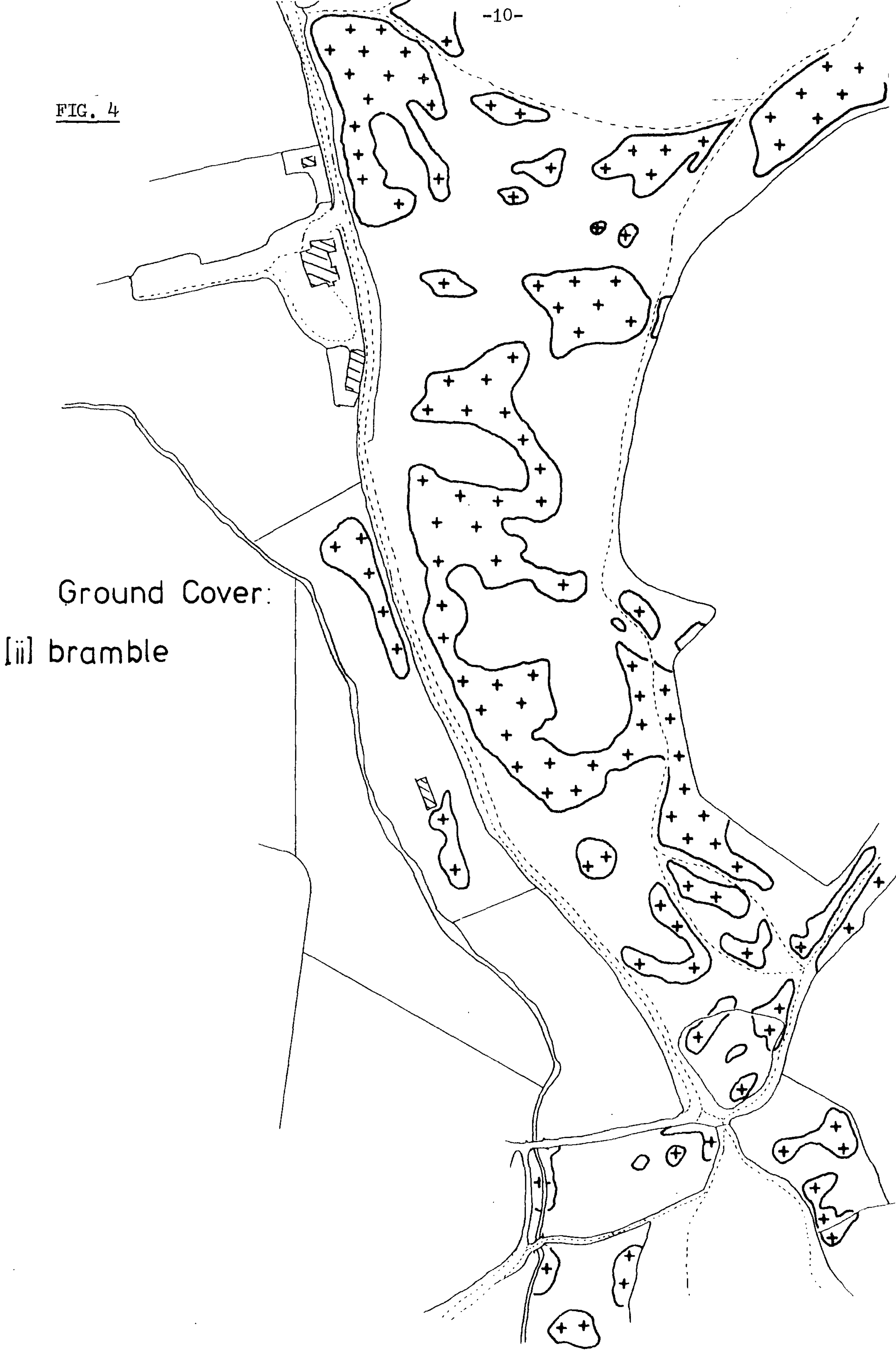
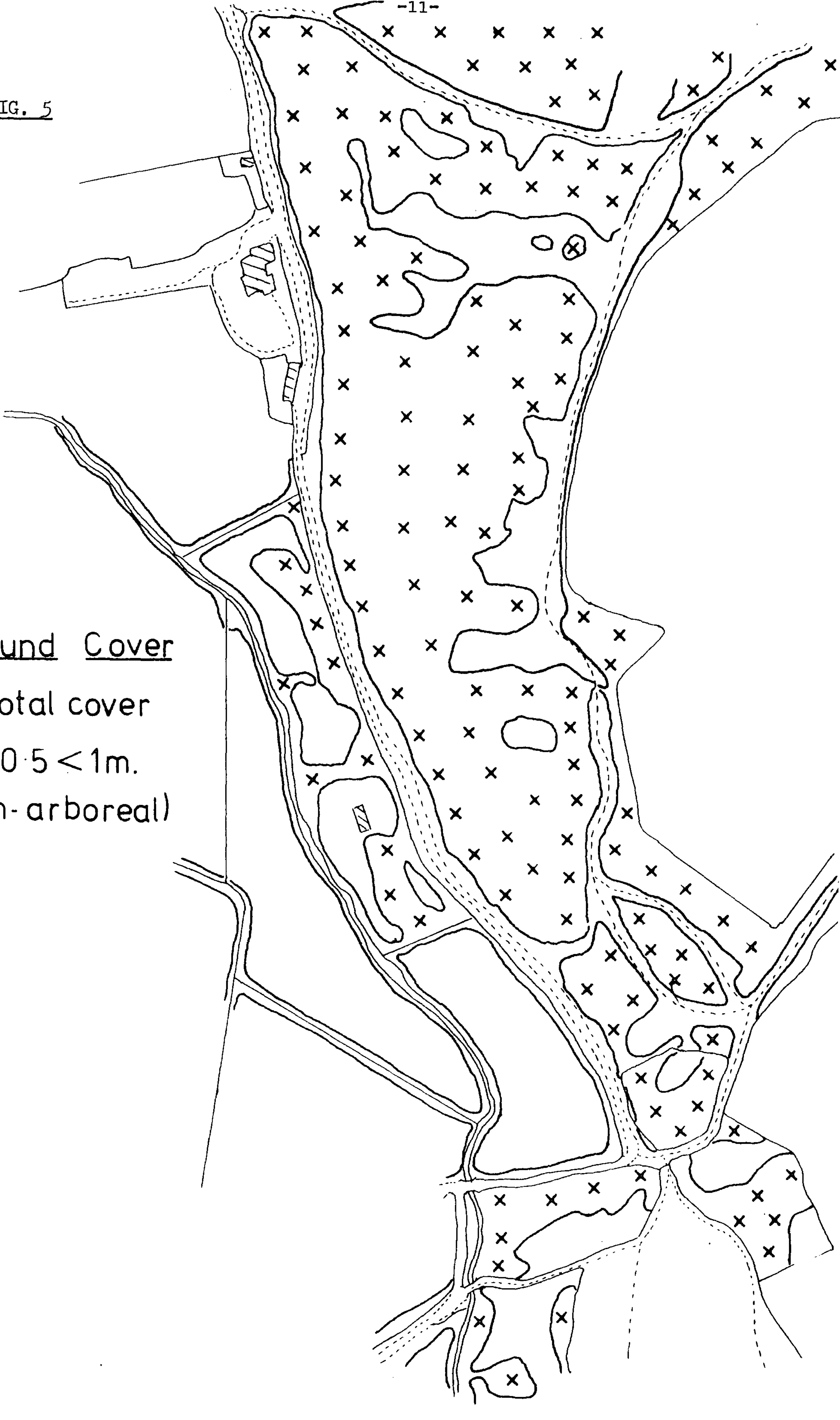


FIG. 5



Ground Cover

[iii] total cover

> 0·5 < 1m.

(non-arboreal)

Plate 2,

Extensive ground cover in Hollinside Wood.

Plate 3.

Extensive ground cover in Hollinside Wood.

Plate 4.

Stream within Field Station.

Plate 5.

Extensive ground and shrub cover within Hollinside Wood.

Plate 6.

Little ground cover within beech dominated areas.

Plate 7.

Grass ground cover within open areas of Hollinside Wood.

MATERIALS AND METHODS

Materials and Methods

1.1 General

Observations were made from early April until late July 1976 and additional information on breeding biology was gathered during early August.

1.2 Bird Censuses

To determine the initial dispersion of male Wrens a census was carried out in the area in April, following the recommendations of the International Bird Census Committee (1969).

Visits to the area were concentrated at times when song activity was believed to be greatest, i.e. in the morning and to a lesser extent in the evening. A walking speed of approximately 1 km. per hour was maintained whilst censusing, and different routes were taken through the plot at each census. The minimum number of visits used in the closed habitat was ten and in the open habitat eight. Positions of the singing males or direct observations of the birds were recorded on a 1:2500 map.

Results from these censuses are set out in the appendix and possible sources of error discussed.

It was assumed that only the males sang, as this is amply documented by Armstrong (1955).

1.3 Trapping and Marking

To establish the range of movements of individual birds it was necessary to trap and colour ring individuals. Many accounts testify to the difficulty of catching Wrens (Bolan 1912) and the Hollinside Wood population behaved characteristically.

Mist nets were set across observed flight paths but Wrens seemed able to distinguish the nets from the surrounding vegetation and avoided them. Armstrong (1955) notes the apparently exceptional visual acuity of the bird.

All birds caught were marked with a B.T.O. and two colour rings. Data on wing length and weight were not collected, even though Hawthorn (1975) and Thorne (1972) have utilised these to differentiate the sexes outside the breeding season. Since my study was carried out during the breeding season, weights would not have been reliable indicators of sex, since the females may have been carrying eggs.

Chicks were ringed whilst in the nest at approximately 7 days old. For each brood a single colour was chosen and only one colour ring used per chick. (B.T.O. rings were used as well.) White rings were not used in case the female mistook them for faecal pellets and attempted to remove or eat them.

Handling and ringing did not effect adversely either the males or the chicks. Within a few hours the males were singing from their normal song posts, and as soon as the nests were left the young continued to be fed.

1.4 Estimation of sizes of territory and home range

Accepting that song is a means of defence (to be justified later) territory size can be estimated from the minimum polygon of song posts used by each male. Home range is the area in which non-defensive activities take place outside the delimited territory. A minimum polygon drawn from non-defensive activity observations thus delimits the home range.

During May, June and July each bird was observed for as many daylight hours as possible. A rota system was established for observing so that individual male were observed at least twice a week for a minimum of four hours at each session.

Each bird was watched from a naturally camouflaged position with 10x50 binoculars. As far as is known, the observer's presence did not effect the bird's behaviour. The location of each song post was recorded on a 1:2500 map, as were observations of other activities, mainly foraging.

Minimum polygons were measured with a planimeter and the results are given in Table 2.

1.5 Song timing

The lengths of songs were timed with a stop watch reading to $\frac{1}{5}$ th. s. (Only full songs were timed.)

1.6 Activity patterns

Activity was divided into:

1. Singing-only recorded when the bird was singing a territorial song.
2. Flying
3. Foraging-when the bird was neither singing nor foraging.

Finer divisions into activities of feeding, preening and searching for food was impossible because of the birds' inconspicuousness in dense vegetation. Wrens were very active at all times of the day and continually foraged, particularly in dense ground vegetation such as bracken or bramble. Success rates in capturing insects could not be measured.

For each record of activity, the height at which the activity took place was noted. Vertical subdivisions of 1 metre units were estimated by eye.

Three methods of estimating the allocation of time to the activities were used.

1. 'continuous survey'- A spoken commentary on the activity

and its height was recorded on a tape as the bird was followed. Later the tape was re-run and each activity timed with a stop watch.

2. '5 minute spot observation method'- At five minute intervals details of the activity and height were recorded.

3. '1 minute spot observation method'- At one minute intervals details of activity and height were recorded.

Although the most accurate, the 'continuous survey' proved to be extremely time consuming. The length of the tape limited the period of observation to a maximum of one hour. Timing of the sequence of observations took almost twice as long. A possible source of error, which had to be guarded against, arose if the tape ran more slowly on the re-run than on the recording. However, this method normally gave an accurate account of time allocation to each activity and was used as a baseline against which the other methods were compared.

As shown in Table 2 the '5 minute spot observation method' proved to be very inaccurate. The percentage of time spent singing was overestimated and the foraging periods underestimated. Another fault with this method was the limited amount of data which could be collected-only 12 observations in each hour.

The '1 minute spot observation method' provided results comparable to the 'continuous survey' and most activity data was collected in this way. The 1 minute pauses between observations allowed time for each record to be written down and the bird pursued, if it had moved out of range. Smaller sub-divisions of time e.g. 30 s. would not have allowed for this.

1.7 Vegetation mapping

The extent of different ground cover (Figs. 3,4 and 5) was estimated visually during the middle of June and recorded onto a 1:2500 map.

1.8 Nest records

Once each nest had been located, the following data were collected:

1. The height of the bottom of the entrance hole above ground.
2. Direction of the entrance hole.
3. Building materials.
4. Surrounding vegetation.
5. The identity of the male which maintained the territory.
6. Breeding biology-Nests were checked at least once every three days before egg laying. Once eggs were found, the nest was checked every other day. The path through the vegetation to each nest was altered regularly to avoid the attention of predators. Eggs were counted with the aid of a light beam reflected by a mirror inserted into the entrance hole.

Table 1.

A comparison of the three methods of recording time allocation by the Wren.

Method	% of time spent in each activity		
	Foraging	Singing	Flying
Continuous survey (n 6549 s.)	77.3%	21.1%	1.6%
5 minute spot observations (n 148 observations)	59.7%	38.5%	1.8%
1 minute spot observations (n 3441 observations)	75.3%	22.8%	1.9%

Note: Comparisons were made for the same time of day (10.00-14.00h.) with the same birds.

(I) RESULTS

(I) Results: Sizes of territories and home ranges.

During the three months of observation territories and home ranges grew steadily (Figs. 6 and 7). Ten territorial males were located in the area studied intensively. Another three, males m9, m11 and m12 held territories adjacent to the area and influenced the shape and size of the 'defended areas' of males m1-m8, m10 and m13

During May the song territories were restricted chiefly to those parts of the wood with emergent vegetation, particularly bramble. This association of song areas with ground cover was particularly well shown by male m7. From Fig.8 it appears that the bird maintained two small territories (0.17ha. and 0.16ha.), since it never sang and only occasionally foraged between these areas in May. Similarly, male m6 sang only along a hawthorn and bramble hedge bordering a grassland field. Male m1 held a long but narrow territory on either side of the Field Station stream. Expansion of the song territory away from the stream occurred only where it bordered an area of young alder (Alnus glutinosa Linn.) with dense secondary vegetation.

During June and July the other dominant species of ground vegetation, bracken, appeared and provided dense cover in most of the wood, except under canopies of beech and larch. This may have effected the territory expansion and will be discussed later.

In all months some restrictions to the boundaries of the territories were imposed by topographical features. Ridges divided the valley areas defended by males m3 and m5; by m5 and m10 and by m10 and m7. The road separated males m1 from m7 and m8 from m13, but was included in the territory of male m5. Open grassland provided part of the boundaries to the territories of males m4; m6; m7;

m8; m13 and m1.

Often the territories were not static even for a few days. Continued adjustments occurred between the territories of neighbouring birds particularly those with larger territories. For example, whilst Wren m7 defended the north-western part of its territory against m10, m8 would extend its territory into the south-east corner of m7's territory. This territorial gain was maintained for several days but then relinquished. For each bird,the boundaries shown on the maps (Fig. 8-10) are the maximum areas defended by song during each month and it must be emphasised that many subtle changes occurred at much shorter time intervals.

Greater overlap occurred between home ranges than territories. Penetration into neighbouring territories was quite extensive during foraging excursions. The foraging intruder did not identify itself as a male Wren by singing, and so was not recognised as such. Home ranges extended into more open areas than did territories. For example, the home range of male m1 included much of the young conifer plantation (Fig.1 area s2). This bird foraged actively for long periods in this open area, but when deliberately disturbed by the observer returned to its territory.

The boundaries of the home ranges of one month provided an indication of the territory size in the next (Table 2). A possible implication is that during home range expansion the locations defended by neighbouring birds were more clearly established. Extension of the territory during the next month could then be made in a direction where the conflict between birds would be least. For example, male m3 extended its territory to the north-east to include an area of ground cover close to the footpath.

Table 2.

Areas (ha.) of territories and home ranges of Wrens.

Wren		May	June	July
m1	Territory	0.38	0.94	1.16
	Home Range	0.97	1.43	1.48
m2	Territory	0.47	0.43	0.58
	Home Range	0.74	0.86	0.91
m3	Territory	0.27	0.60	0.78
	Home Range	0.61	1.13	1.46
m4	Territory	0.56	0.94	1.22
	Home Range	0.89	1.33	1.35
m5	Territory	0.31	0.58	0.70
	Home Range	0.57	0.93	1.23
m6	Territory	0.19	0.25	0.29
	Home Range	0.50	0.55	0.59
m7	Territory	0.33	1.08	1.59
	Home Range	0.59	1.41	1.75
m8	Territory	0.37	0.98	1.72
	Home Range	0.58	1.49	2.04
m10	Territory	0.34	0.32	0.38
	Home Range	0.64	0.63	0.57
m13	Territory	0.51	0.84	0.84
	Home Range	0.65	1.03	1.03

Table 3.

Areas (ha.) of bramble and bracken within each Wrens territory.

	May		June		July	
Wren	Bramble	Bracken	Bramble	Bracken	Bramble	Bracken
m1	0.03	0.0	0.08	0.0	0.08	0.0
m2	0.30	0.0	0.30	0.04	0.35	0.17
m3	0.07	0.0	0.08	0.26	0.12	0.27
m4	0.40	0.0	0.40	0.30	0.91	0.30
m5	0.04	0.0	0.12	0.34	0.30	0.39
m6	0.03	0.0	0.10	0.15	0.10	0.15
m7	0.20	0.0	0.73	0.35	0.78	0.81
m8	0.07	0.0	0.29	0.35	0.47	0.46
m10	0.19	0.0	0.19	0.13	0.22	0.16
m13	0.03	0.0	0.15	0.19	0.15	0.19

FIG. 6 Area (ha.) of territories for May, June and July; showing growth in size.

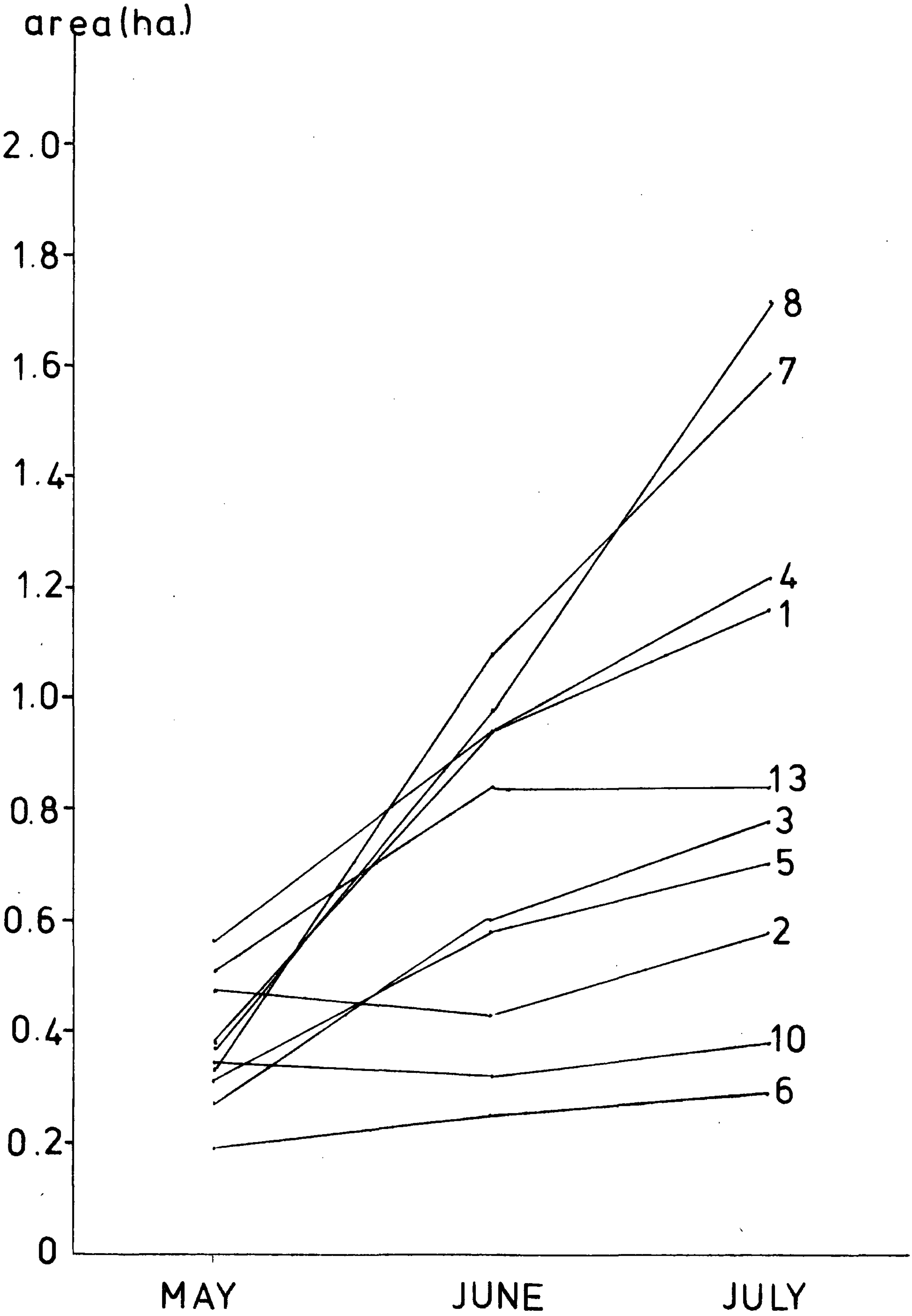


FIG. 7 Area (ha.) of home ranges for May, June and July; showing growth in size.

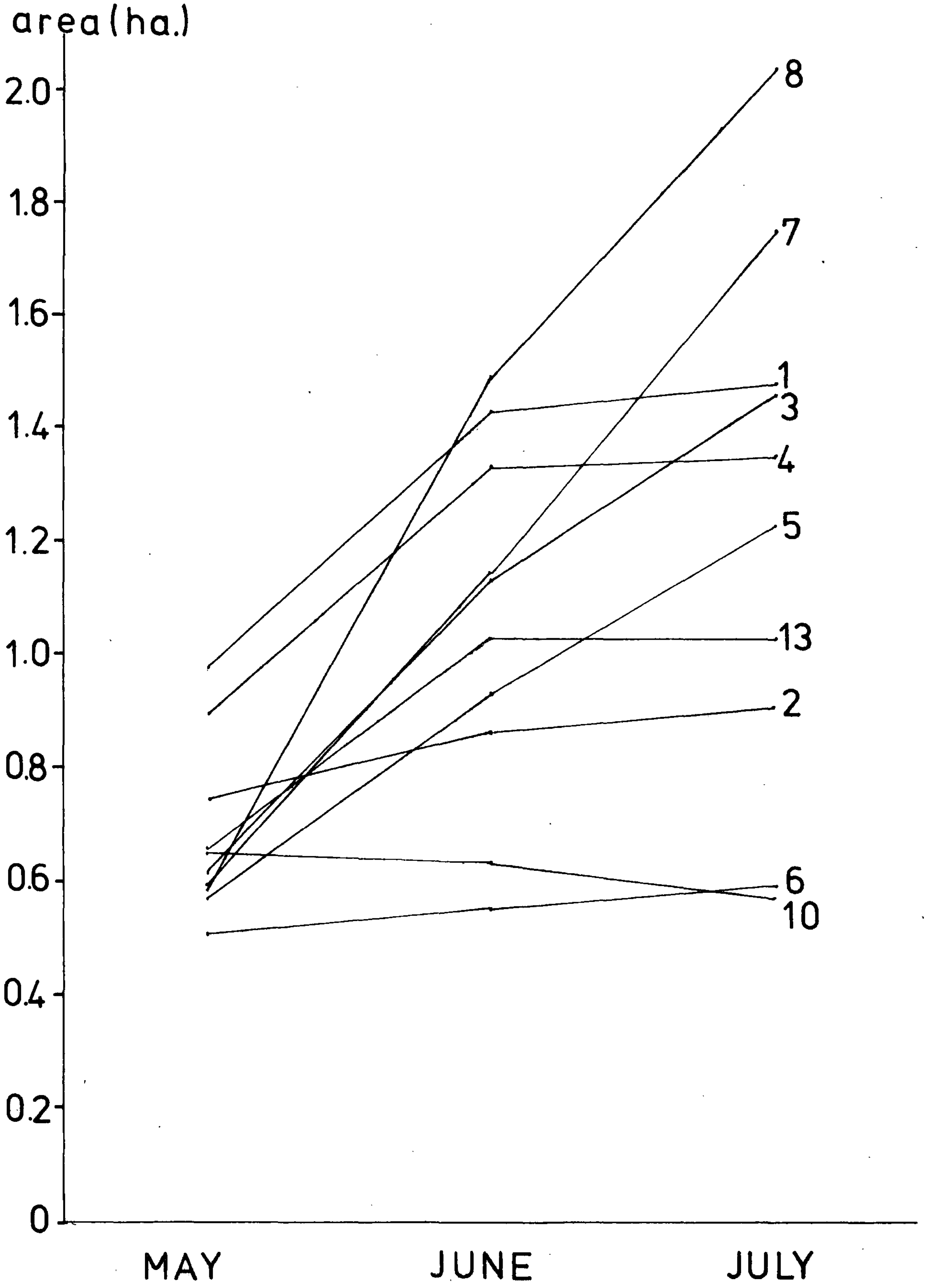
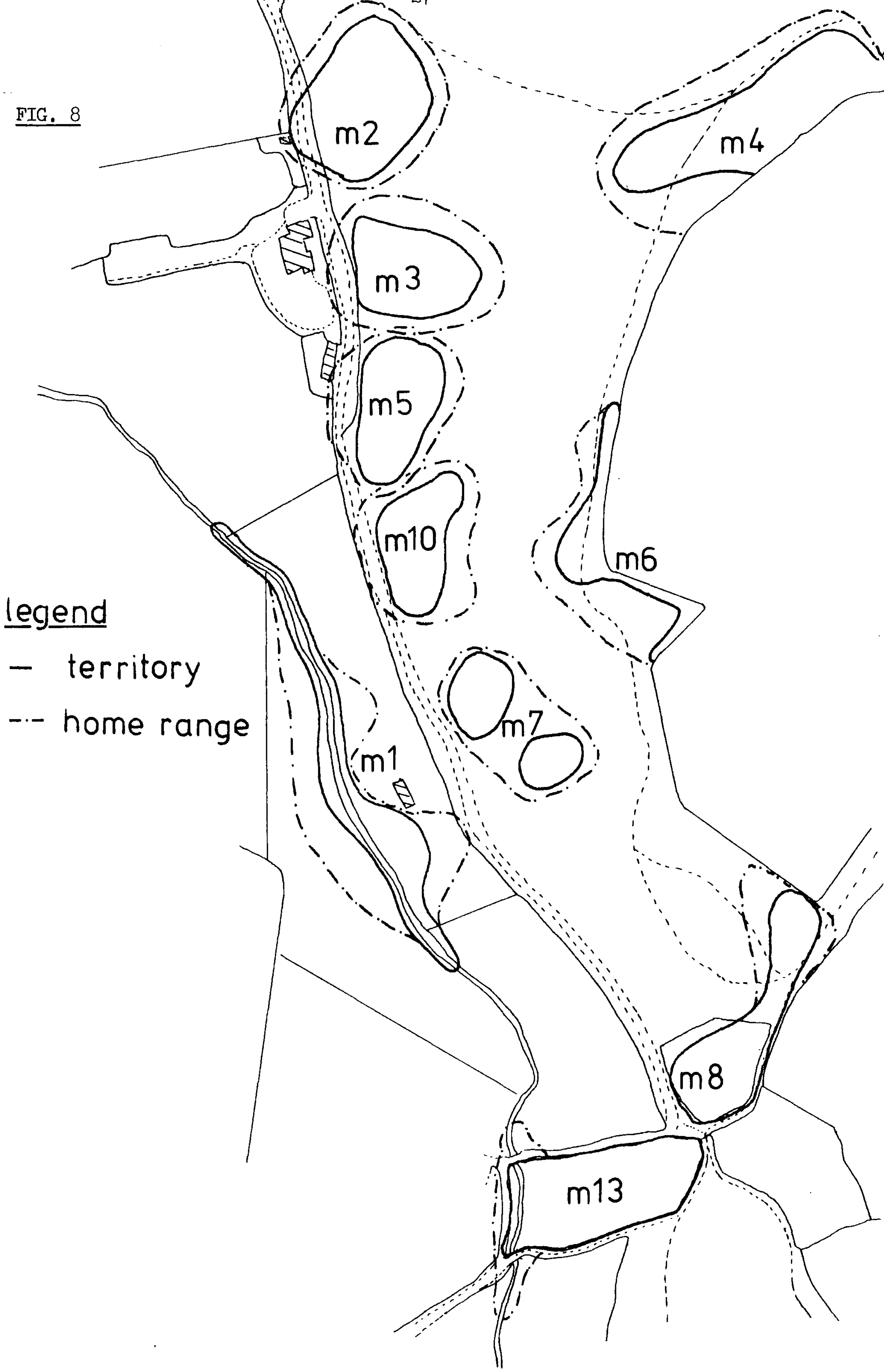
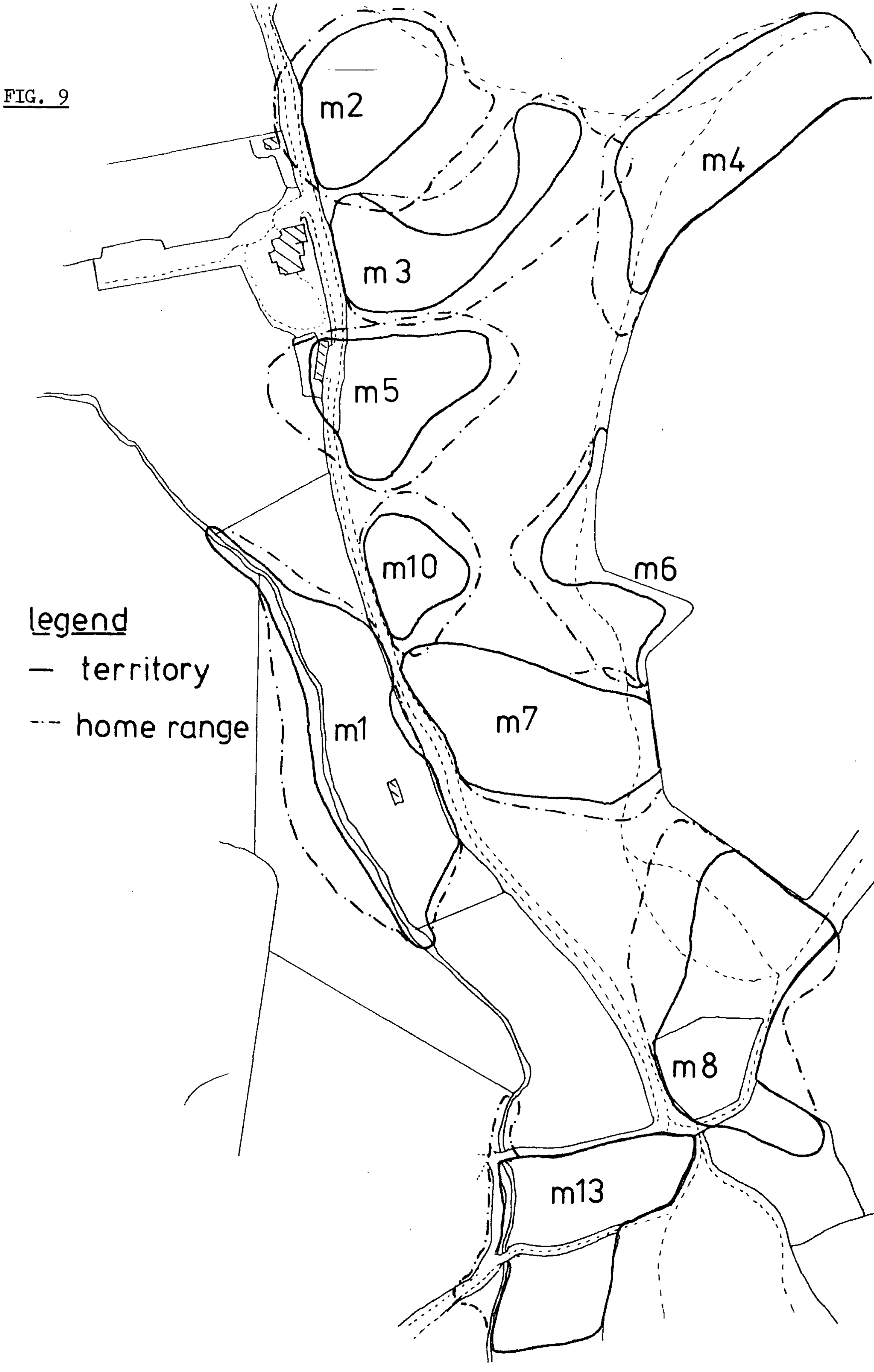


FIG. 8



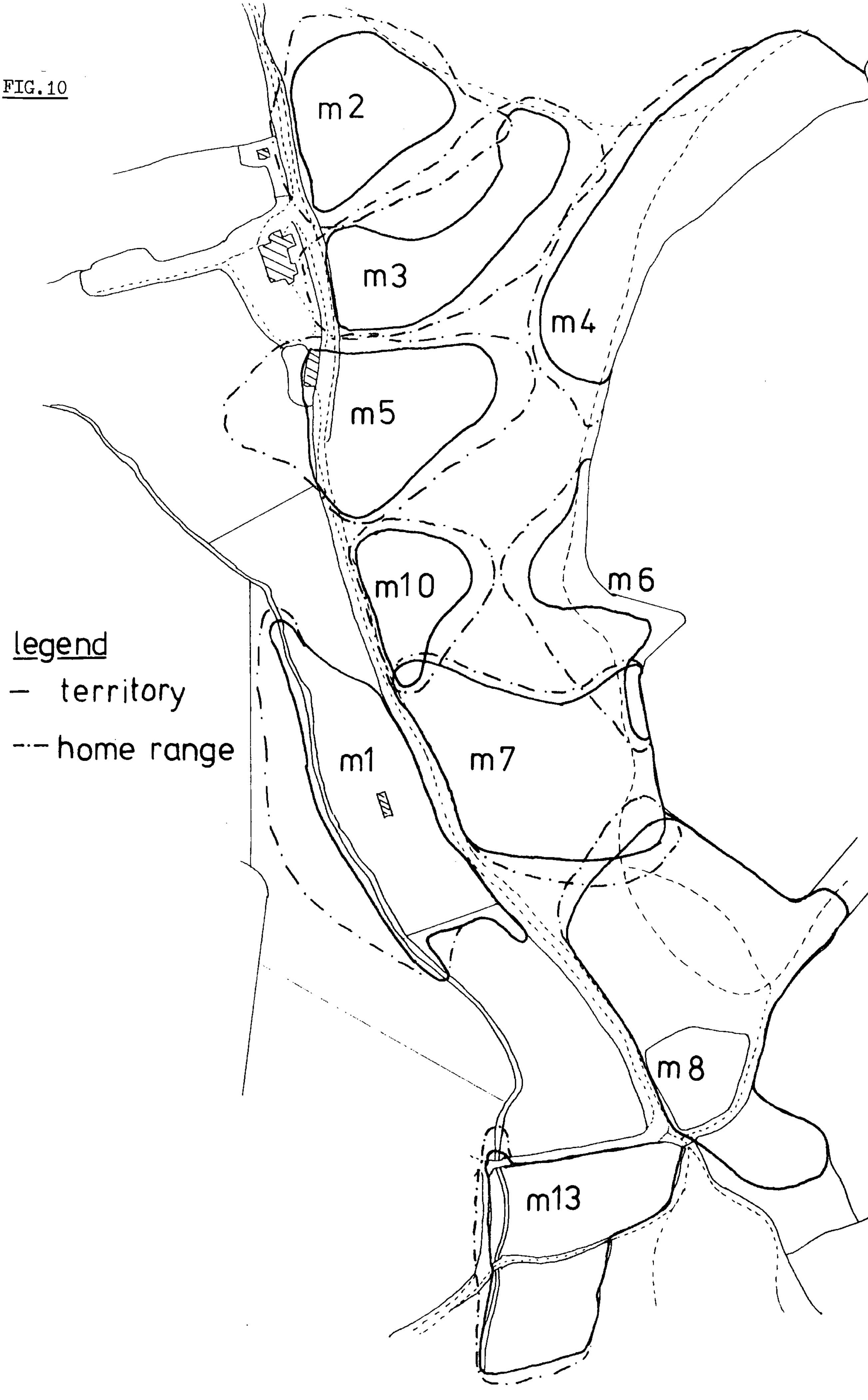
Territory & Home Range May 1976

FIG. 9



Territory & Home Range: June 1976

FIG.10



Territory & Home Range July 1976

This created less conflict than would have resulted from an expansion to an area occupied by male m2 or that occupied by m5. Also male m1, as the sole occupant of the Field Station, was able to expand its territory as far as the road before male m7 prevented further expansion. Restrictions on male m1 extending its territory in other directions were provided by the lack of ground cover.

The increase in territory size was, for most of the birds, greater between May and June than between June and July (Table 4). The area of bracken and bramble cover within each territory increased with territory expansion (Fig.11-13). Although the amount of bramble cover increased steadily (Fig. 11), the most marked increase was in the amount of bracken cover within each territory between May and June (Fig. 12).(No bracken cover had been available before its emergence in June.) The large increase in the amount of bramble within male m4's territory between June and July was due to the incorporation of hitherto undefended bramble areas into the song territory boundary. Male m1 and male m13 had territories adjacent to the stream and although the ground cover for these sites was hawthorn and grasses, expansion of these territories still occurred. It was the presence of ground cover, not the type of vegetation, that allowed territory expansion.

To examine experimentally whether the Wrens continued territorial expansion during July to occupy the maximum possible suitable areas, or whether territories held then were the physical maxima which could be defended,(An increase in the time allocated for defence would detract from foraging time)one male, m3, was removed from its territory and taken to a suitable habitat 3 km. from Hollinside Wood. Fig. 14-16 show the expansion of the territories of neighbouring males, m2 and m4, which took place subsequently. Within two days male m2 had occupied the entire area vacated by m3. Both its original and 'new' territory, which it defended by utilising the same song posts at the same height as male m3 had done, were maintained until at least the end of July. Male m5 did not expand its territory into the vacated area although some of its song posts were close to the boundary of male m3's territory. However, a ridge separated the territories of male m5 and m3, as noted earlier, so that if m5 had occupied m3's vacated territory, the enlarged area could not have been kept under complete surveillance at all times. The rapid colonization by male m2 may have prevented male m5 from detecting that a vacated area had become available. It was not possible for a human observer to hear whether male m3 was singing or not unless one was close to the m3/m5 border.

Table 4.

The increase in area (ha.) of the territories between the months.

Wren	May to June	June to July
m1	0.56	0.22
m2	-0.04 *	0.15
m3	0.33	0.18
m4	0.38	0.28
m5	0.27	0.12
m6	0.06	0.04
m7	0.75	0.51
m8	0.61	0.74
m10	-0.02*	0.06
m13	0.33	0.0

* Indicate a reduction in territory size from May to June

FIG. 11 Area (ha.) of bramble within each territory for May, June and July.

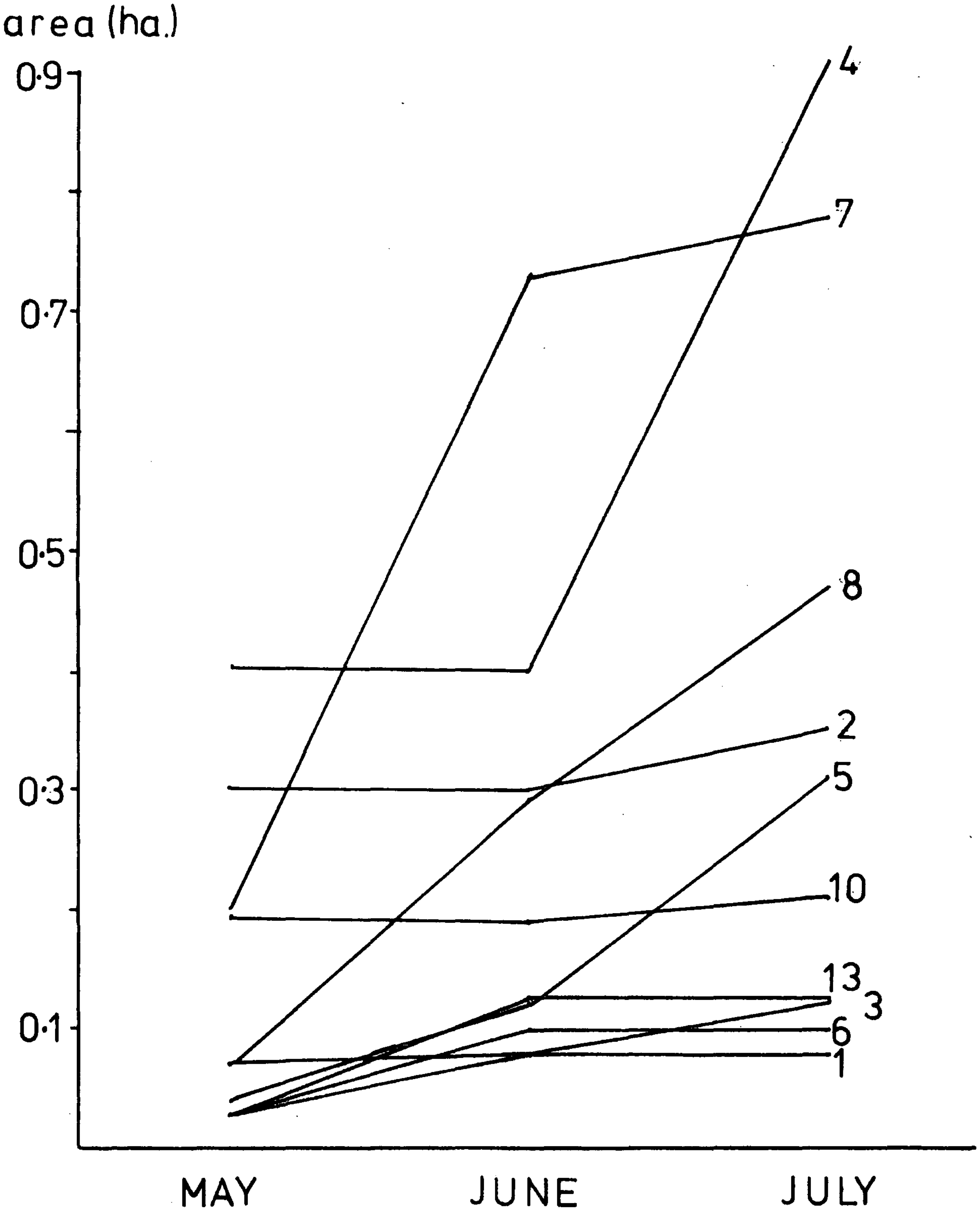


FIG. 12 Area (ha.) of bracken within each territory for May, June and July.

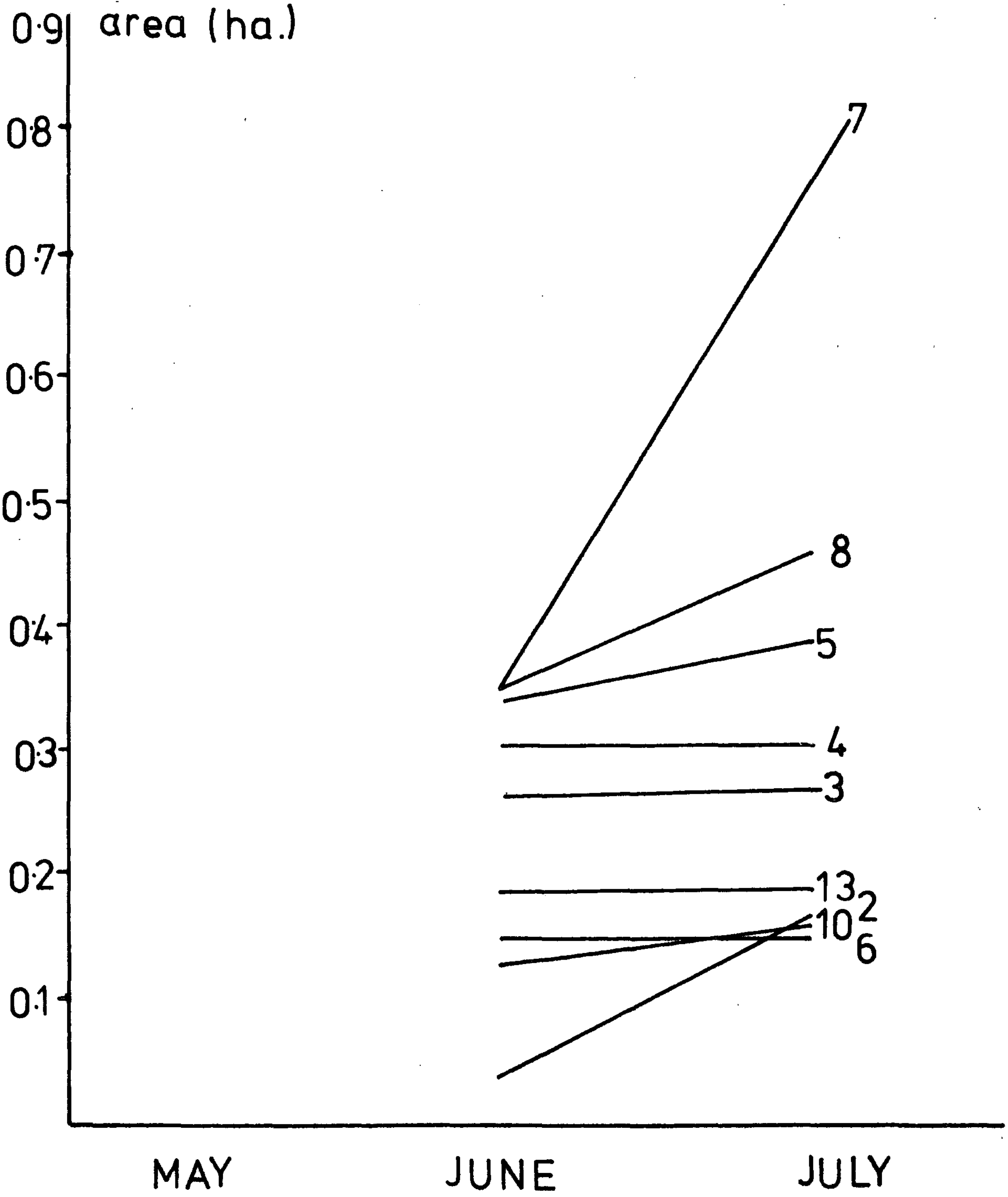


FIG. 13 Area (ha.) of bramble and bracken within each territory for May, June and July.

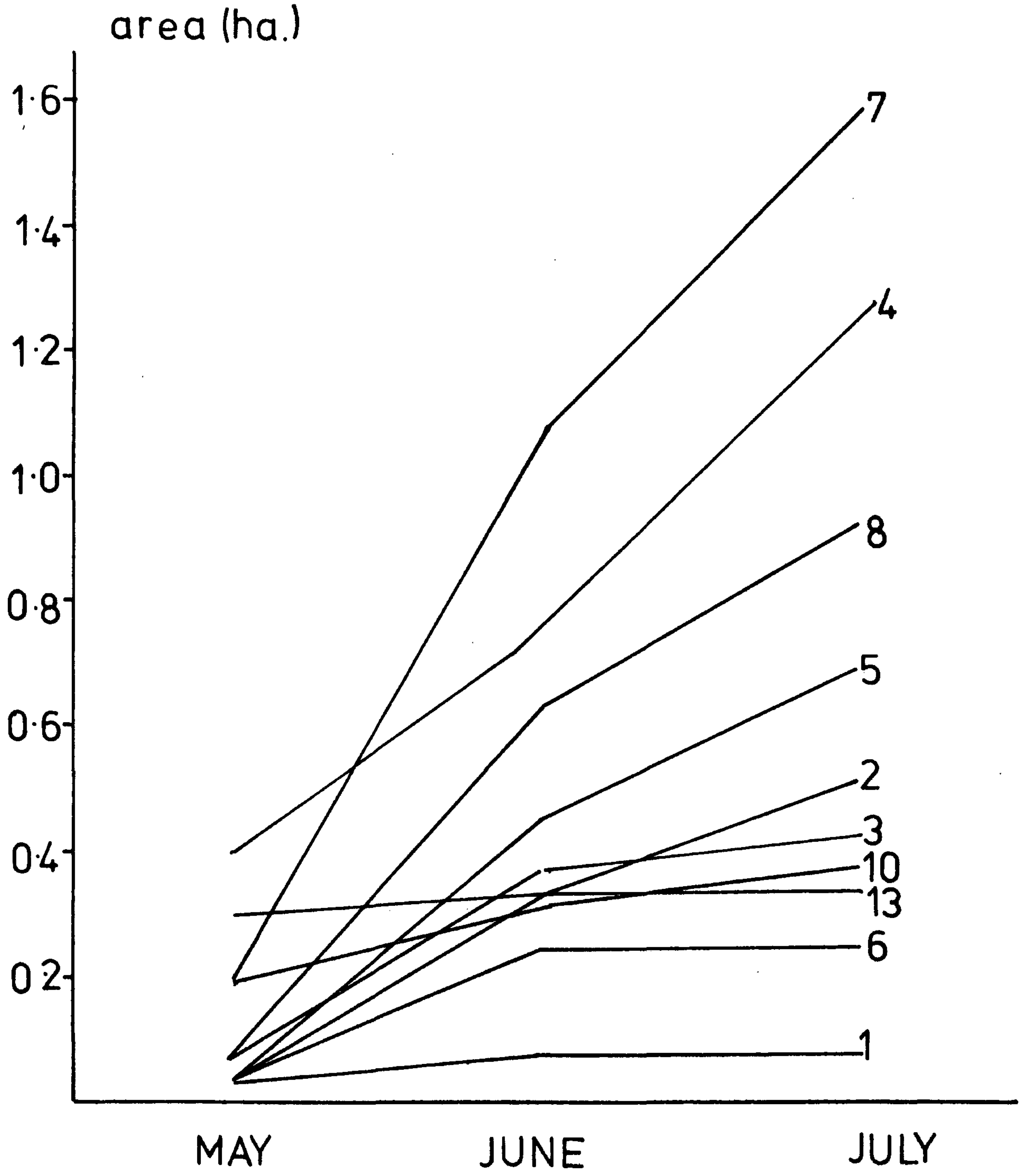


FIG. 14 Removal experiment (1) - Territories held by male Wrens before male m3 was removed (14-7-76)

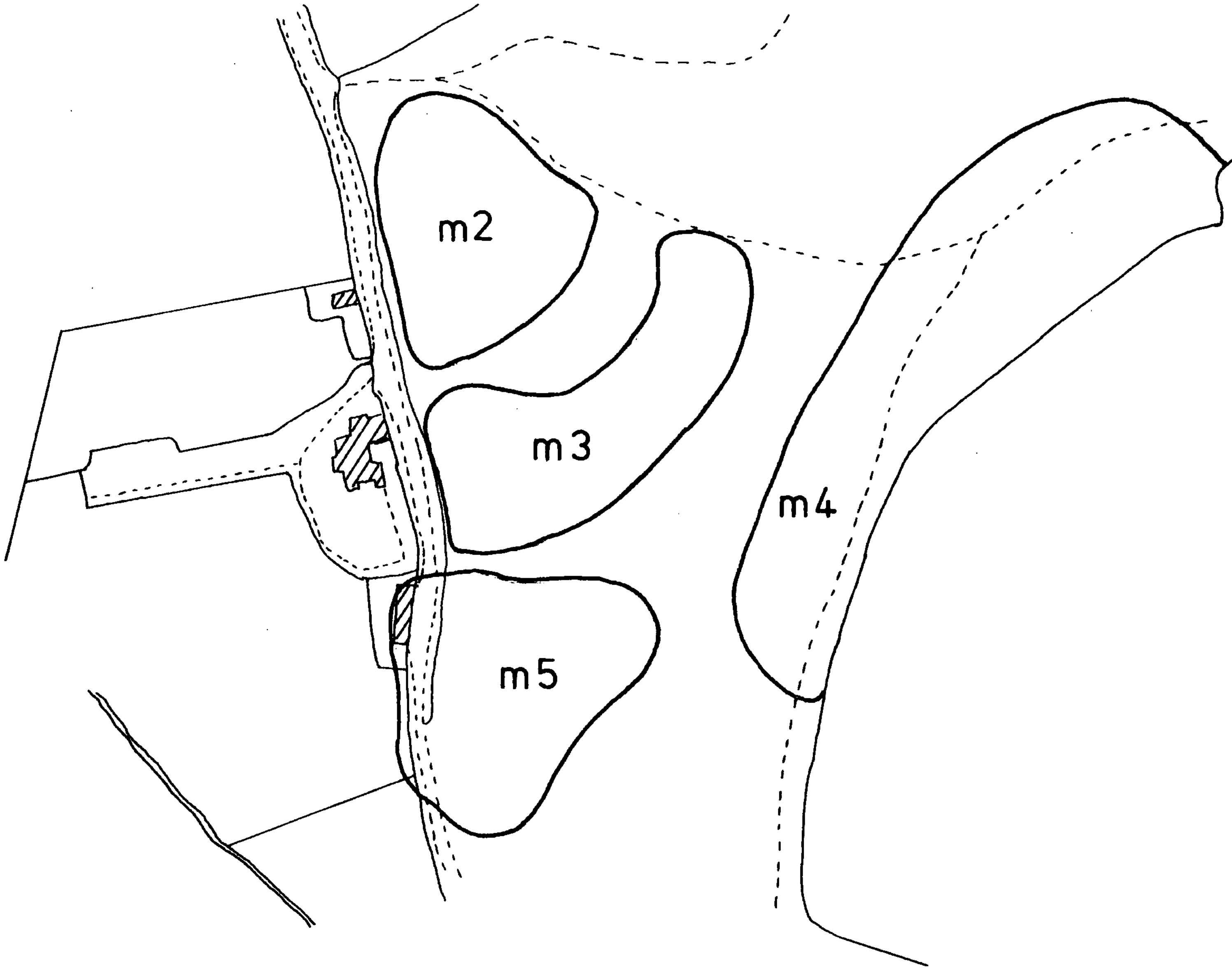


FIG. 15 Removal experiment (2) - Territories held by male Wrens 24h. after male m3 was removed (15-7-76)

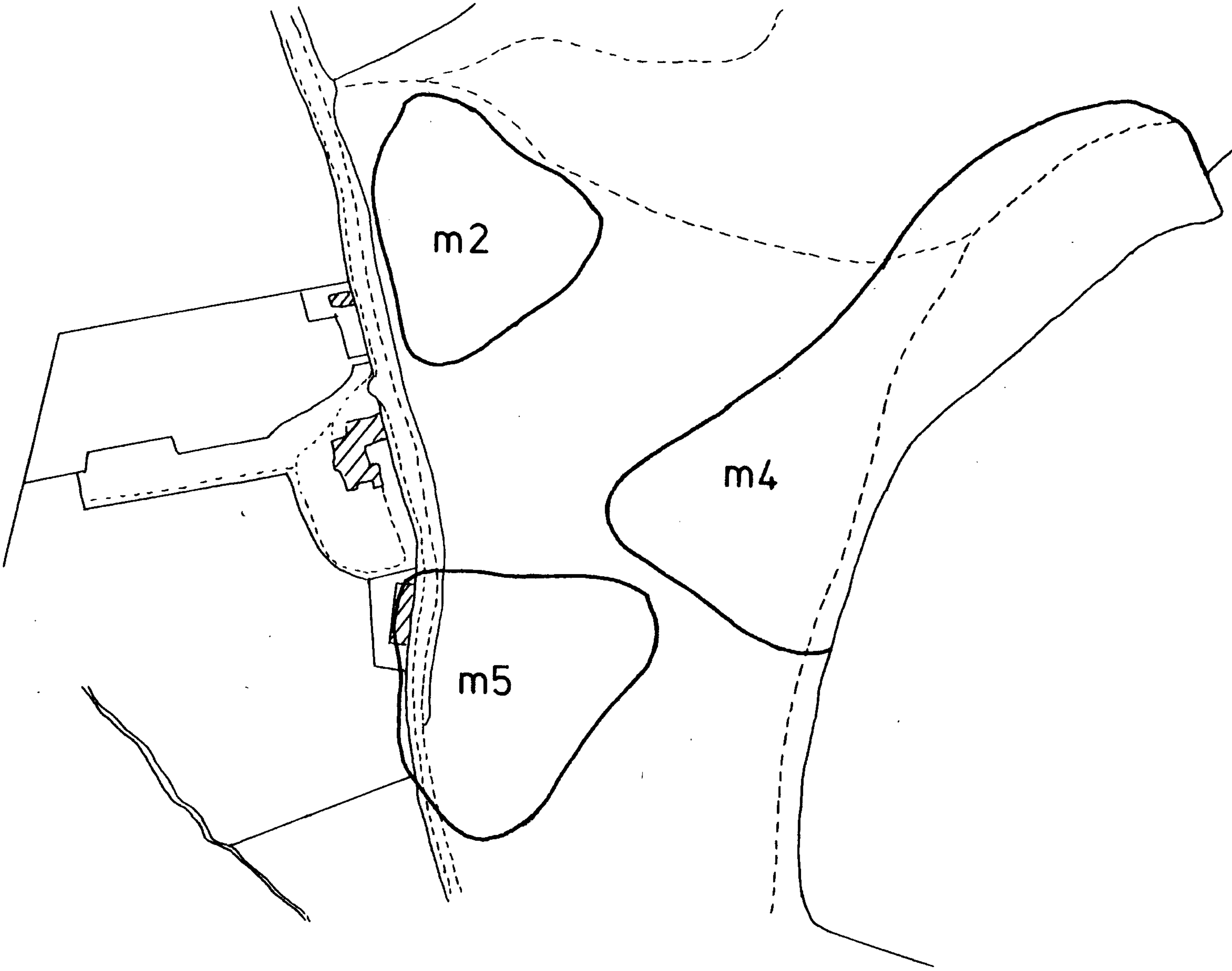
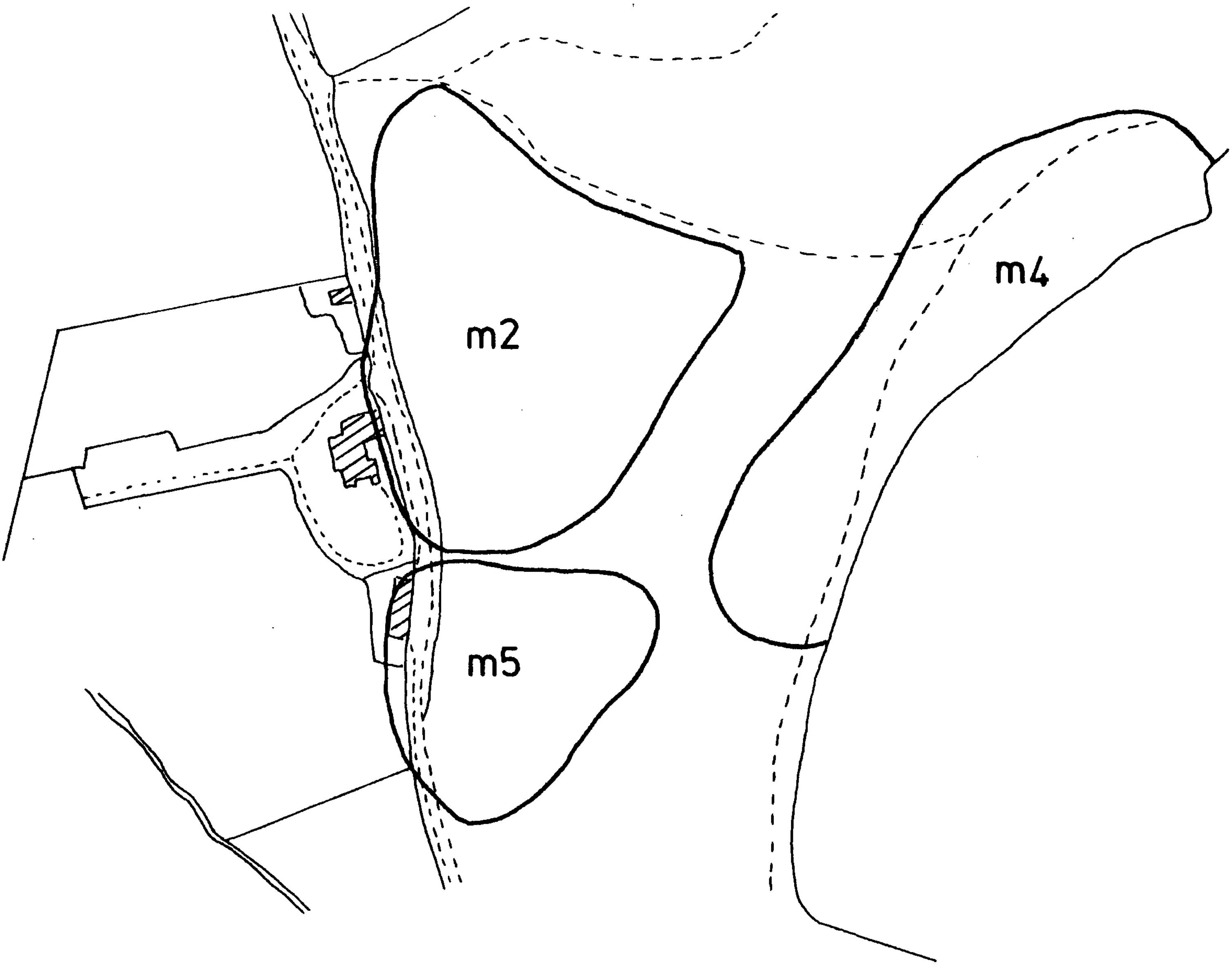


FIG. 16 Removal experiment (3) - Territories held by male Wrens 48h. after male m3 was removed (16-7-76)



(I) DISCUSSION

(I) Discussion

Lack and Venables (1939) classify the Wren as a 'scrub' bird which resticts all its activities to secondary growth. However, they point out that although the Wren should not be regarded as a truely woodland bird, most 'scrub' in Britain is found within woods. Lack of secondary growth in some woods, such as beech, restrictsthe number of Wrens found there. Dunlavy (1935) assumes ground cover to be the true niche of the bird, for it seeks safety within this zone. The importance of ground cover for foraging will be shown later.

Within each woodland,areas of suitable habitat are limited, natural woodlands being vegetationally heterogeneous. Wrens might attempt to maintain their entire populations within such patches of suitable habitat (which would require reductions in territory size to allow any increase in density); or some birds might be forced into less suitable habitats.

If territory has a minimum size (Kendleigh 1941; Nice 1943; Kluijver and Tinbergan 1953; Armstrong 1956), and if the amount of such habitat is limited, a maximum number of birds can be accommodated by any chosen area, if the Wrens are only found in suitable habitats. A greater amount of suitable ground cover within the chosen area would lead to a higher number and overall density of birds; or to a stable density for the area but larger territories for the resident birds. The Wrens of Hollinside Wood increased the areas of their territories to include the areas of emergent bracken without an increase in the number of territories.

As the size of the territories increased the amount of ground cover included increased. The increase in the size of territories from May to June was possible because of the increased cover provided by the emergent bracken allowing expansion into new suitable areas. The increase in size of territories from June to July was into undefended areas of both bramble and bracken. The growth of the bracken produced the ground cover necessary to link undefended areas of bramble before expansion of territory could occur. For some of the Wrens the increase in territory size from June to July included a substantial increase in bramble cover. The bramble cover could be important for nesting sites, foraging areas or protective cover for the chicks. Territories in May all had bramble within them and the amount increased with territory expansion.

The function of the territory increase could be to make available the exclusive use of a larger foraging area, for example for the young. However, not all foraging takes place within the territory and neither the female nor the chicks recognize territorial boundaries, as will be shown later. In any case, it has not been proved that territorial behaviour is necessary to ensure an adequate food supply for the young (Hinde 1956). If the food supply was the limiting factor it would be expected that with an increase in insect abundance during the summer months there would be no need to increase the size of the territory. The idea of a 'food territory' suggested by Altrum (1898) and Howard (1929), finds little support in the case of the Wren.

A larger territory could increase the males' chance of obtaining a mate if the females' movements through the area were at random. However, as will be shown later the male attracts the female to the nest site with song. Thus a male with a small territory but one who sings often will have a better chance of attracting a female than a male with a larger territory who sings less. Males with larger territories have more song posts, and could therefore spend less time singing from each post if adequate defence of the entire perimeter of the territory was necessary - or the number of songs per day would have to be increased. An increase in the number of songs would reduce the time available for foraging. However, from a selected song post within a small territory defence of the territory and attraction of females to nest sites would be possible for the whole of the territory. Less time need be spent patrolling the territory and the defence of the territory would be just as efficient as the use of many song posts.

An increase in territory size incorporating an increase in the area of bramble cover would make more nesting sites available. Bracken was not a suitable nest-supporting material. However, since male Wrens will build nests in a multitude of habitats (Witherby _et al_ 1945), bramble cover is unlikely to have been a limiting factor to the number of nest sites available. However, if there is a minimum distance between nests, because of the foraging area required by the female when feeding the nestlings, then an increase in territory size will increase the number of potential nest sites. Armstrong (1955) states that females will not select nests close to occupied nests. Thus a larger territory will create a better dispersal of nests and more available potential nest sites.

(II) RESULTS

(IIi) Results: Song production per hour.

Observations on three male Wrens were collected in the middle of each month. Data were collected during dry, still days to try to alleviate the effect of climatic factors affecting song production. In all months, May (Fig. 17); June (Fig. 18) and July (Fig. 19), there was a reduction in song output per hour throughout the day. The maximum number of songs per hour was given soon after dawn but the time at which the minimum number was given changed in different months. The 95% confidence limits to the means of the hourly song outputs are large because of individual variation between the birds; small sample size and exogenous factors e.g. climate and the proximity of an intruder affecting song production.

Comparisons were made between song production in different time intervals by entering data for time spent singing and not singing into a 2×2 contingency table. The amount of time spent singing was calculated from the number of songs per hour and the mean song length. The difference between time spent singing(i) and one hour was the time available for non-singing activities(ii) in each hour.

(i) Song number/h. × 5.51 = Number of seconds spent singing

(ii) 3600-Number of seconds singing = Time spent not singing

The total number of songs produced per da in May was less than in June or July, between which the song output was similar. There was a significant decrease in May in the number of songs between early (5.00-6.00h.) and late (7.00-8.00h.) morning. ($\chi^2 = 4.09$ $p < 0.05$ degrees of freedom =1).

After this initial decrease in song output the level remained stable for the rest of the day.

In June there was again a significant decrease in song output from early (5.00-6.00h.) to late (8.00-9.00h.) morning ($\chi^2 = 5.28$ $p < 0.05$ degrees of freedom =1). Subsequently song output was stable from 9.00-20.00h. During this period the song output per hour was greater and the stable level reached later in the morning than in May.

In July the number of songs given each day was similar to that in June but very few were given after 15.00h. There was a significant decrease in the song output between 5.00-6.00h. and 10.00-11.00h. ($\chi^2 = 4.49$ $p < 0.05$ degrees of freedom =1) No stable level of song production per hour was observed during the day.

Although no quantitative data were collected during April it was apparent that the number of songs per hour was less than May, a result consistant with that given by Clarke (1949). Fewer Wrens could have been singing in Hollinside Wood during April.

The length of song did not vary significantly between months and a mean duration of 91 songs was 5.51±3.24 (S.E.=0.34)s.This figure includes only full songs. The interval between songs varied greatly. The minimum was approximately 7s. for antiphonal singing i.e. when each song evoked an immediate song response by another male. Much longer intervals between songs were observed later in the day when much of the singing was not antiphonal.

FIG. 17

Number of songs per hour – MAY 1976 – [mean ± 2 SE n= 3]

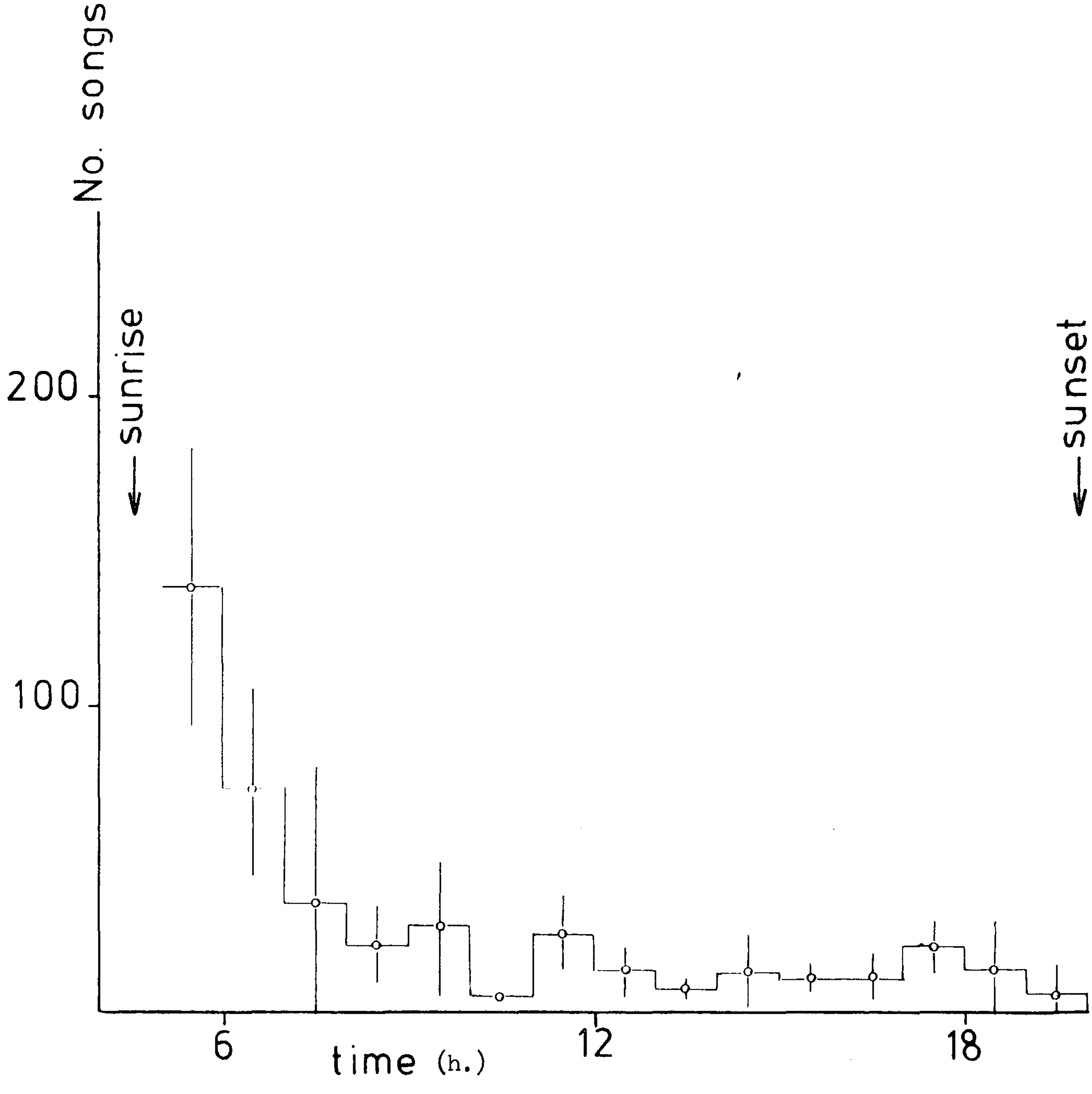


FIG.18

Number of songs per hour — JUNE 1976 - [mean ± 2 SE n=3]

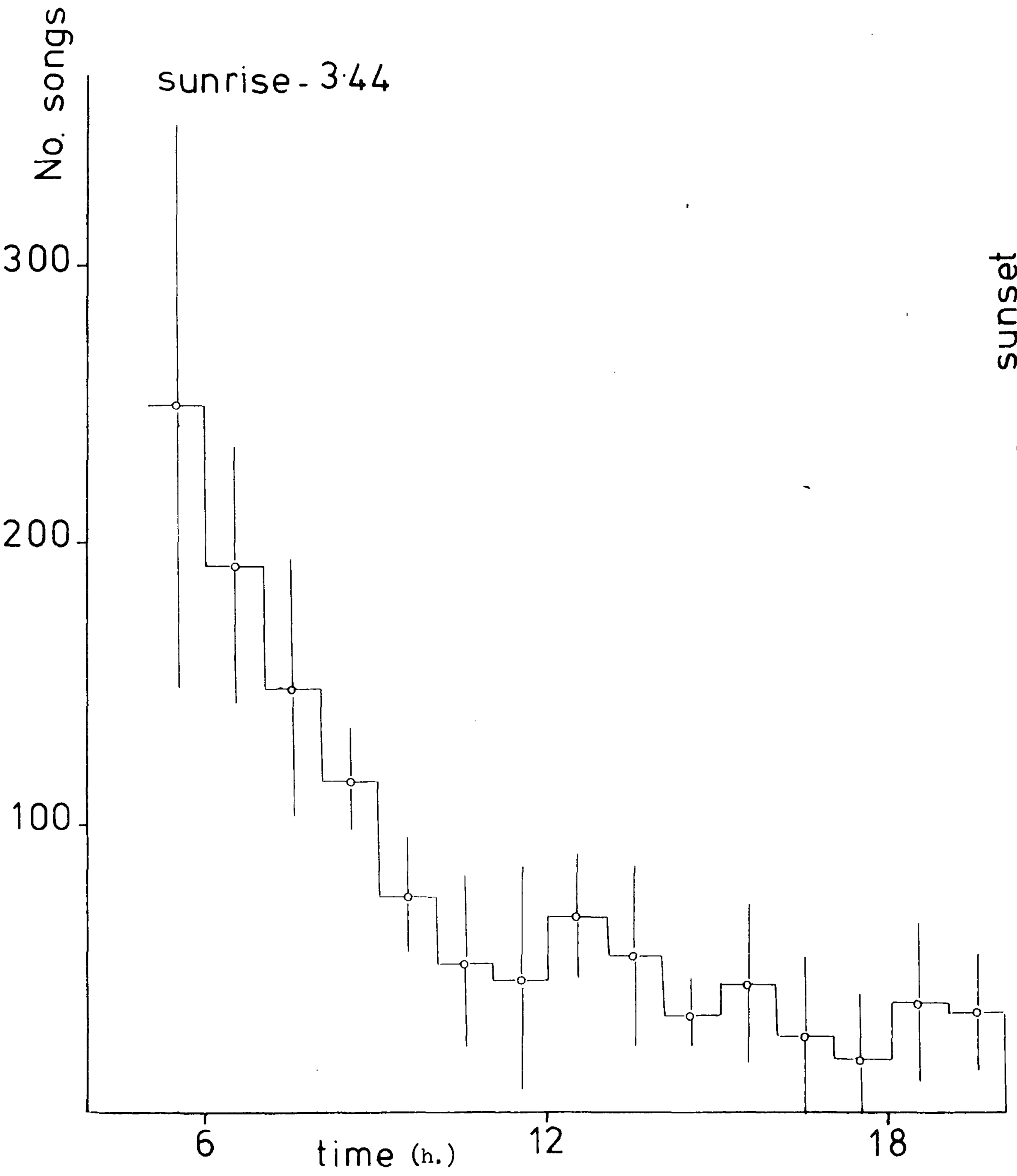
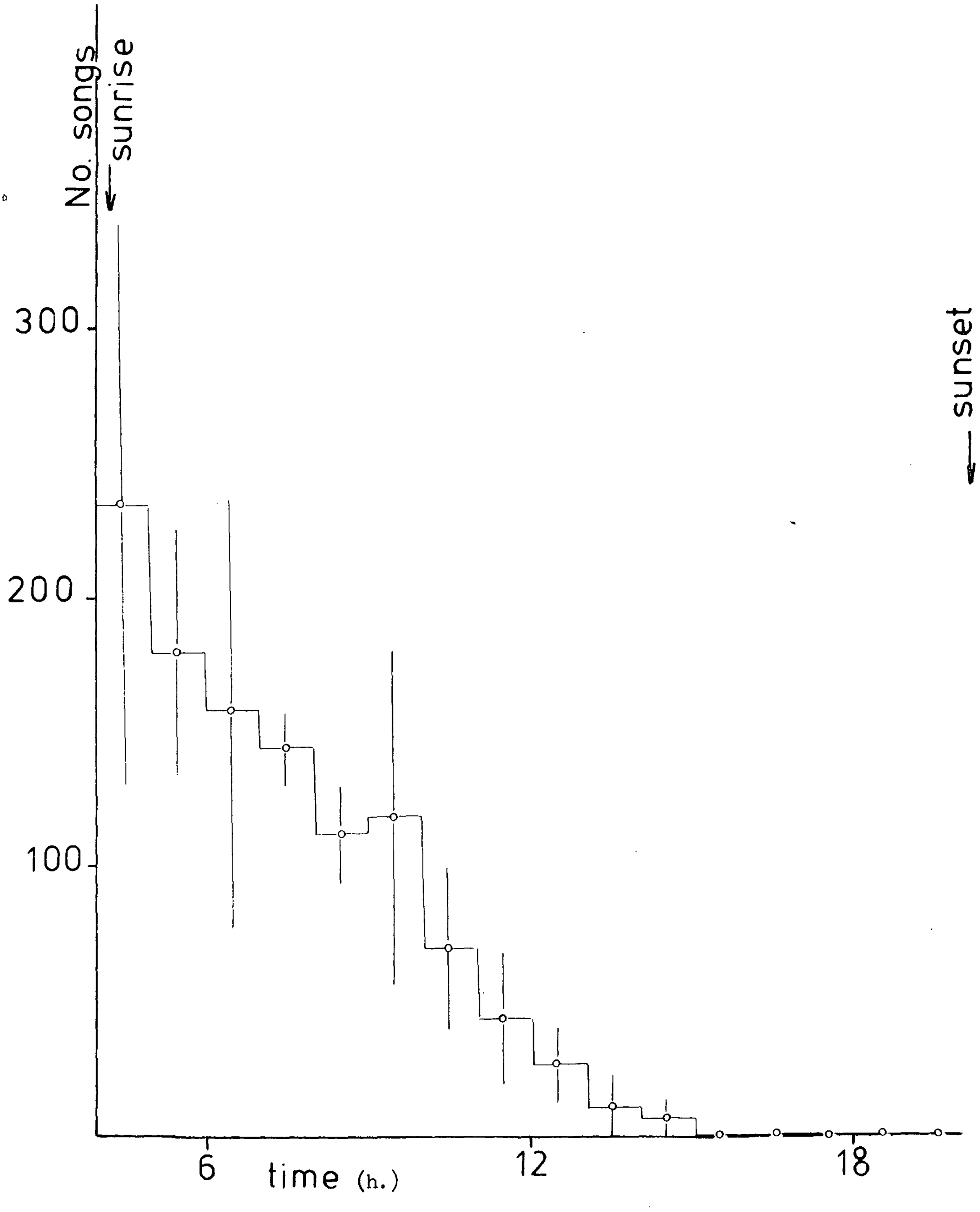


FIG. 19

Number of songs per hour –
JULY 1976 – [mean ± 2 SE n = 3]



(IIii) Results: Time allocation to singing, determined by the '1 minute spot observation method'

Three catagories of activity were timed; singing; foraging and flying. The time allocation to flying was minimal and uniform throughout the day (see Results (IIIvi)); the time allocated to singing was therefore related inversely to the time spent foraging.

The decrease in the time spent singing as the day progressed in June (Fig. 20) was not as evident when measured by this method as by the number of songs per hour (Fig. 18); the large 95% confidence limits somewhat obscure the trend. For example, there was no significant difference in song activity (when compared by a 2×2 contingency table including data for singing and non-singing activities) between 5.00-6.00h. and 8.00-9.00h. ($\chi^2 = 0.0137$ $p < 0.9$ degrees of freedom =1), but song activity decreased significantly between morning (6.00-7.00h.) and afternoon (16.00-17.00h.) ($\chi^2 = 35.09$ $p < 0.001$ degrees of freedom =1).

In July (Fig. 21) a highly significant decrease in song activity ($\chi^2 = 22.57$ $p < 0.001$ degrees of freedom =1) was evident between early morning (5.00-6.00h.) and midday (12.00-13.00h.).

Fig. 22 and 23, composite histograms of all activity that was measured, show the general trends of a steeper reduction in song activity in July than in June and an increase in foraging activity through the day in both months.

FIG. 20

JUNE- Singing as % of total activity (1 min. obs.)
[mean ± 2 SE n= no. of hours obs.]
sunrise 3. 44
sunset 20. 18

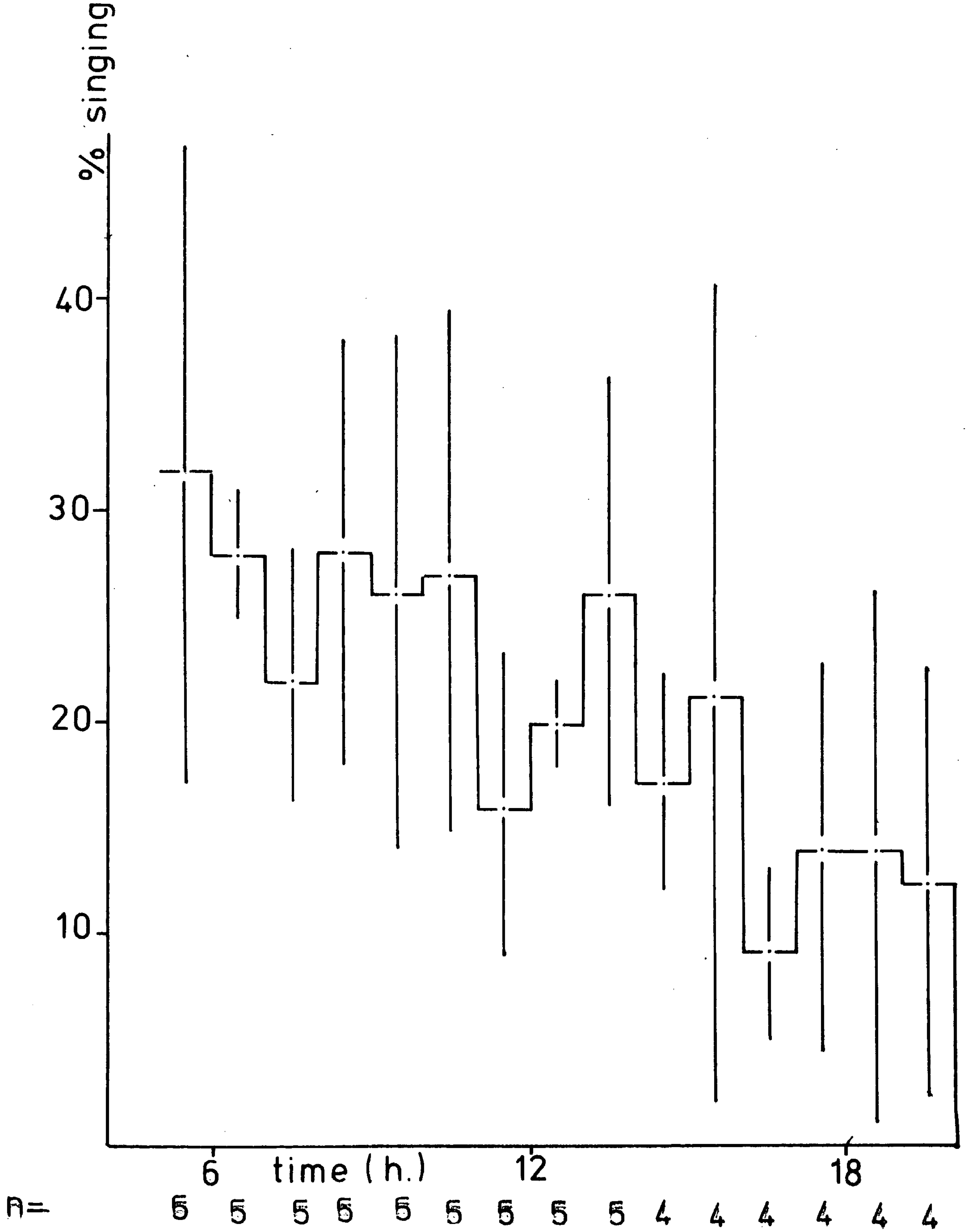


FIG. 21

JULY- Singing as % of total activity(1.min.obs

[mean ± 2SE n= no. of hours obs.]

sunrise 4.16

sunset 20.02

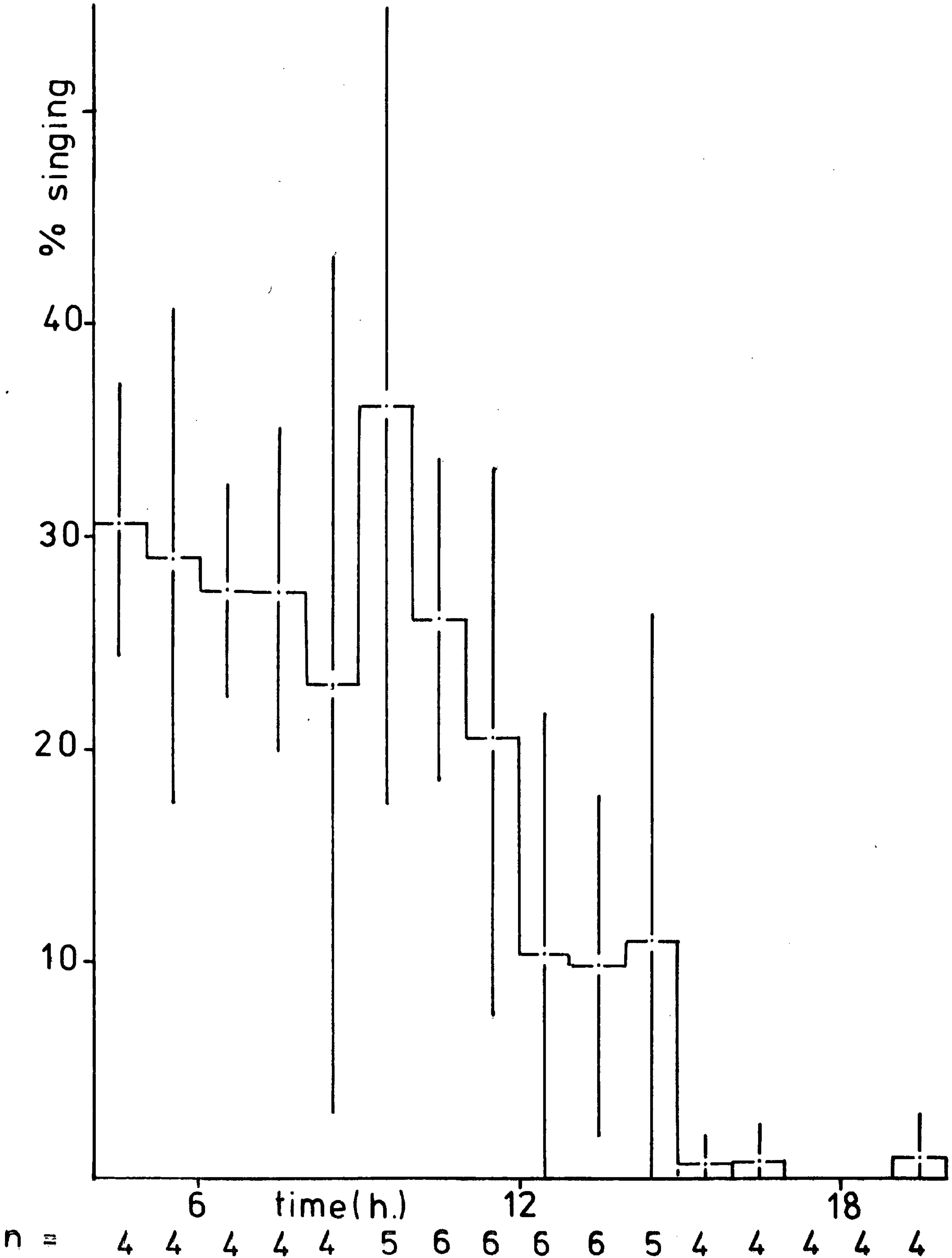


FIG. 22 Histogram of flying, singing and foraging activity measured by the '1 minute spot observation method' (JUNE)

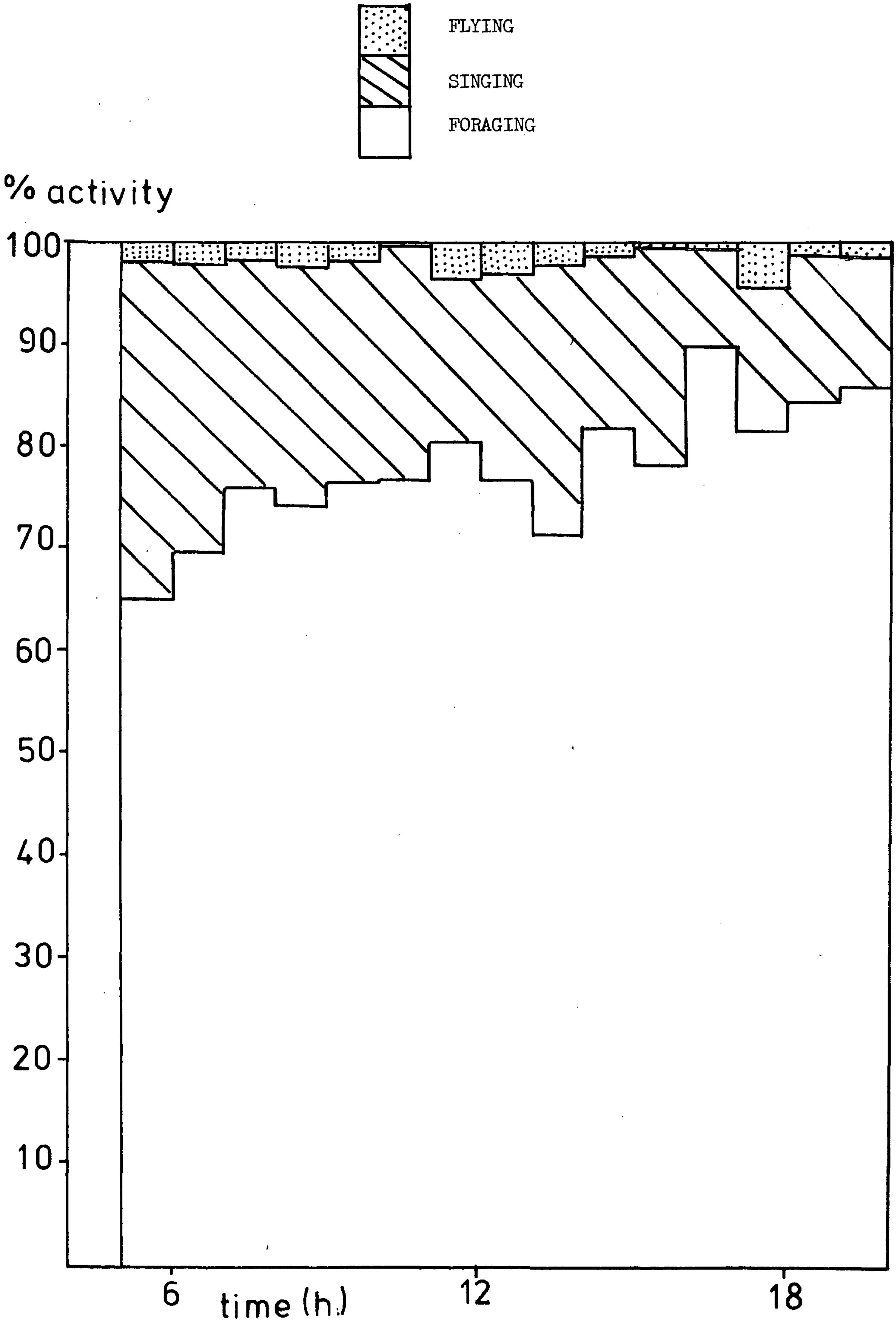
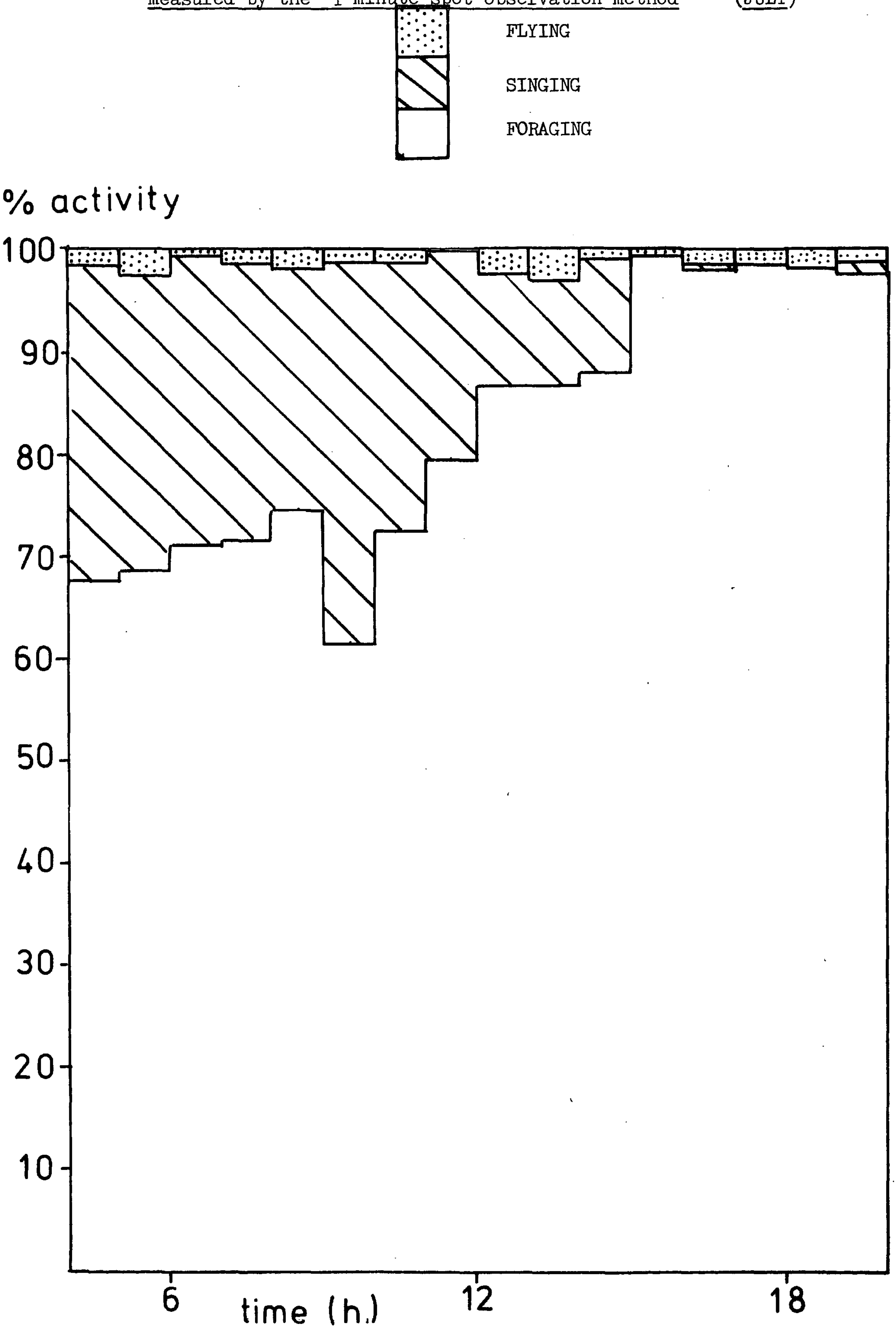


FIG. 23 Histogram of flying, singing and foraging activity measured by the '1 minute spot observation method' (JULY)



(IIiii) Results: Heights of song posts

Male Wrens sang throughout the day from selected song posts, whose height was estimated to the nearest 1m. The data were grouped into four vertical sub-divisions; 0-1m. (ground cover zone); 1-2m. (bush zone); 2-4m. (lower tree zone); and above 4m. (middle tree zone and above). Fig.25-29 show the heights chosen during different 3h. periods of the day in June; and Fig.31-35 in July. Fig. 24 and 30 show the mean percentages, with 95% confidence limits, of song and foraging activity at the different heights.

Most songs were delivered from the 2-4m. zone in June (Fig.24). Little preference was given to the lowest zone (0-1m.) for song activity.

In July most songs were delivered from either the 1-2m. or 2-4m. zones (Fig. 30). Preference was shown for singing from the 2-4m. zone in the morning (Fig.31 and 32) but from the 1-2m. zone later in the day (Fig. 34 and 35). However, it must be stressed that most songs were produced in the morning during July, and that very little singing activity took place after 15.00h.

Comparisons between the use of the zones for singing activity were made by 'Student's' t-test between the means using the correction for small sample size. The results of the comparisons are summarised in Tables 5 and 6.

All the song post heights were measured above ground level. However, the ridges that cross the wood would assist the male Wren to gain song post height. For example, a song post at 10m. in the valley could be at the same height above sea level as a 1-2m. song post on the top of the ridge. This might have had an influence upon song post selection.

FIG. 24 Percentage of song and foraging activity at different heights above ground level from 5.00-20.00h. (JUNE)
(mean ± 2 SE where n=5)

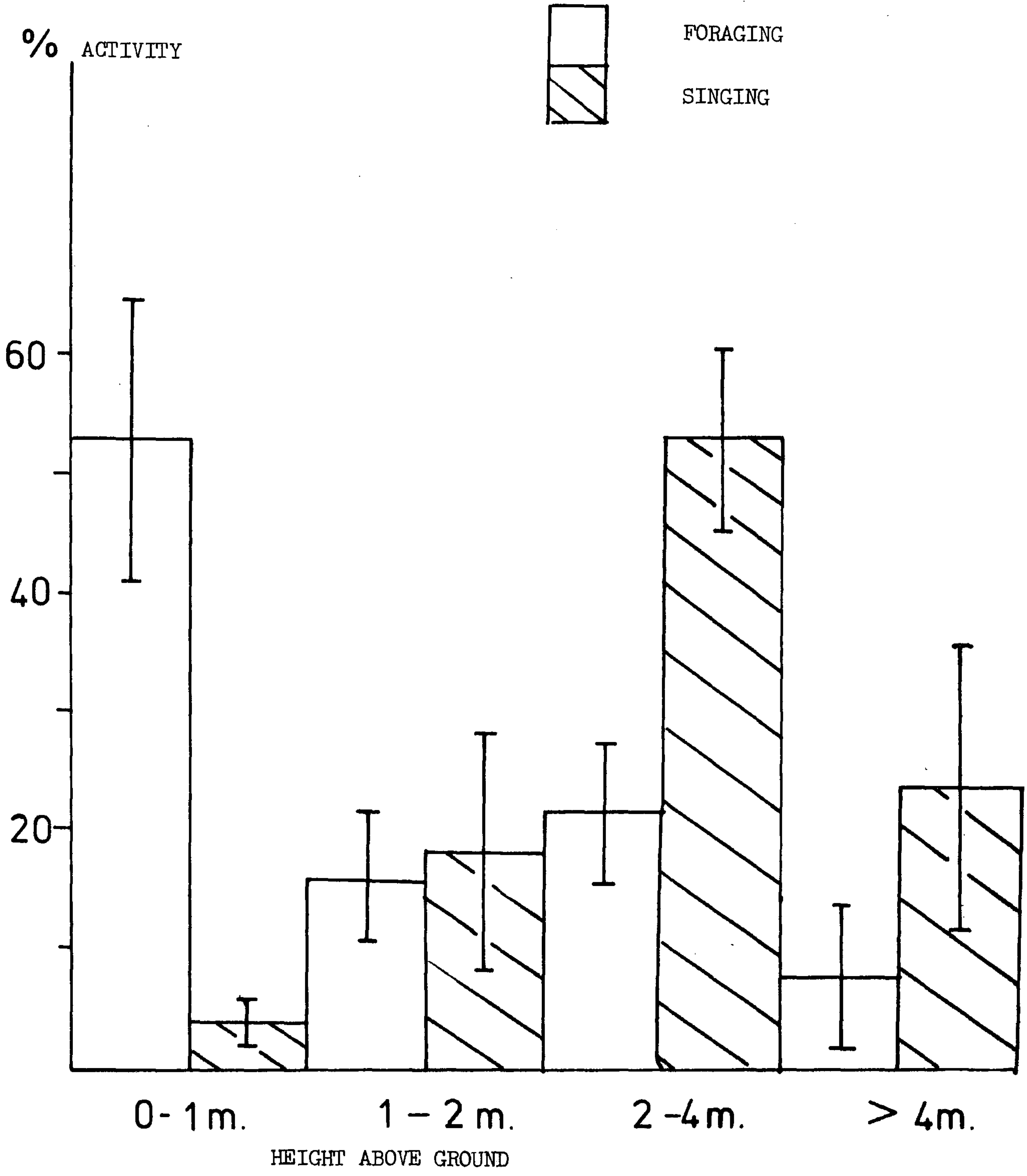
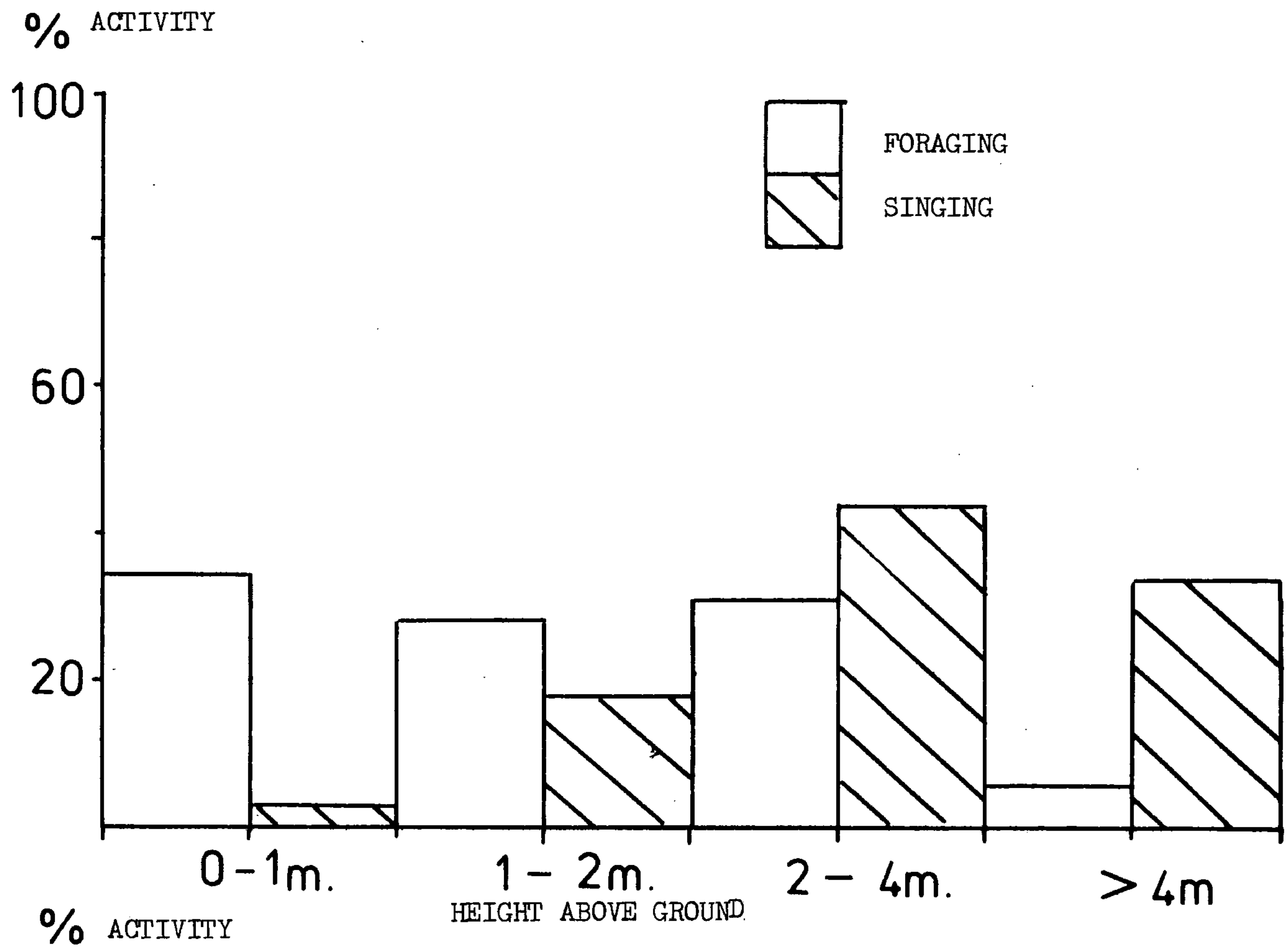


FIG. 25 Percentage of song and foraging activity at different height above ground level from 5.00-8.00h. (JUNE)



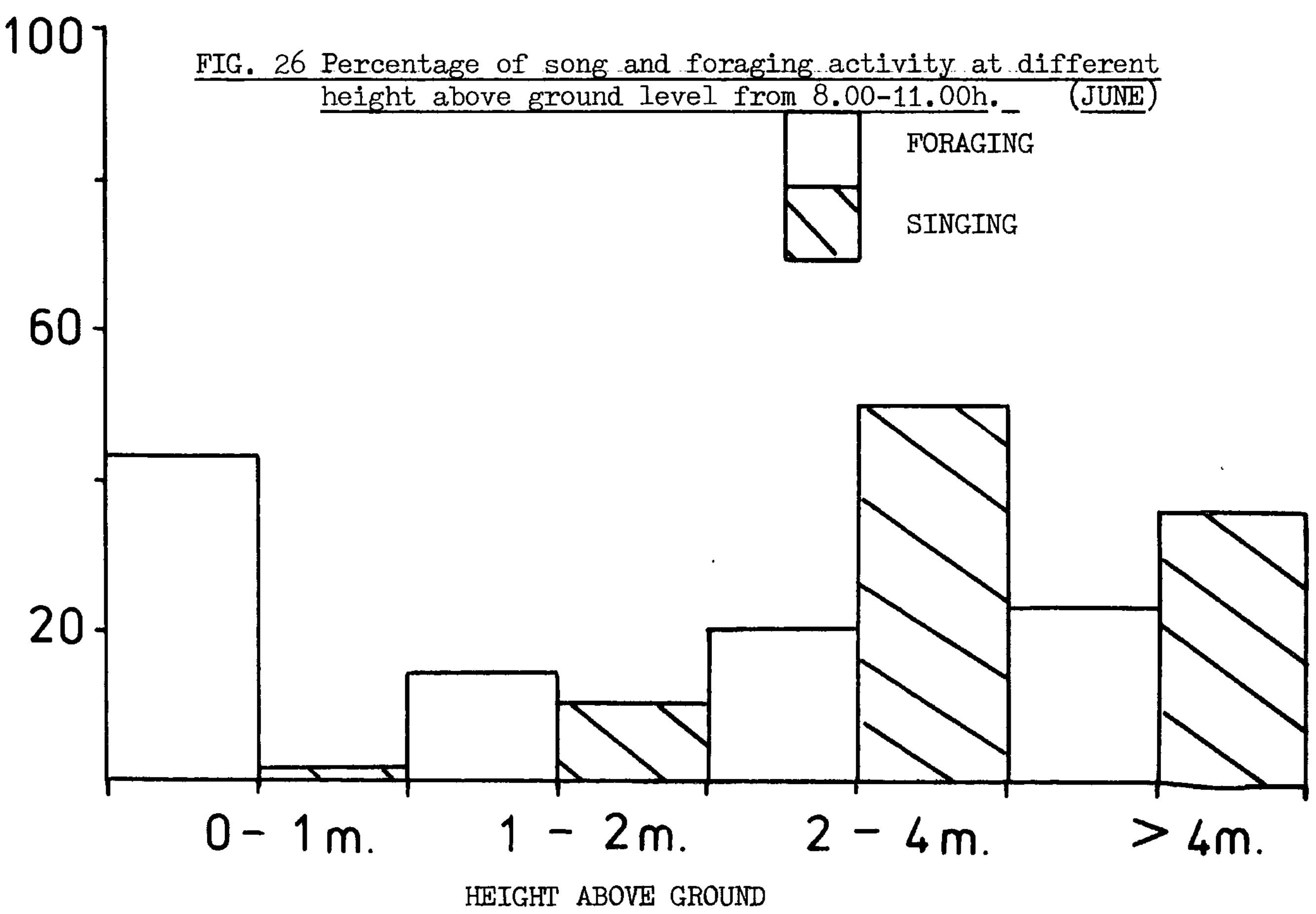


FIG. 26 Percentage of song and foraging activity at different height above ground level from 8.00-11.00h. (JUNE)

FIG 27 Percentage of song and foraging activity at different heights above ground level from 11.00-14.00h. (JUNE)

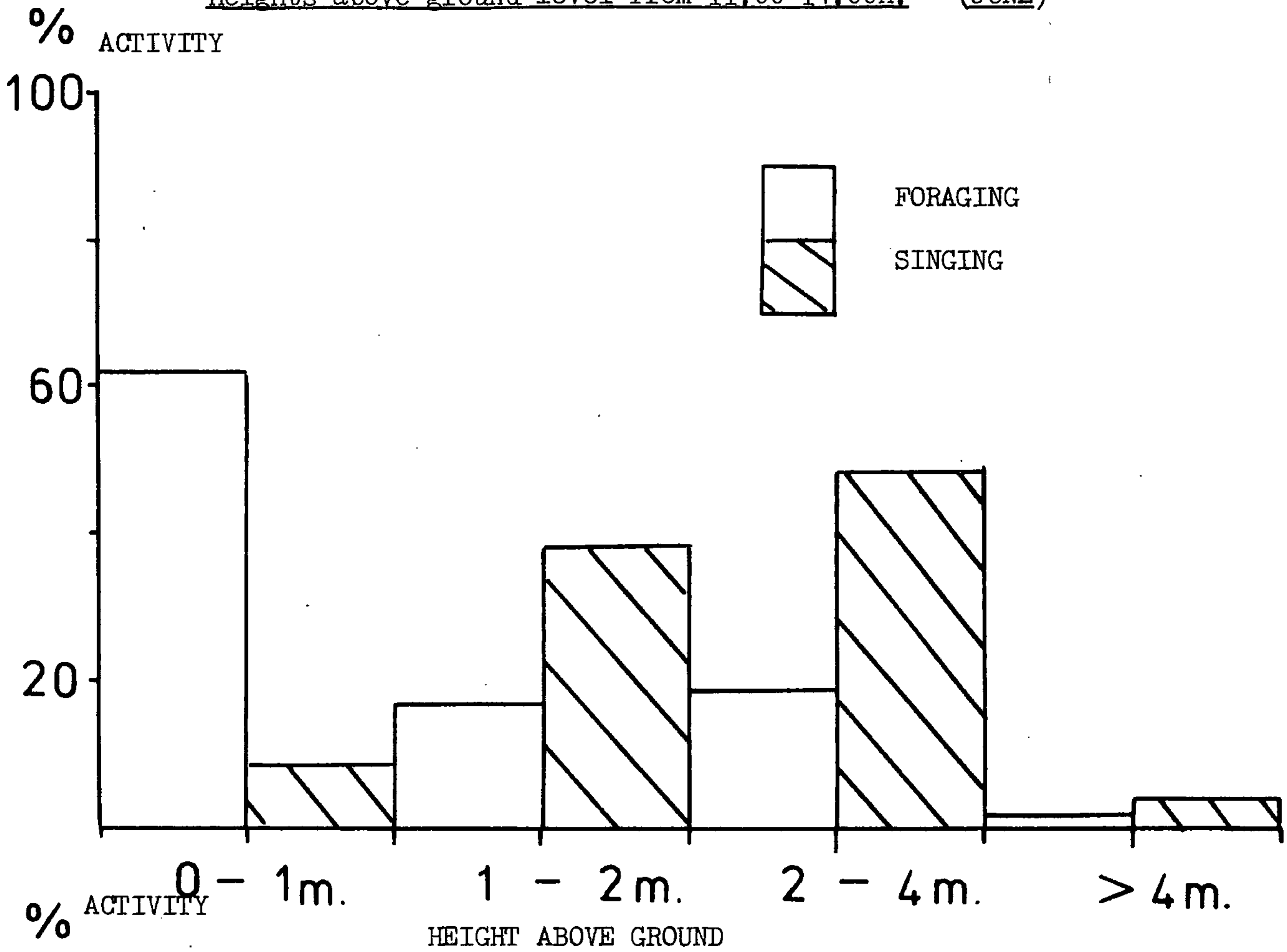


FIG. 28 Percentage of song and foraging activity at different heights above ground level 14.00-17.00h (JUNE)

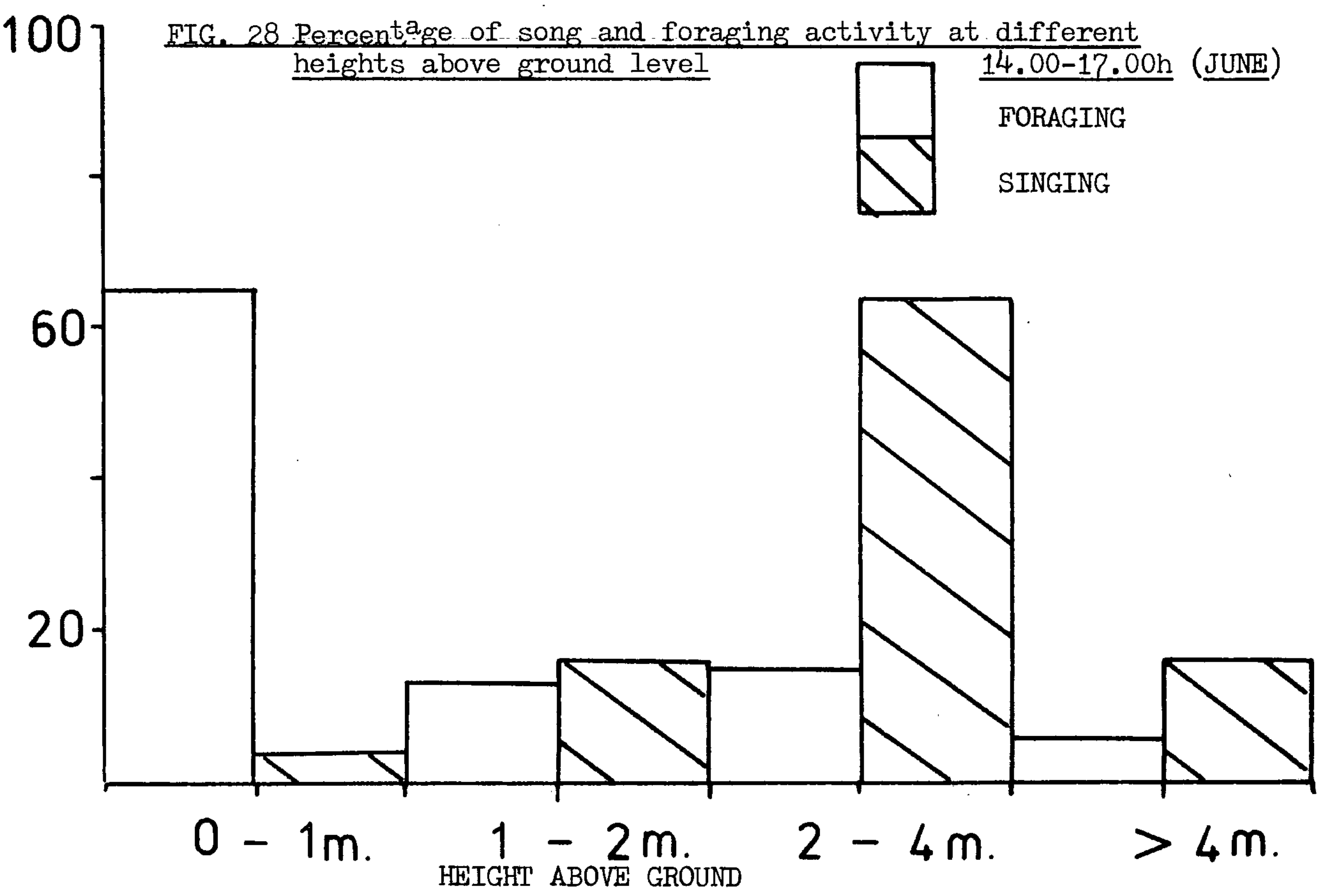


FIG. 29 Percentage of song and foraging activity at different heights above ground level from 17.00-20.00h. (JUNE)

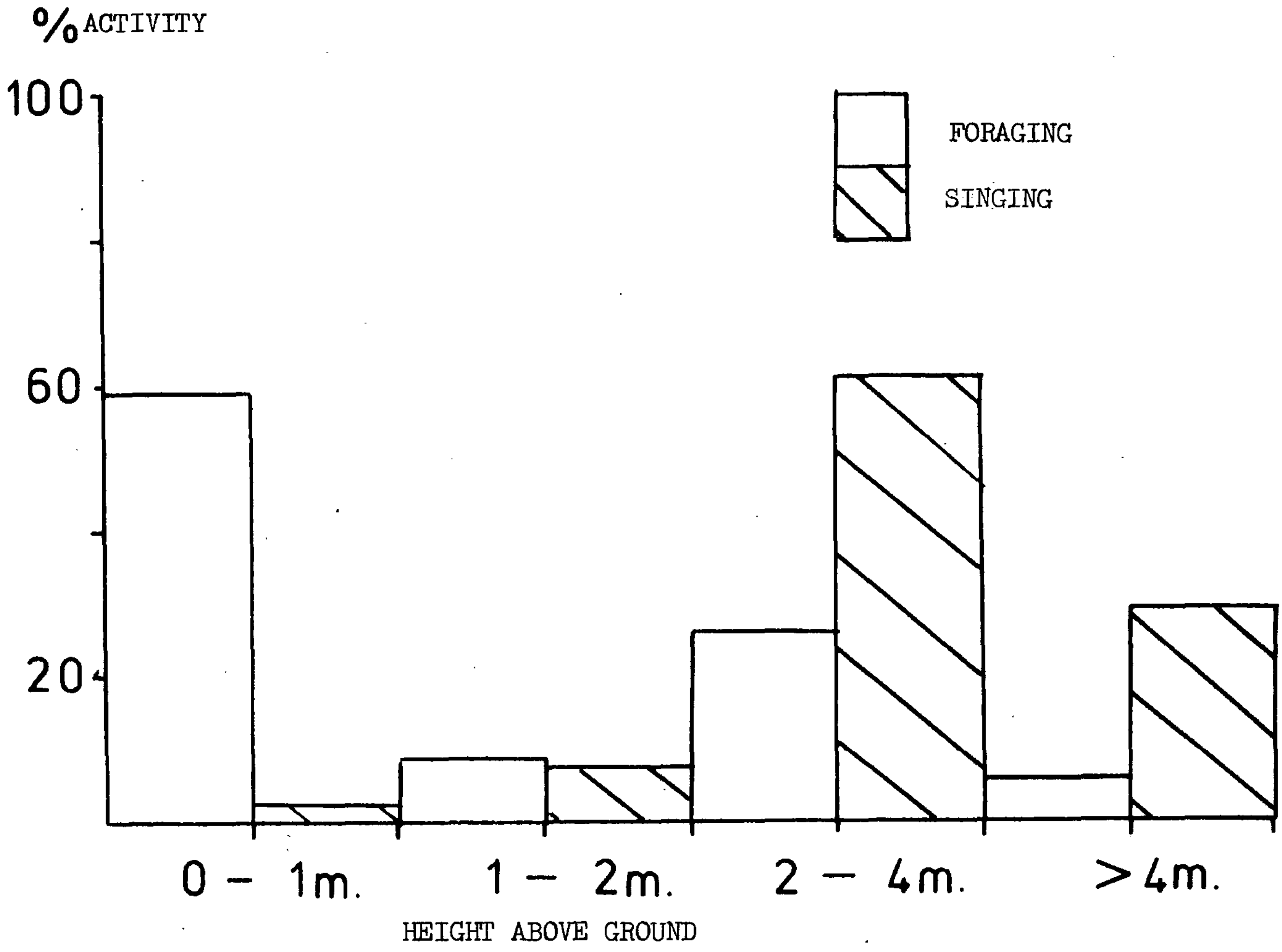


FIG. 30 Percentage of song and foraging activity at different heights above ground level from 5.00-20.00h. (JULY)

(mean ± 2SE where n=5)

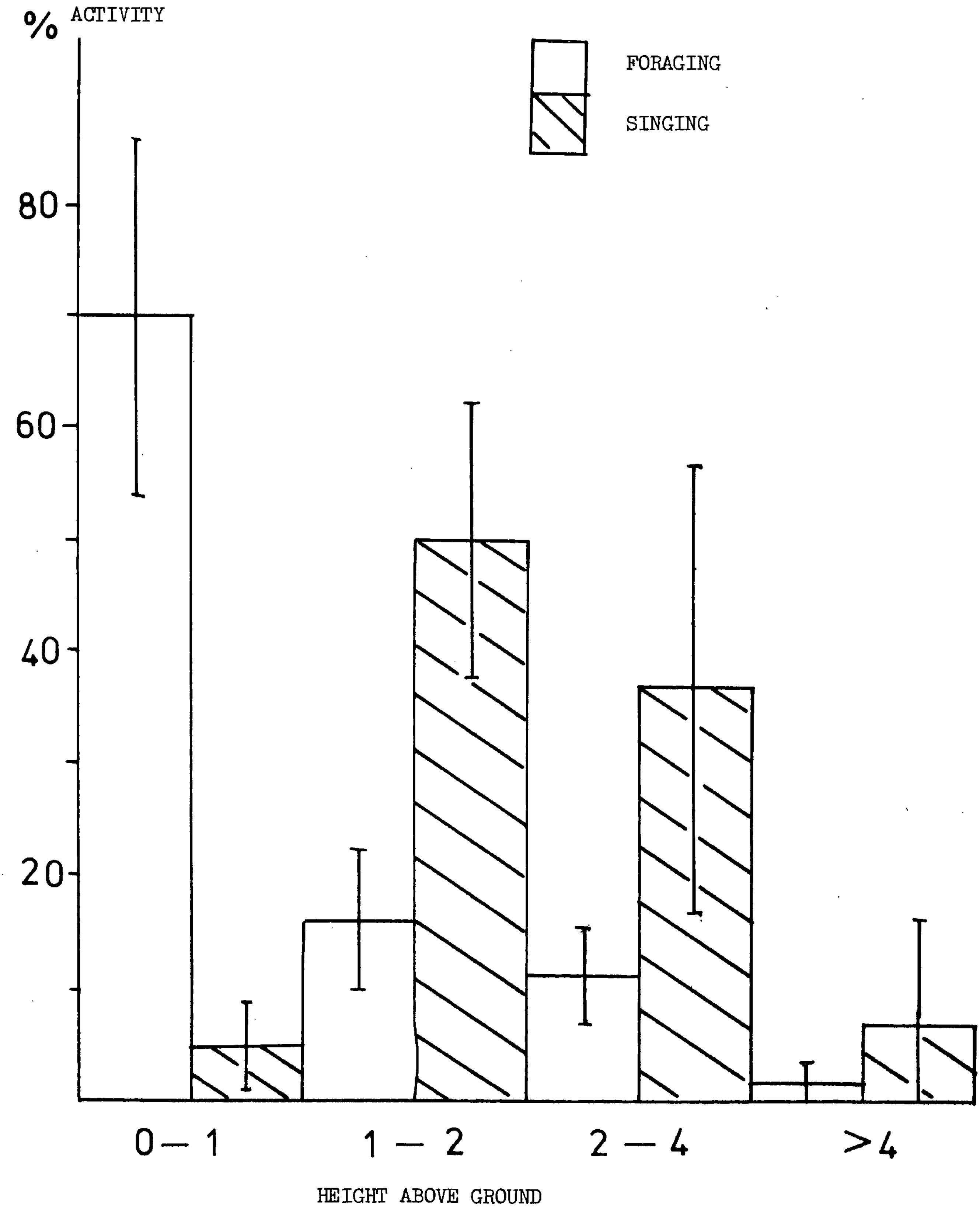


FIG. 31 Percentage of song and foraging activity at different heights above ground level from 5.00-8.00h. (JULY)

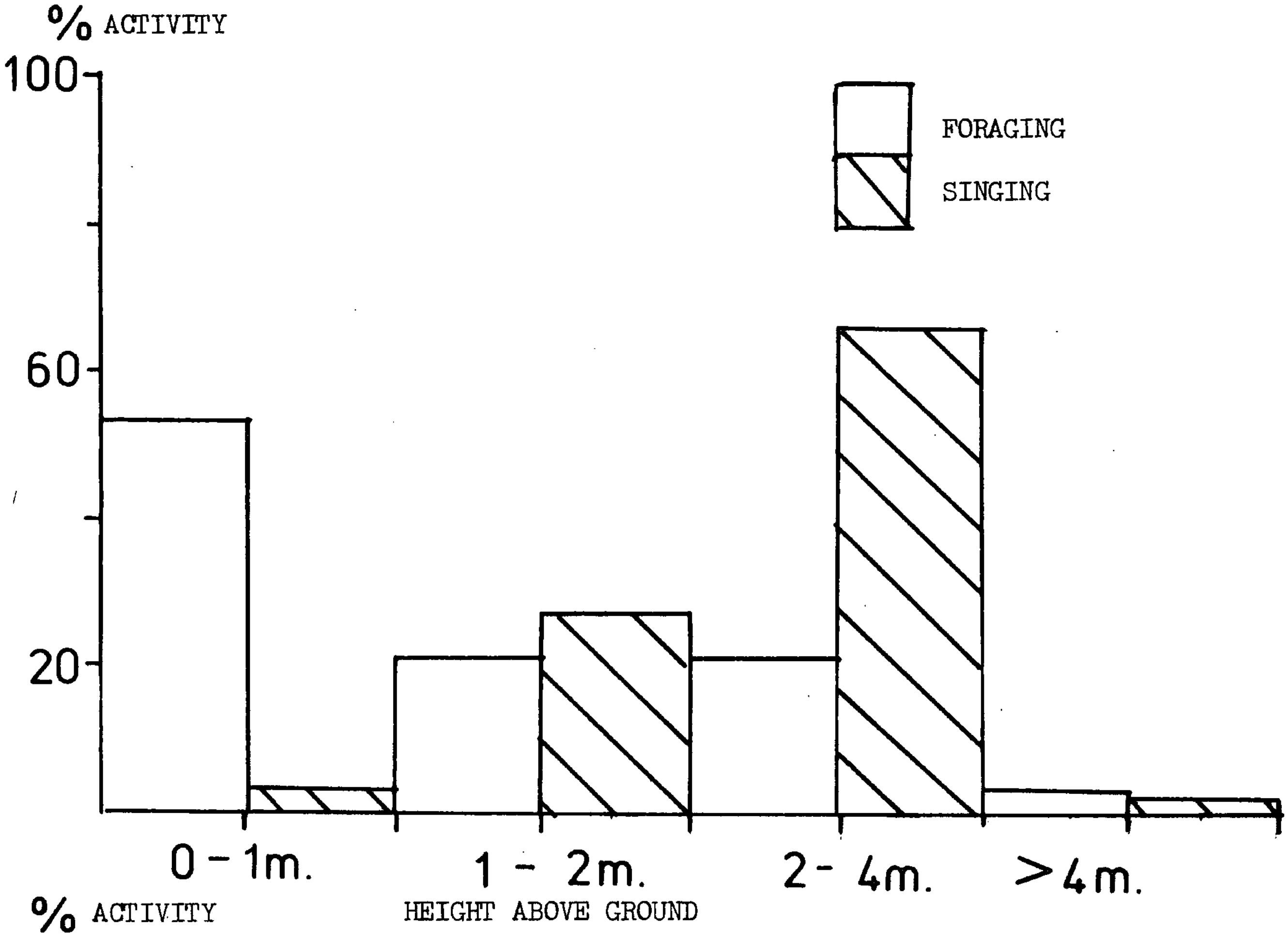


FIG. 32 Percentage of song and foraging activity at different heights above ground level from 8.00-11.00h. (JULY)

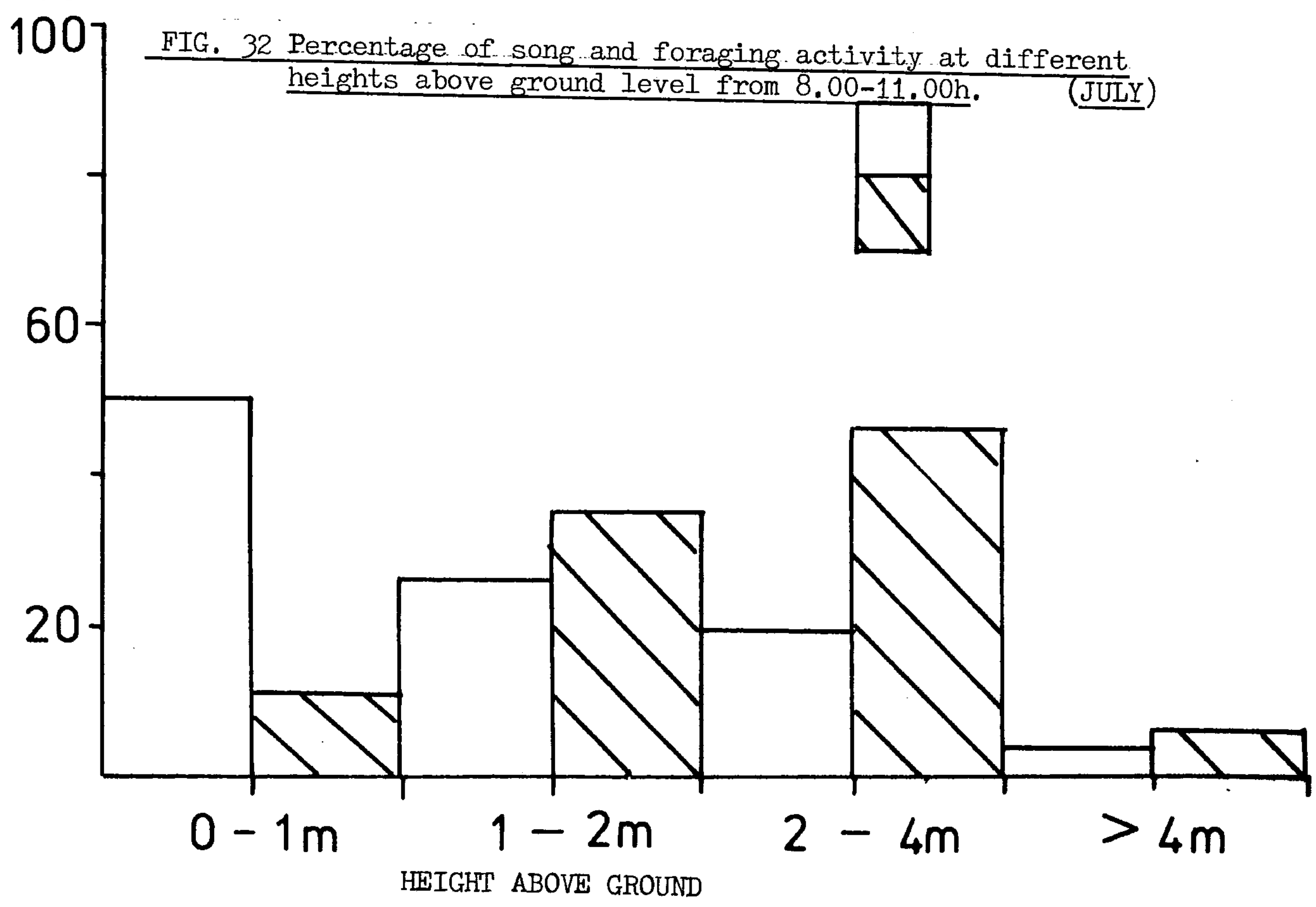


FIG. 33 Percentage of song and foraging activity at different heights above ground level from 11.00-14.00h. (JULY)

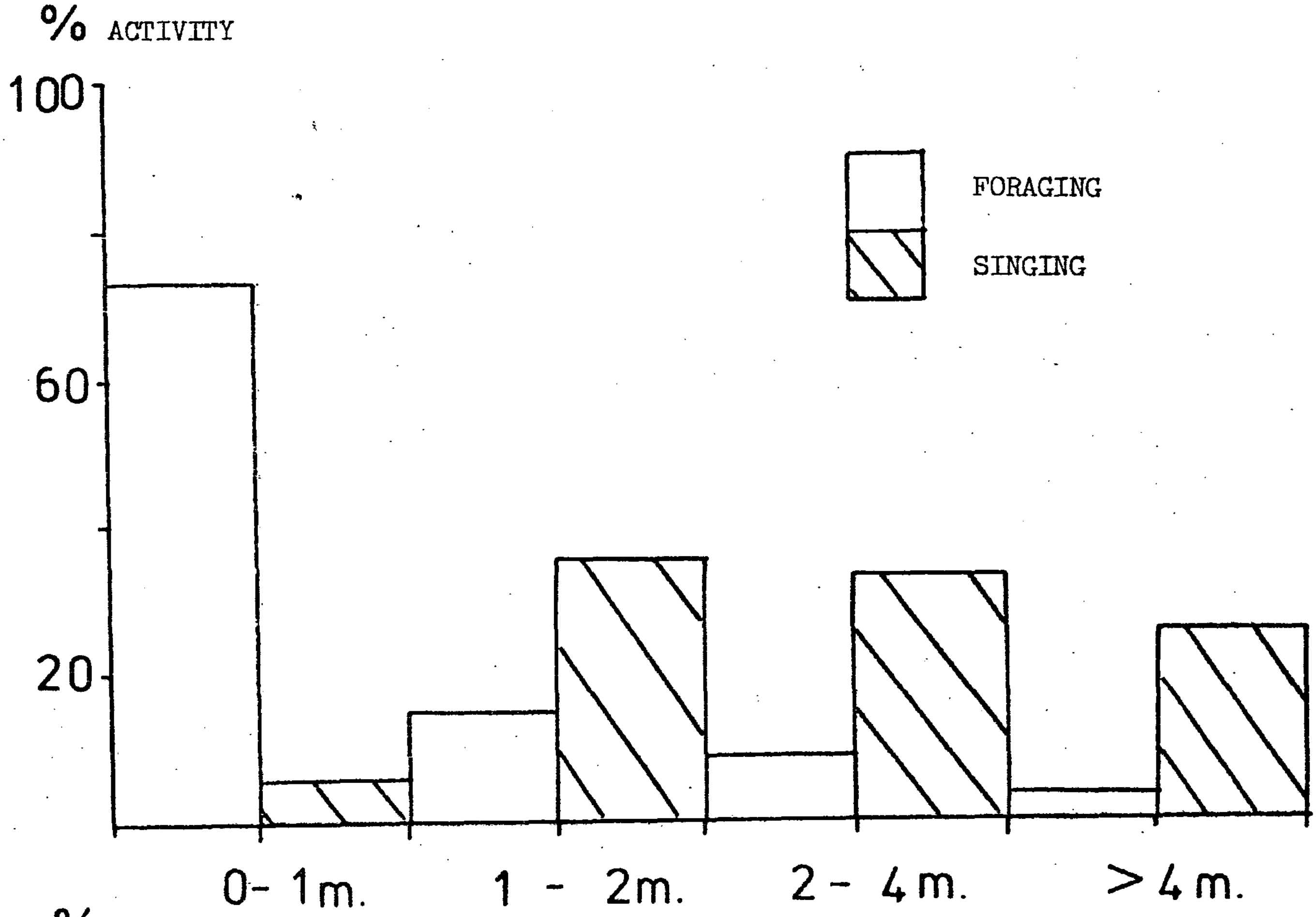


FIG. 34 Percentage of song and foraging activity at different heights above ground level from 14.00-17.00h. (JULY)

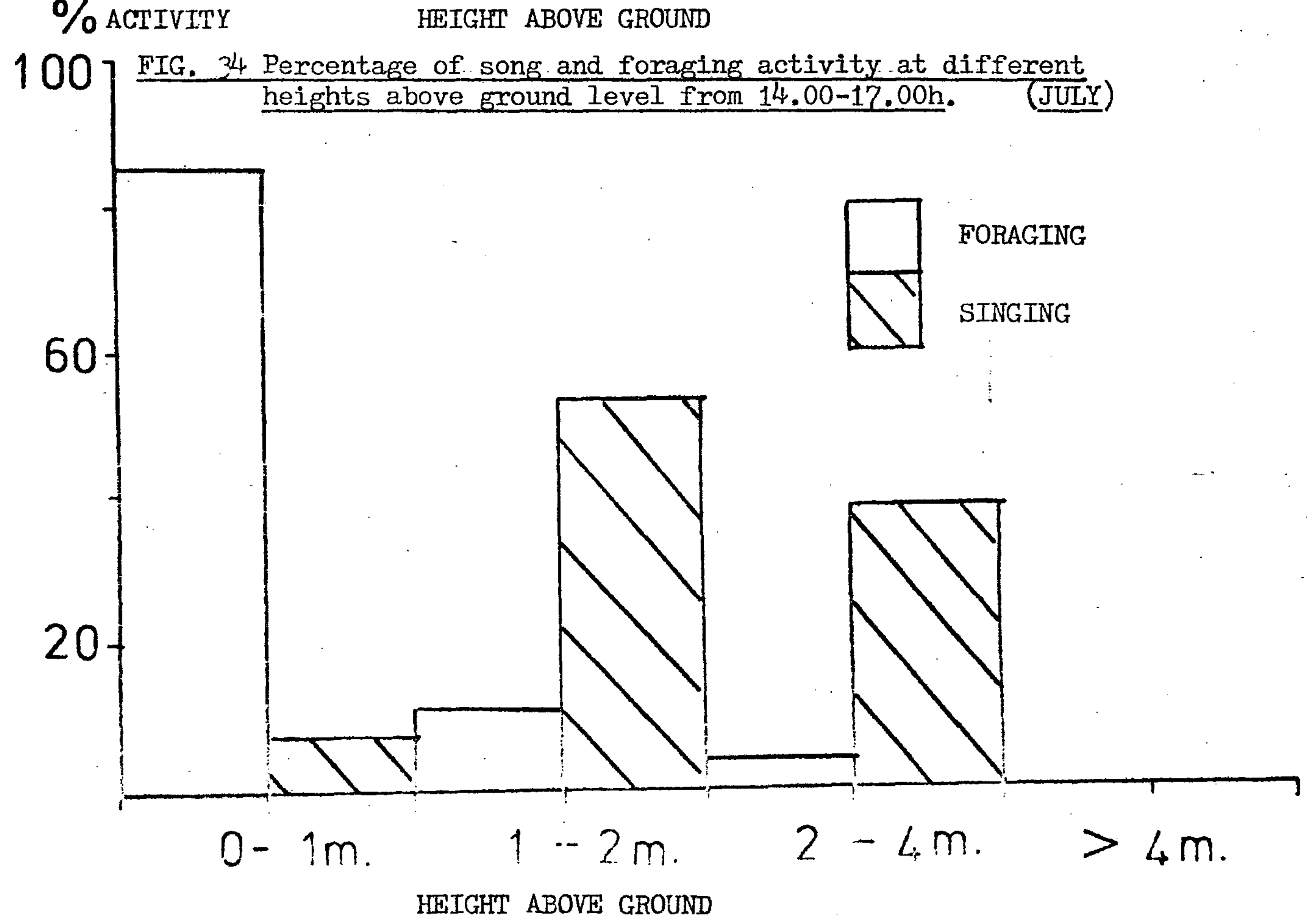


FIG. 35 Perecentage of song and foraging activity at different heights above ground level from 17.00-20.00h. (JULY)

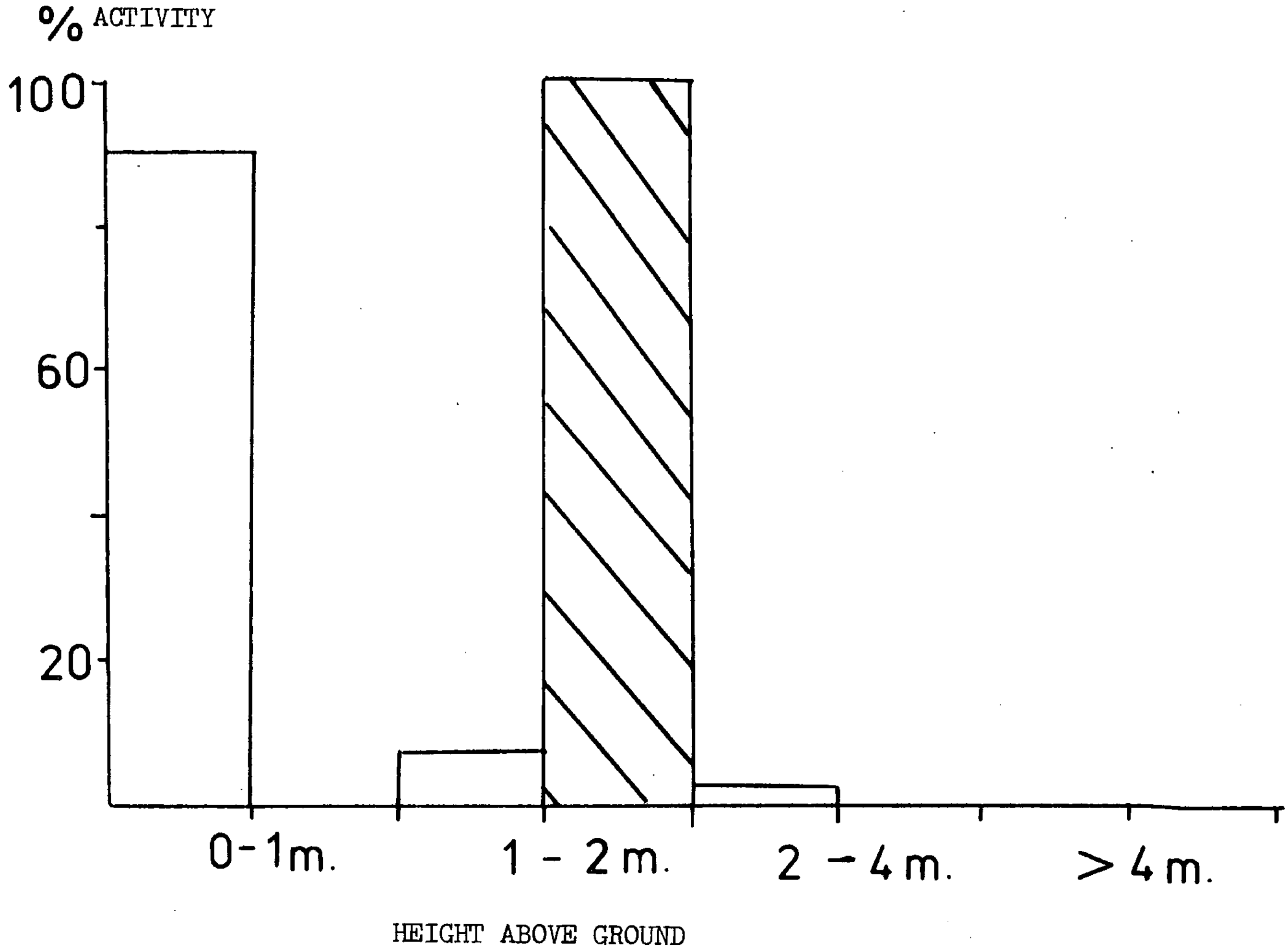


Table 5

Comparison between different heights of song post by 'Student's' t-test with the correction for small sample size.

Degrees of freedom=8

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

June	t values			
0-1m.	-			
1-2m.	2.429*			
2-4m.	12.0***	5.32***		
+4m.	3.126*	0.719	4.1**	—
	0-1m.	1-2m.	2-4m.	+4m.

Table 6

Comparison between different heights of song post by 'Student's' t-test with the correction for small sample size.

Degrees of freedom=8

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

July	t values			
0-1m.	-			
1-2m.	3.38**			
2-4m.	2.837*	0.79		
+4m.	0.0003	3.1*	2.49*	—
	0-1m.	1-2m.	2-4m.	+4m.

(IIiv) Results: Patrolling behaviour

Preferences for certain song posts were measured by studying the patrolling behaviour of the male Wrens. The number of song posts per territory; and the number of songs per post were counted. The number of songs per post is presented as a percentage of the total number of songs produced whilst the bird was observed during July, for a limited time period only (Table 7). The use of song posts in each territory is ranked from highest to lowest amount of use (Table 7).

The larger the territory the more song posts were used. For example, male m2 had a territory in July of 0.58ha. and used only four song posts: male m3 had a territory of 0.78ha. in July and used five song posts; male m7 had a territory of 1.59ha. in July and used ten song posts. When male m3 was removed from its territory male m2 increased its territory size substantially, and by using both the song posts that male m3 had used and those of its original territory increased the number of song posts that it used.

Different numbers of songs were broadcast from each song post; a greater variation in use was observed. Where conflict over territorial boundaries was more likely, or where the boundaries were close or overlapping, the use of the closest song post to the boundary increased. For example, male m1 and m7 sang antiphonally (each broadcast of song by one Wren was returned by another-a song conflict situation) from song posts 24 and 34 respectively (see Fig. 37). Probably as a result male m1 sang 54.8% of its songs from song post 24 and male m7 26.2% of its songs from song post 34. However, the large number of songs broadcast from post 24 by male m1 might have been because this was the only border close to another Wren's territorial boundary. Thus it was able to spend longer at that particular song post, since defence of other parts of its territory was unecessary.

Song posts near nest sites were also favoured. For example, 18.6% of the songs produced by male m8 were from song post 46, which was close to nest site (t) (see Fig.38), 54.8% of songs produced by male m2 were from song post 2 (see Fig. 36) close to nest site (a) (see Fig. 38), and 34% of the songs produced by male m13 were from song post 53 close to nest site (u).

The position of the song posts corresponded approximately with the territorial boundaries. The territories expanded and new song posts close to the new territorial boundary were selected. The song posts of the previous smaller territory were then utilised less except where the same boundary (i.e. beside an open field) was kept, or advertisement of an unused nest site was maintained.

Table 7

The percentage of songs produced from each particular song post within some of the male Wren territories.

Number in brackets (0) is the rank of the song post

Male m1 n=629 songs

Song Post	18	4.6%	(7)
	19	3.0%	(8)
	20	5.1%	(6)
	21	5.4%	(5)
	22	10.5%	(2)
	23	8.9%	(3)
	24	54.8%	(1)
	25	1.6%	(9)
	26	6.0%	(4)

Male m2 n=126 songs

Song Post	1	1.6%	(4)
	2	54.8%	(1)
	3	38.0%	(2)
	4	5.6%	(3)

Male m3 n=295 songs

Song Post	13	3.1%	(5)
	14	21.4%	(2)
	15	8.1%	(4)
	16	49.2%	(1)
	17	18.3%	(3)

Male m4 n=114 songs

Song Post	5	2.6%	(7)
	6	35.1%	(1)
	7	1.8%	(8)
	8	17.5%	(2)
	9	5.3%	(6)
	10	11.4%	(4)
	11	9.7%	(5)
	12	16.7%	(3)

Male m8 n=458 songs

Song Post	36	15.3%	(4)
	37	7.9%	(6)
	38	17.9%	(2)
	39	15.5%	(3)
	40	1.3%	(9)
	41	0.4%	(11)
	42	11.8%	(5)
	43	7.6%	(7)
	44	2.4%	(8)
	45	1.3%	(9)
	46	18.6%	(1)

Male m7 n=141 songs

Song Post	26	7.8%	(4)
	27	2.1%	(9)
	28	2.8%	(8)
	29	7.8%	(4)
	30	7.1%	(6)
	31	19.9%	(2)
	32	17.7%	(3)
	33	7.1%	(6)
	34	26.2%	(1)
	35	1.4%	(10)

Male m13 n=259

Song Post	47	8.1%	(4)
	48	7.0%	(5)
	49	5.0%	(6)
	50	26.3%	(2)
	51	0.8 %	(8)
	52	3.9%	(7)
	53	34.0%	(1)
	54	15.1%	(3)

FIG. 36 The position of song posts within the July territory for males m2; m3 and m4.

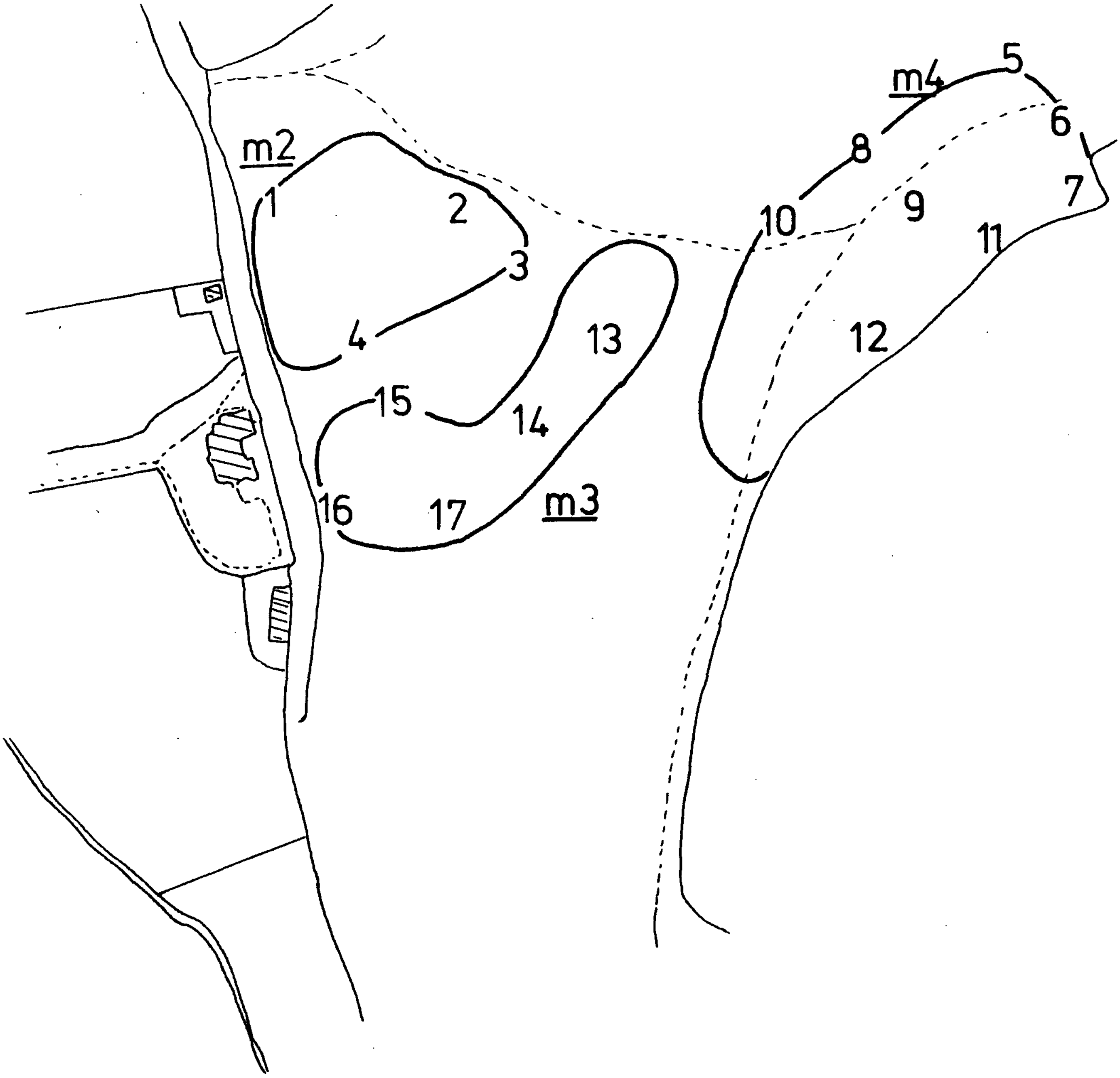


FIG. 37 The position of song posts within the July territories for males m1; m7; m8 and m13

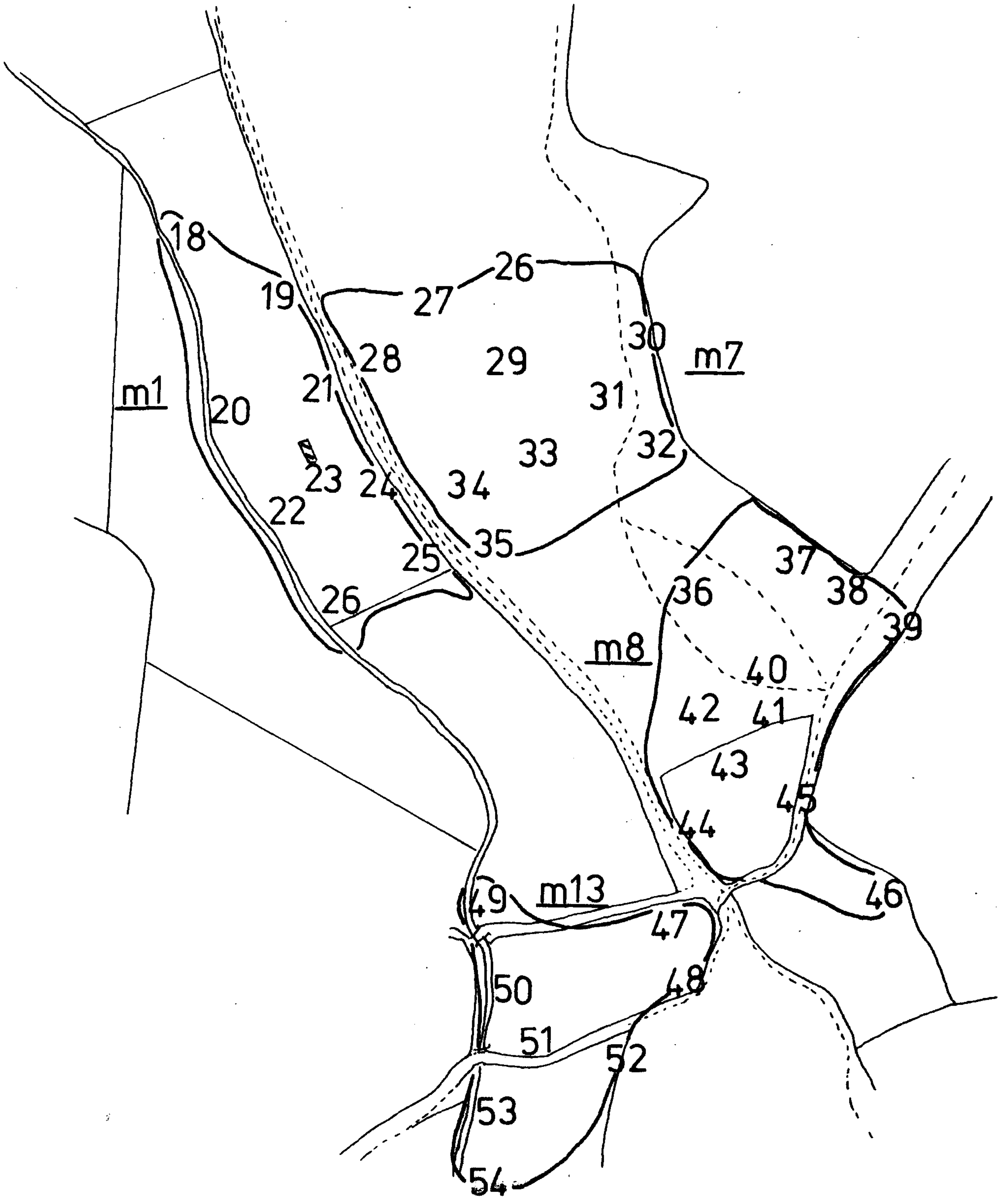
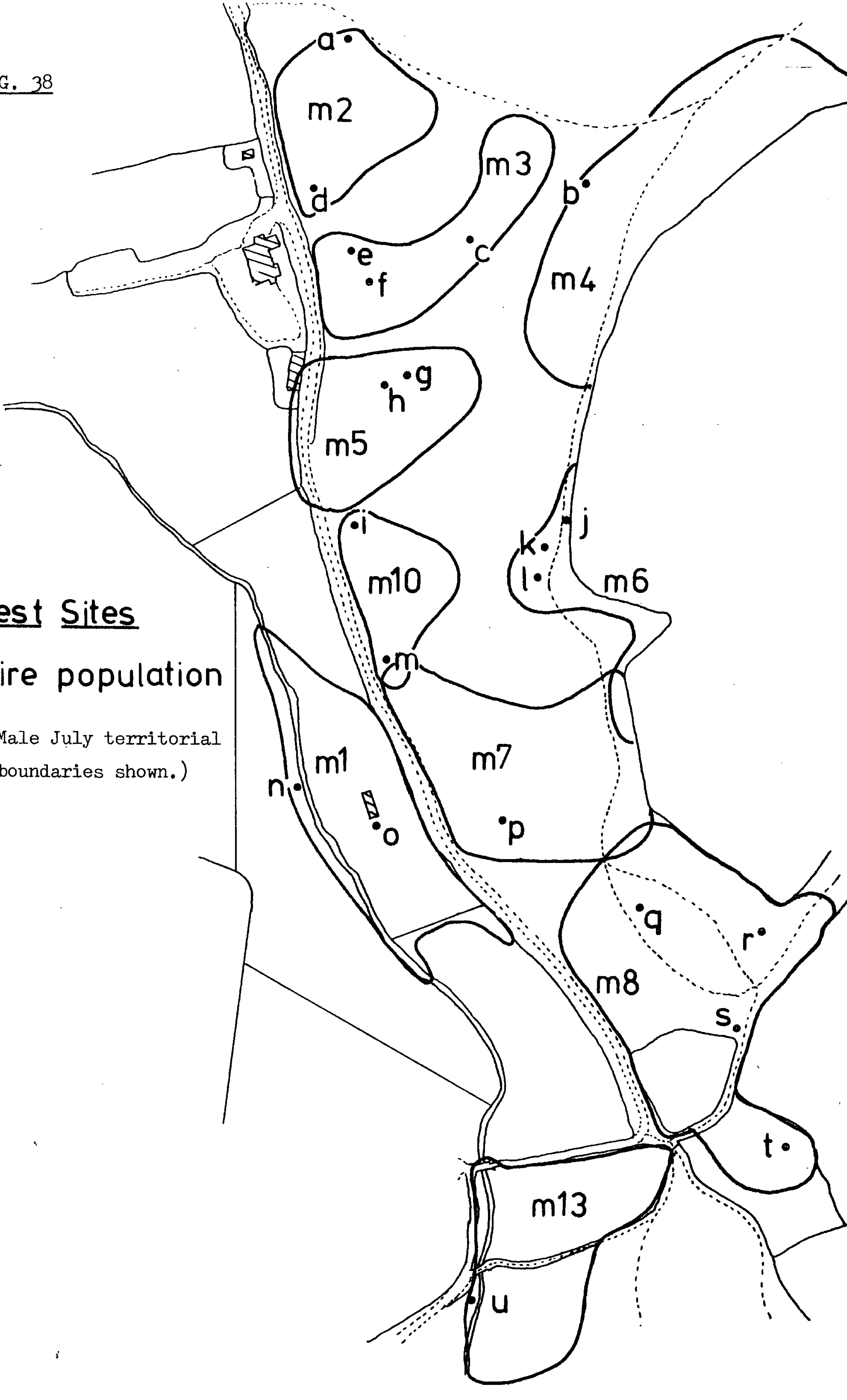


FIG. 38



Nest Sites

Entire population

(Male July territorial boundaries shown.)

(II) DISCUSSION

(II) Discussion

The 'purpose' of song by a male bird is to advertise its presence to other birds of the same species. The functions of song indicated by Armstrong (1944) can be summarised as:

1. intimidation of another bird of the same sex to drive it from the territory.
2. attracting a female to a nest site.

To achieve these functions the song must be broadcast from the best vantage points within the territory as often as possible; but an increase in the time allocated to singing reduces the time available for foraging. Thus for the most effective use of time spent singing, song must be concentrated into one part of the day. In Wrens the early morning peak of production in song is used to re-establish territorial boundaries after the night when no singing, and therefore no defence of the territory takes place.

During May less time was spent singing than in June or July perhaps because more time was needed for foraging. However, even though the number of songs given per day was less than in June, a similar time pattern of song production each day was observed. Songs were broadcast throughout the day in May and June both to maintain the territorial boundaries and attract females to the nest sites. In July the abscence of songs after 15.00h. could be due to the necessity to spend more time foraging, possibly to build up food reserves to sustain the bird through the moult in August. Clarke (1949) found that Wrens spend little time singing during August. The concentration of the songs into the early part of the day in July might be related to the lessened need for female attraction at the end of the breeding season; or that the position of territorial boundaries had been learnt by the other male Wrens and that reinforcement throughout the day was therefore unecessary later in the season.

Colquhoun (1940a) established a relationship between the penetration of bird song and the size of its territory. For example, woodpeckers (Picidae spps.) are obliged to establish large territories because of their nesting and feeding habits and the maintenance of a large territory is possible because the song carries so far. The Redstart (Phoenicurus phoenicurus Linn.) has a song of low penetration, in that it will not carry very far, but a territory of approximately 0.4ha. (Buxton 1950) which it advertises by singing high in the vegetation and/or sings whilst flying. The Wren's loud song penetrates easily through the wood, and aids the establishment of a large territory.

To increase the penetration of the song through the wood higher song posts could be selected. The Wrens of Hollinside Wood selected a preferred song height of 2-4m. This height was above the dense ground vegetation zone (0-1m.). The effect of dense vegetation in preventing song penetration can be illustrated by the fact that antiphonal singing across the open field (a distance of 200m.) was common between male m11 and m6; m4; m7 and m3, but within the wood antiphonal singing rarely occurred unless the birds were much closer together.

The ridges between the valleys also had some effect in preventing the song carrying so far in the wood.

To assist the carrying power of the song over distances the male Wren holds its head back (see Plate 8) when singing, projecting the song upwards towards the canopy. Song posts with little foliage (Plate 1 and 8) were preferred to aid song penetration (dense foliage would detract from this) and perhaps make the Wren more conspicuous when posturing.

Song has a duel function, to repel males and to attract females, and song posts might be selected whereby both functions could be carried out from the same song post. However, an expansion of the territory required 'new' song posts to be selected. Nests would not be built in areas where conflict between males might result in the loss of part of the territory and with it a nest.However, building nests close to the boundary of the territory would ensure simultaneous attraction of females and defence of the boundary,from the same song post.

The larger the territory, the more effective use must be made of the limited number of songs. Either the number of songs per day must be increased (e.g.from May to June) or the time spent at each song post must be related to its function, namely male repulsion or female attraction or both. Song posts situated where the defence is unecessary because there is no Wren's territory close by and no suitable nesting site are used to a lesser extent (if at all) than song posts close to another males territory and/or near a nest site. The time spent singing cannot increase above a level which would effect the time available to forage.

(III) RESULTS

(III) Foraging activity.

General:

The diet of the Wren comprises chiefly of larvae of Lepidoptera (Geometridae and Noctuidae); Diptera (larvae of Tipulidae); Coleoptera (Sitona etc.); Trichoptera (larvae of caddis flies); Hemiptera (Aphididae); spiders and some seeds according to Witherby et al (1945). These foods are picked from leaf surfaces. In my studies aerial feeding was not observed and foraging often commenced at the base of the tree, branch or twig and continued up the stem. Particular attention was given to searching the abaxial leaf surface for insects.

(IIIi) Results: Time allocation to foraging; estimates by the '1 minute spot observation method'

As stated earlier because the percentage of time spent flying was uniform throughout the day, the time allocated to foraging was inversely related to the time spent singing. Thus the proportion of each hour spent foraging increased throughout the day (Fig. 39 and 40).

Comparisons between the proportions of each hour spent foraging at selected times were made by a 2×2 contingency table in which times spent foraging and not foraging in each hour were entered.

In June the percentage of time spent foraging increased significantly from 5.00-8.00h. to 14.00-17.00h. ($\chi^2 = 24.85$ $p < 0.001$ degrees of freedom =1).

During July days the proportion of time spent foraging increased rapidly; the increase between 5.00-8.00 and 14.00-17.00 ($\chi^2 = 124.8$ $p < 0.001$ degrees of freedom =1) was more highly significant than in June.

FIG. 39

JUNE-Foraging as % of total activity (1 min.ob
[mean ± 2 SE n= no. of hours obs.]
sunrise 3. 44
sunset 20.18

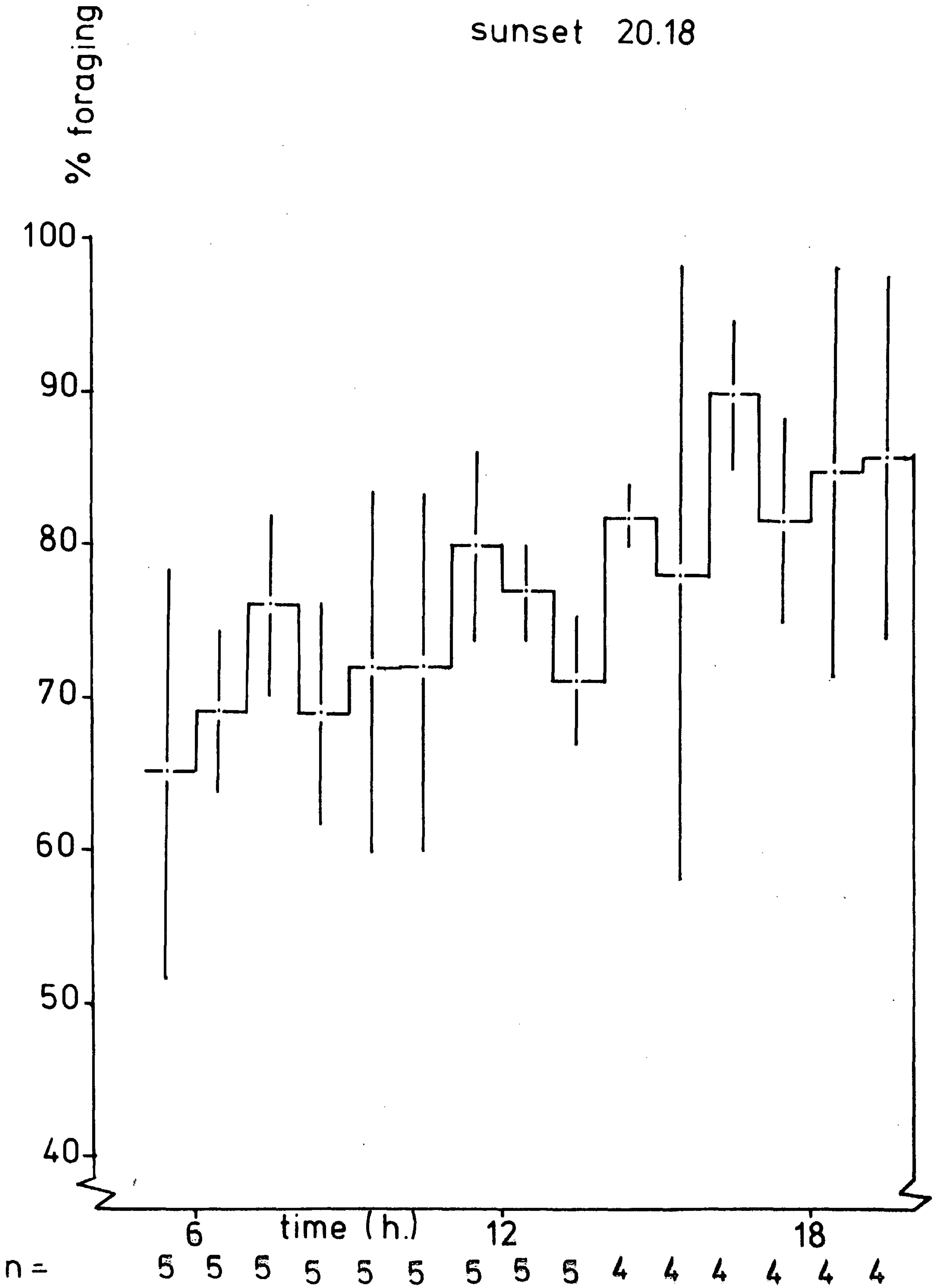
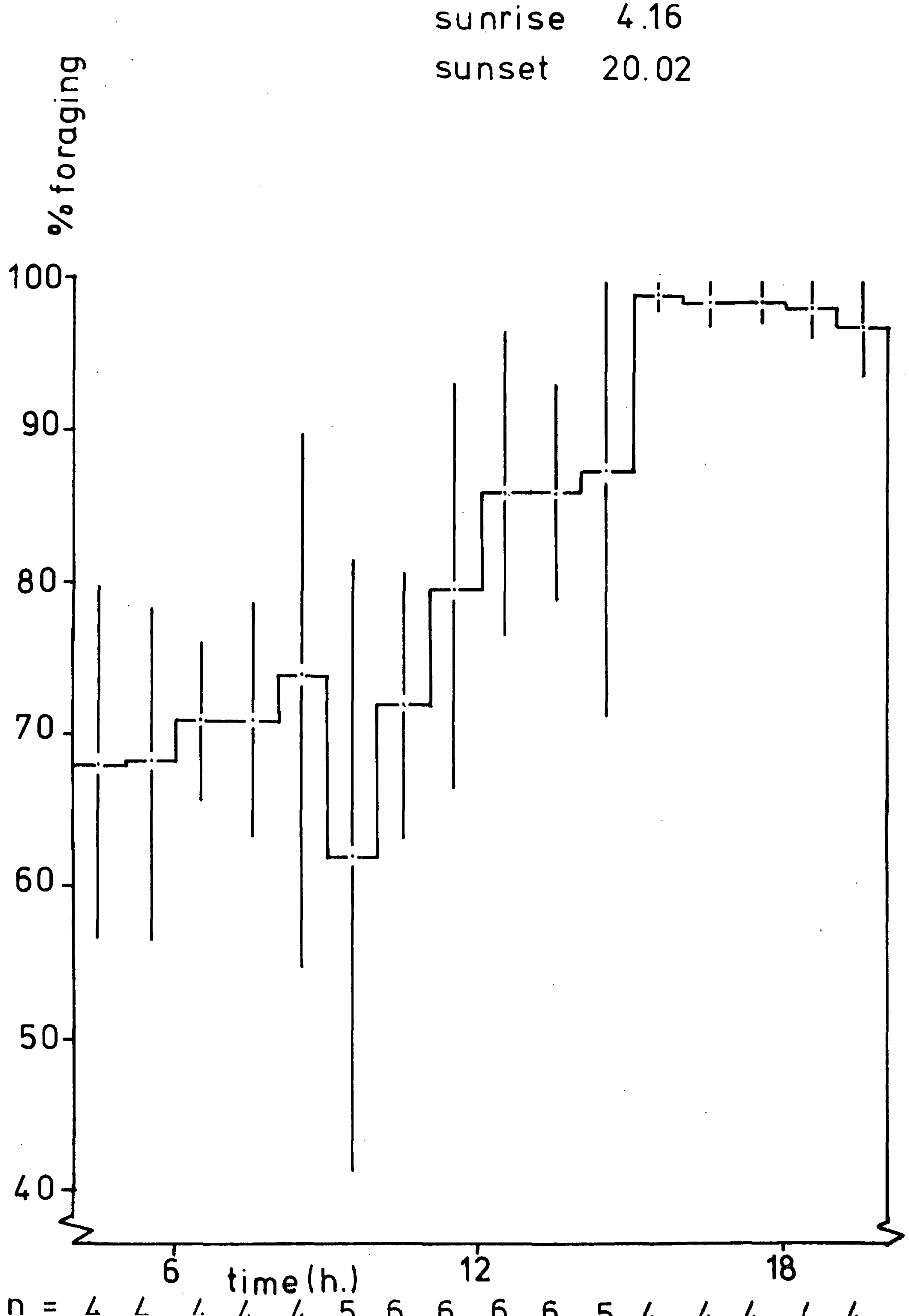


FIG. 40

JULY– Foraging as % of total activity (1.min.obs.)
[mean ± 2 SE n = no. of hours obs.]



(IIIii) Results: Heights of foraging by males.

The preferred foraging zone was 0-1m. in both June and July. (Fig. 24 and 30 respectivly)

Comparsions were made between the mean use for each zone by using the 'Student's' t-test corrected for small sample size. Tables 8 and 9 summarise the t values calculated.

In June the use for foraging of the 1-2m. and 2-4m. zones was similar, but the +4m. zone was used significantly less than the 2-4m. zone.

In July the +4m. zone was used significantly less than each of the other zones and again the use of the 1-2m. and 2-4m. zones was similar.

Table 8

Comparsion between different heights of foraging by 'Student's' t-test with the correction for small sample size.

June	t values			
0-1m.	-			
1-2m.	5.28***			
2-4m.	4.6**	1.3		
+4m.	6.28***	1.64	2.93*	—
	0-1m.	1-2m.	2-4m.	+4m.

Degrees of freedom =8

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Table 9

July	t values			
0-1m.	—			
1-2m.	6.2***			
2-4m.	6.67***	1.0		
+4m.	8.49***	4.17**	2.35*	—
	0-1m.	1-2m.	2-4m.	+4m.

Degrees of freedom =8

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

(IIIiii) Results: Size and use of the home range by females.

About half of the females that were mated and attached to males in the study area were watched to obtain estimates of their maximum home ranges whilst foraging for their nestlings (Fig. 41). The areas given in Table 10 are the minimum polygons derived from foraging observations.

Rapid daily changes in the size of the home range whilst the female was feeding the chicks made it impossible to find out whether the home increased from hatching to fledging. The maximum home range was used just before the chicks left the nest. This was not surprising because the demand upon the food supply of the home range was presumably the greatest at this time.

The female did not restrict the home range solely to her use although it was apparent that the male in whose territory the female was foraging did not enter the females home range during the time that the young were in the nest.

The female did not recognise the males' territorial boundaries (as will be documented later under observations of chick and female foraging). She foraged within the male's territory because the nest site was far enough away from the territorial boundary to prevent the female foraging in another male's territory or an undefended area.

Females did not forage in areas with no ground cover, so territorial boundaries of males along a fence separating the wood from open grassland coincidentally provided one boundary to the female's home range.

The shape of the females' home range was dependant on the amount of ground cover close to the nest site. Female f8 had a narrow home range extending south-west and north-east from the nest because no suitable ground cover was available closer to the nest or in other directions.

Table 10.

The areas (ha.) of female home ranges and expressed as a percentage of the males July territory and home range in which the nest was located.

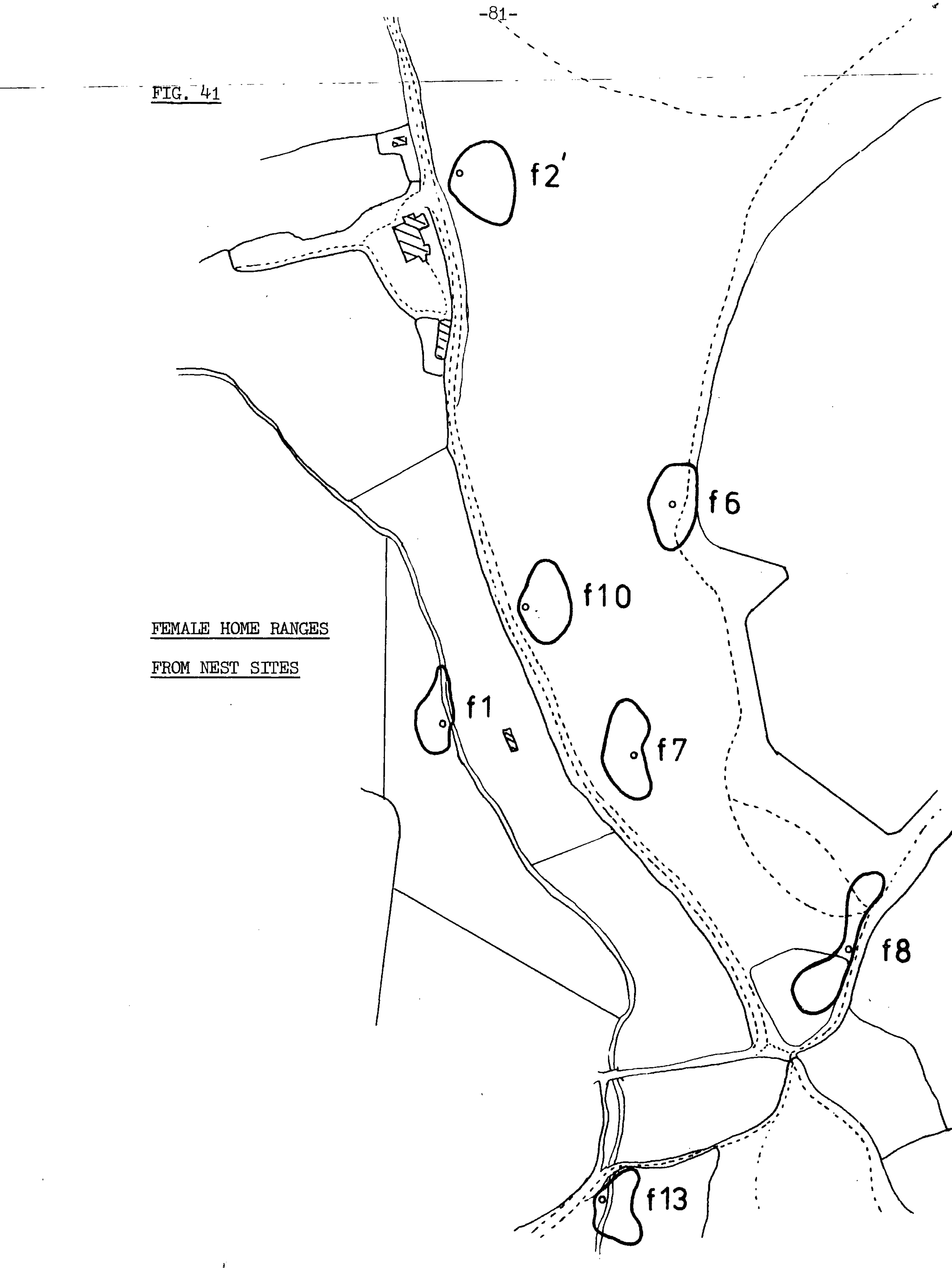
Male	Female	Size of Maximum home range (ha.)	Female home range as % of male territory	Female home range as % of male home range
m1	f1	0.065*	5.6%	4.39%
m2	f2	0.121	20.9%	13.3%
m6	f6	0.060	20.9%	10.3%
m7	f7	0.174	10.9%	9.9%
m8	f8	0.117	6.8%	5.7%
m10	f10	0.093	24.5%	16.3%
m13	f13	0.093	11.1%	9.0%

* The chicks died before leaving the nest

FIG. 41

FEMALE HOME RANGES

FROM NEST SITES



(IIIiv) Results: The feeding ranges of fledged chicks.

After leaving the nest the brood was fed by the female for up to 20 days. Groups of one female and several chicks were often seen foraging within the wood in June and July.

No attention was paid by the female or the chicks to the territorial boundaries of the male with which she had mated and within whose territory she nested. On several occasions the brood of chicks with female f5 were found in the territories of male m3 and m4, up to a distance of 350m. from their original territory, which belonged to male m5.

However, the presence close to the territorial boundary of the male with which the female had mated seemed to prevent foraging excursions further afield. For example, the presence of male m13, which delivered both territorial songs and alarm calls at the boundary between his territory and that of male m8 (close to the road), halted the movements of female f13 and her chicks which then returned to the territory of male m13.

(IIIv) Results: Height of foraging by females.

During at least 10 days of observation the female Wrens foraged only within the ground cover zone (0-1m.). She only moved above this zone when removing faecal pellets from the nest. Once she had collected a faecal pellet the female flew to a high perch where she either ate or dropped it. The same perch and tree were often used during repetition of this behaviour.

(IIIvi) Results: Time allocation to flying for males; data obtained by '1 minute spot observation method'

The time allocated to flying was similar in June and July. There was no significant difference between the proportions of each hour spent flying at different hours of the day. Only a small percentage of time was spent flying (Fig. 42 and 43).

Wrens fly quite swiftly, but usually for distances less than 50m. The height of flight is low, rarely exceeding 2m. above ground level. Longer flights seemed to be assisted by leaving a high perch (e.g. the ridges and higher trees) and flying to lower positions in the vegetation some distance away. Wrens appeared to lose height whilst flying, and to reach a high perch within a tree would climb and not fly to it.

FIG. 42

JUNE-Flying as % of total activity (1 min. obs.)

[mean ± 2 SE n = no. of hours obs.]

sunrise 3.44

sunset 20.18

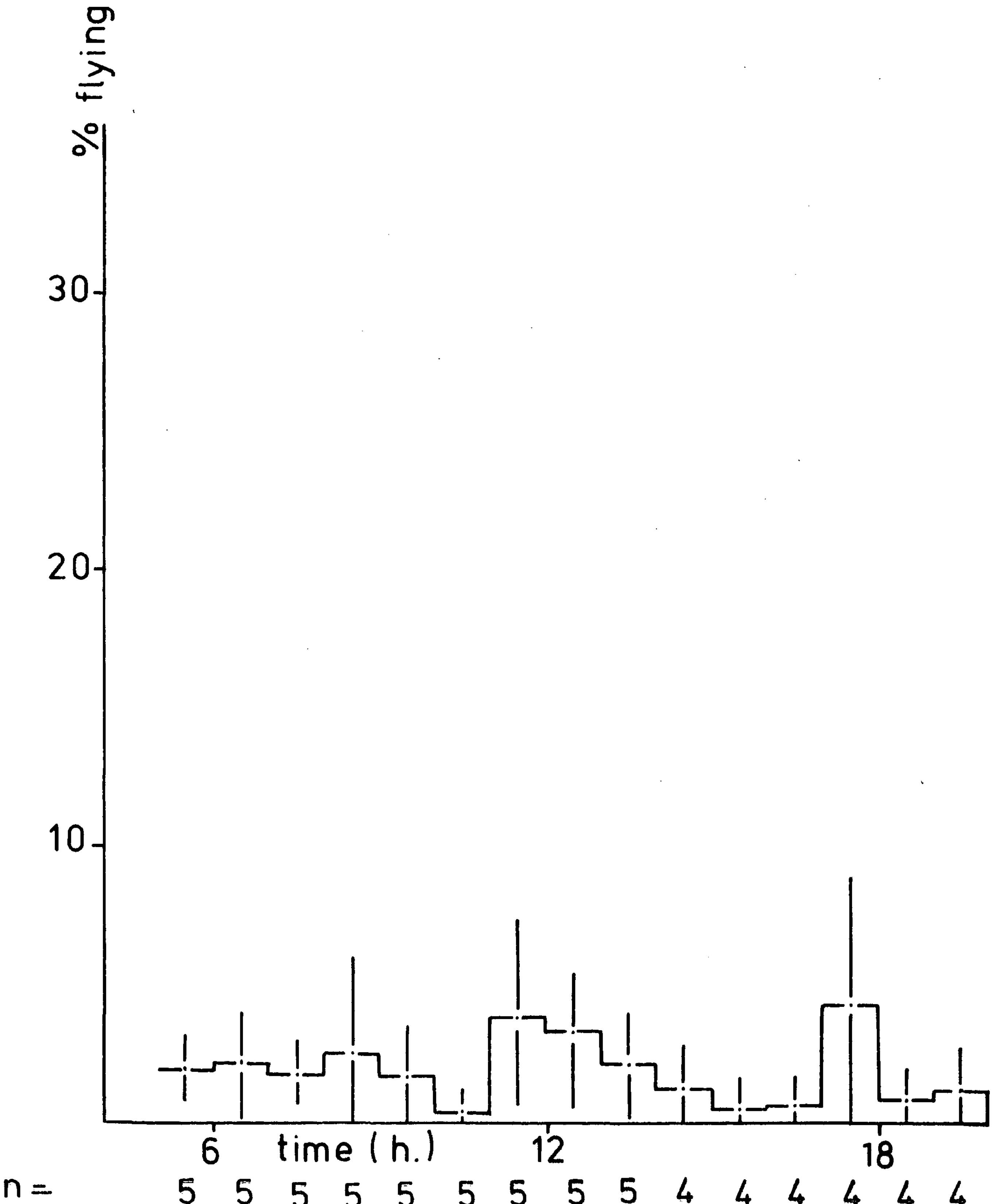
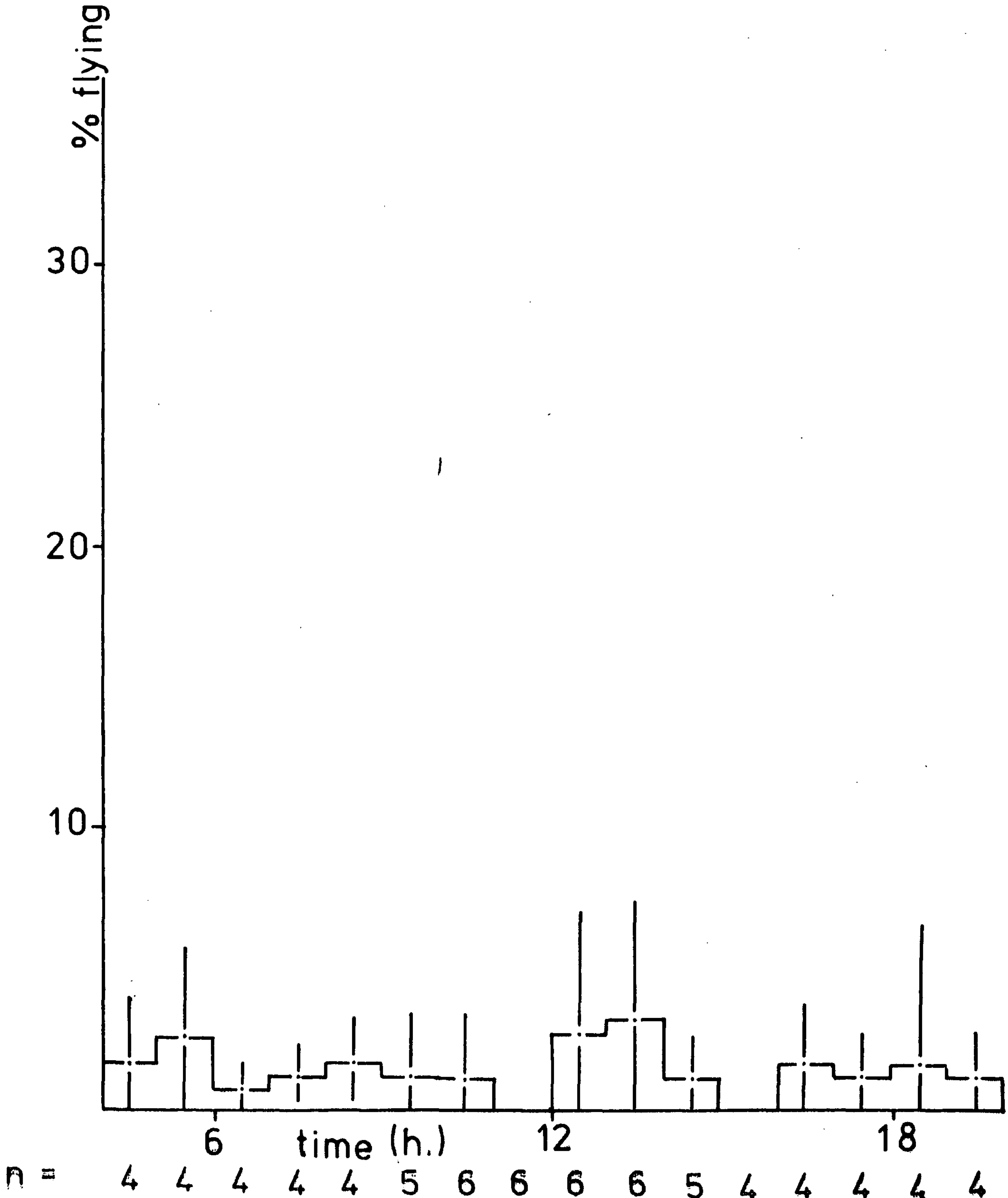


FIG. 43

JULY-Flying as % of total activity (1 min. obsvs
[mean ± 2 SE n= no. of hours obsvs.]
sunrise 4.16
sunset 20.02



(III) DISCUSSION

(III) Discussion

As mentioned earlier, when the size of territories increased, the amount of ground cover within each territory also increased. The ground cover zone was the most favoured for foraging by both males and females, so greater foraging areas were available at the end of July than in May within each territory. However, the male Wrens did not restrict their foraging to their territories and made extended foraging excursions into the territories of other males.

The most favoured foraging zone perhaps offers greater protection against predators because of the 'denseness' of the vegetation. However, as the majority of the Wrens' prey (e.g. Lepidopteran larvae) live upon the surface of leaves an increase in the total surface area of the leaves above a fixed area of ground, i.e. the 'denseness' of the vegetation, may lead to an increase in the prey available. Thus the height selected by the Wren, the lowest zone (0-1m.) might present a more abundant food supply, the leaf surface area being greater for a fixed area of ground, and also provide cover whilst foraging. Cover might be particularly important for the fledgelings which cannot fly well. When disturbed even adult Wrens always seek safety within ground cover.

If food availability was greater in higher zones it would have been expected that Wrens would have spent more time foraging within these zones. The success of the brood, that is whether any young survive or not, depends upon successful foraging by the female, since she alone feeds the chicks. Although not restricted to the 0-1m. zone by any physical constraints, all the females foraging occurs within this ground cover zone. After the young fledge use of the ground cover zone allows the female and her brood to feed undetected by predators.

However, for the male there is a difference in height between the foraging zone (0-1m.) and the preferred song post zone (2-4m.). If singing was exclusive to one zone and foraging to another energy would be wasted in moving between the two. The male Wren is an opportunist when foraging and will sing and forage between songs within the same height zone. Therefore some foraging occurs at all height zones in which song activity is high. When there is a reduction in the proportion of time spent singing, more time is spent within the lowest, most favoured, foraging zone. In the morning, when more songs are produced each hour, more time is spent foraging at the higher zones, which contain the favoured song posts, than in the afternoon when song output is less. In July when songs are broadcast both from 1-2m. and 2-4m.zones, the former being preferred in the afternoon and evening, the use of the +4m. zone for foraging was less than in June. The male Wren spent more time at the lower zones, as the song production decreased.

To establish a high level of energy input every opportunity would be made to forage. However, there would be a compromise between the height preferred for song activity and that for foraging. When the song production was at its highest a greater proportion of the time spent foraging would be at the preferred song post height, even though the majority of the time foraging would still be spent at the 0-1m. zone. The proportion of time spent foraging early in the morning, when the song production was highest, would be less. A greater precedence would be given to song because its function might be of more importance at that time of day than foraging. The amount of time spent foraging might also be effected by the capture rate per unit time of insects by Wrens being less in the morning. This might be due to the lower ambient temperature slowing down the movements of the insects and their detection more difficult. As the song rate per hour was reduced the time available to forage was greater, and this coincided with a higher ambient temperature. With more time available to forage more of the time would be spent within the 0-1m. zone. Foraging at higher levels would be unnecessary because few songs would be produced at a higher level, and the effectiveness of foraging at these levels would be less.

An example of how the maximum use of time was made so that the proportion of time spent foraging was greatest was shown by the foraging behaviour of the female. After leaving the nest the female would fly to the selected foraging area then forage continually back to the nest. The maximum time was spent foraging and the least amount of energy was spent on flying. This behaviour pattern would also allow for the largest area to be searched for food in the time available.

In the male high alighting posts were used when flying because they would reduce the effort of flying without any sacrifice of distance between alighting and landing points.

It appeared that as preference for the 0-1m. zone was given by the male and female Wren population there was no competition between the sexes for foraging zones. The demands by the Wrens on their food supply of that particular zone were not great enough to incur any exclusion mechanism. However, as was stated earlier the male did not approach his respective female's home range. This may have been a mechanism to restrict the use for foraging of a particular area to one Wren of either sex. However, it could have been due to the fact that the male no longer had any interest in the occupied nest site and no further need to visit that particular area of the territory.

(IV) RESULTS

(IVi) Results: Nest building.

Nest building was carried out entirely by the male and several nests were built by each male. Building took place throughout the breeding season until June, but no evidence of new nests was found in July.

The male completed nest construction by sometimes lining it with moss. Once the nest was completed it was visited regularly and any necessary repairs made by the male. The female which had selected a particular nest lined it with feathers just prior to egg laying.

It was possible on only one occasion to observe continually a male Wren building a nest. Male m5 was building between bracken petioles a nest which was later abandoned still incomplete. The allocation of time by this bird to various activities was measured by the 'continuous survey' method and the results are given in Table 11.

It appeared that whilst nest building the normal time allocation to activities was altered. (Table 1 and Table 11). Flying activity increased, possibly because the male searched for nest material at some distance from the selected nest site. Both singing and total foraging activity decreased to allow for the high proportion of time spent actually building the nest.

Table 11.

Time allocation to various activities whilst nest building

Time 10.00-10.55

Total duration of observation period 55mins.

Time spent foraging*	32.7min.	(59.5%)
Time spent flying	4.1min.	(7.5%)
Time spent singing	0.7min.	(1.3%)
Time spent nest building	17.5min.	(31.7%)

* Foraging activity included searching for both food and suitable nesting material.

Plate 8.

Male Wren (m8) singing from song post.

Plate 9.

Nest (k) built by male m6.

Plate 10.

Nest (d) built by male m2.

Plate 11.

Nest (j) built by male m6.

Plate 12.

Nest (u) built by male m13.

Plate 13.

Nest (m) built by male m10.

(IVii) Results: Nest site location and building materials.

Twenty-one nests were found and their ownership, height, and details of nest construction are given in Table 12. Their position within the wood is given in Fig. 44; and Plates 9-13 show photographs of the nests of some of the male Wrens.

A wide variety of nest sites were used, e.g. under the stream bank; within bramble; in holes and branches of trees. The height above ground level also varied widely, from 30cms. to 450cms., but none were found at 200cms. or above that were chosen by female Wrens.

Males m1 and m13 both made use of the overhanging stream bank for nest sites. The grass roots and overhang of the bank were very suitable nest supporting structures. The majority of nests built within the wood were made of dead bracken petioles. There was an abundance of this material throughout the season. Where bracken was not available in the vicinity of the nest site dead leaves and grasses were used to build the nest, e.g. in the larch wood and the Field Station. Bracken was not favoured as a nest supporting material even when it was abundant during June and July. The only attempt at nest building (nest g) within bracken was soon abandoned.

Nest sites were found close to territorial boundaries if a suitable supporting material for the nest was available. Nests found in a central position in the territory were close to former territorial boundaries at the time they were built. For example, male m8 built nest (r) close to the boundary if its May territory;

nest (t) was built in June at the furthest extension to the territory in a southerly direction; and nest (q) was built in late June at the edge of the territorial expansion in a northerly direction.

The distance between nests varied considerably. Male m6, which had a small territory, built nests relatively close together. The distance between nests (k) and (l) was approximately 10m. Wren male m5 commenced building a nest, (g), which was approximately 10m. from nest (h), but did not complete it. The largest number of nests was found within male m8's large territory. Here the nests were separated by a minimum distance of 25m. (nest (r) from nest (s)).

Table 12.

Data on nests found within study area.

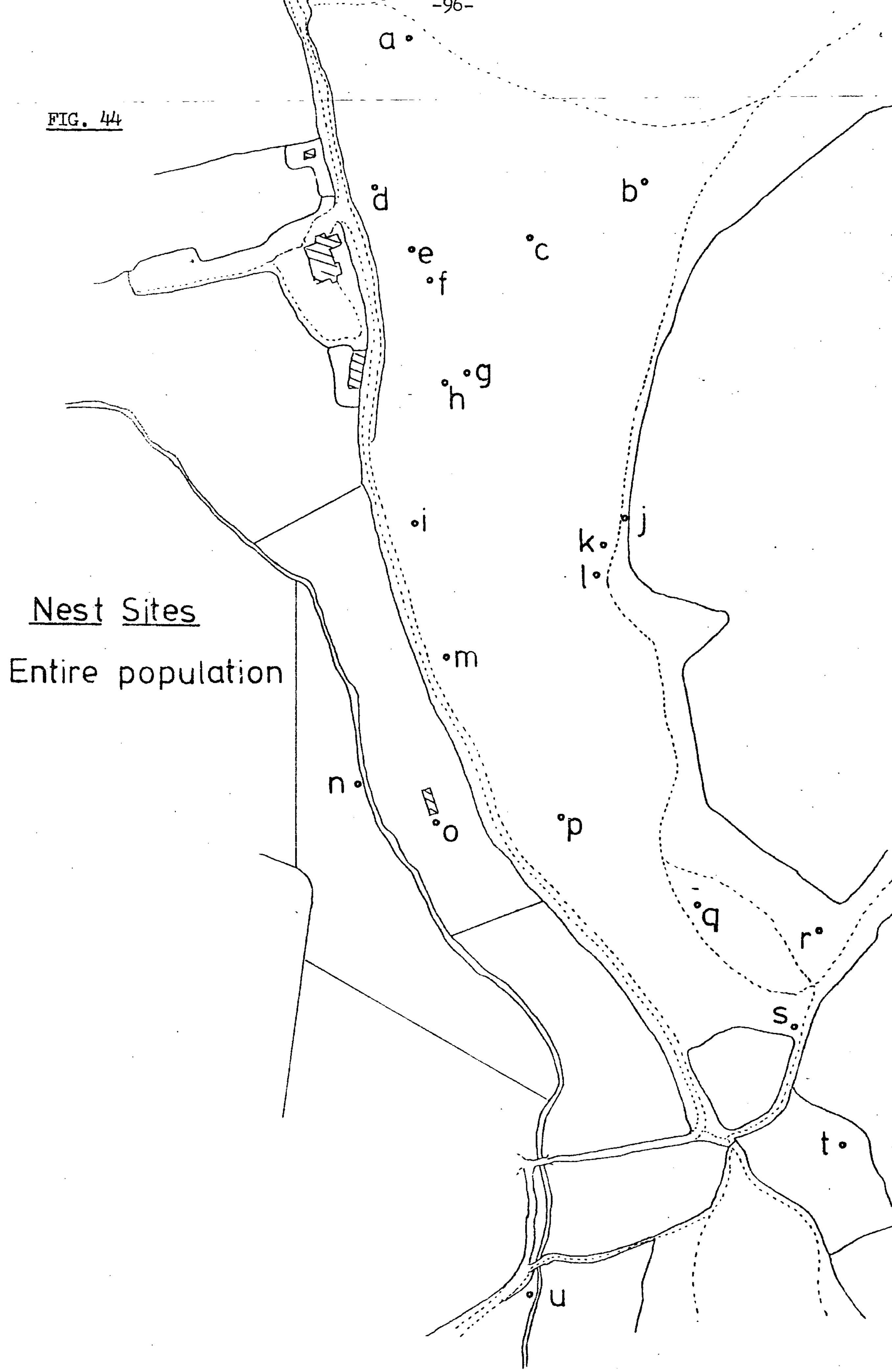
Male	Female	Nest	Height above ground (cms.)	Nest material	Surrounding material
m1	f1	n	90	grass/roots	grass/soil
m1	-	o	120	grass	rose bush
m2	f2'	a	100	bracken	bramble
m2	f2"	d	30	leaves	rowan/sycamore tree
m3	-	c	270	bracken	beech tree
m3	-	e	450	bracken	sycamore branch
m3	-	f	inc.	bracken	tree stump
m4	f4	b	70	bracken	bramble
m5	-	g	inc.	bracken	bracken
m5	-	h	90	bracken	bramble
m6	-	j	130	bracken	bramble
m6	-	k	30	bracken	bramble
m6	f6	l	40	bracken	bramble
m7	f7	p	70	bracken	bramble/tree
m8	f8*	r	40	bracken	tree stump
m8	-	t	60	leaves	bramble/tree
m8	f8**	s	70	bracken	bramble
m8	-	q	300	bracken	sycamore tree
m10	f10'	i	150	bracken	bramble
m10	f10"	m	180	bracken	silver birch tree
m13	f13	u	110	moss	grass/soil

Note: f8* was presumed to be the female of the first clutch, f8** the second.

f2';f2";f10' and f10" were thought to be females attached to polygamous males m2 and m10 respectively.

inc. represents incomplete nest

FIG. 44



(IViii) Results: Breeding biology.

Of the twenty-one nests found only ten were later occupied by females. Of the ten clutches laid four were lost to predators before hatching. The predators could have been small mammals and only eggs were taken. No evidence of predation during the nestling stage was observed but one brood died of unknown causes (nest n). Nest (p) was destroyed before egg laying commenced but had been feather lined by the female.

The time between the completion of the nest and occupation by the female varied considerably. Only nests (a) and (b) were selected by the female Wrens immediately after building by the male had been completed. Nest (d) built by male m2 in May was not occupied until the end of June, whereas nest (a) built in June was occupied immediately.

The number of eggs laid, length of incubation period, length of the nestling period and the number of days the female remained with the chicks are presented in Table 13. The chronology of breeding biology is presented in Fig.45.

Two separate groups of fledgelings were found within male m5 and m7's territory but no nest site could be found for them. The fledgelings sometimes returned to their nests at dusk, but unfortunately this was not so in the case of the two'missing' nests.

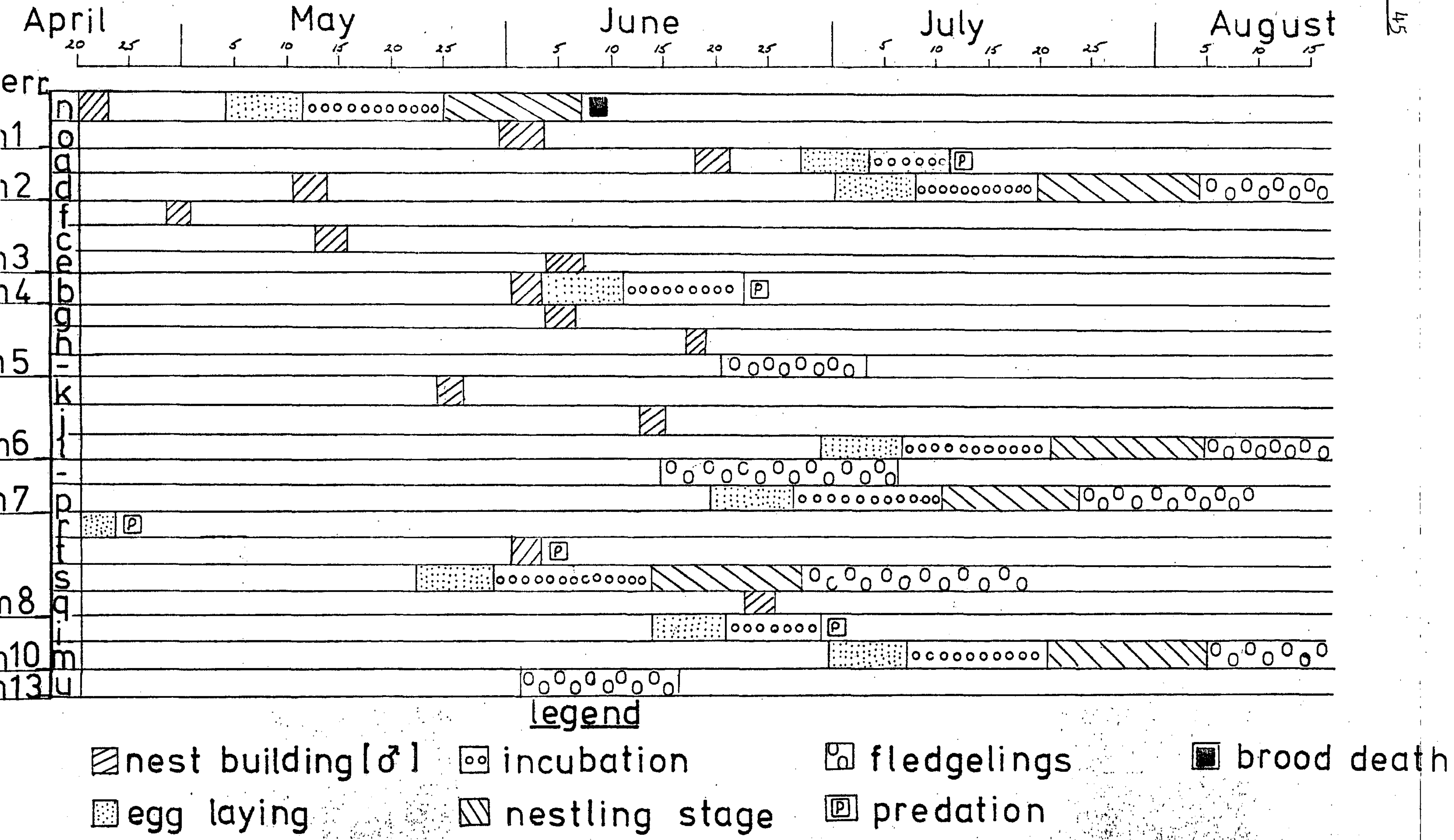
Table 13. Breeding biology.

Male	Female	Nest Site	Clutch size	Date of first egg.	Incubation period(days)	Nestling period(days)	Number fledged
m1	f1	n	5	4/7/76	16	DIED	-
m2	f2'	a	7	28/6/76	PRED.	-	-
m2	f2"	d	6	1/7/76	15	15	6
m4	f4	b	7	3/6/76	PRED.	-	-
m6	f6	l	6	30/6/76	14	14	6
m7	f7	p	7	20/6/76	15	14	6
m8	f8*	r	3P	20/4/76	-	-	-
m8	f8**	s	6	22/5/76	14	14	6
m10	f10'	i	7	14/6/76	PRED.	-	-
m10	f10"	m	7	29/6/76	15	16	7

Note:
- f8* is thought to be the female of the first clutch and f8** the second.
-f2';f2";f10'andf10" are thought to be females attached to polygamous males.
-3P- clutch was predated before complete
-PRED.- clutch was predated during incubation

FIG. 45

Date of commencement of breeding activities



(IV) DISCUSSION

(IV) Discussion

Multiple nest building is recorded amongst birds in widely diverse families and may serve a variety of functions. The average number of nests per male Wren found in Holland was 6.2 (Kluijver et al 1940); the average number of nests per male in Hollinside Wood must have been much less even though the 2.1 nests per male were probably not all the nests built.

Each nest which was started was completed, or abandoned incomplete, before a new nest site was chosen. However, nest repairs and lining with moss continued throughout the breeding season until the nest was occupied by a female. Singing from a song post close to the nest site also continued until the nest was occupied. No completely built nest was abandoned by the male. Thus by creating more nests the male provides a greater choice of nesting sites for a female. He also has a greater chance of mating, if the female selects which nest she will use. The Nethersole-Thompsons (1943) state because the male builds the nest he selects the nest location. However, it is clear that the female must make the final choice which, if any, of the many nests she will use.

An additional advantage to the male of having several nests available might be that when one of them is occupied, advertisement of the others can continue with the possibility of further matings with other females. However, this is only possible because the male is not responsible for feeding the female on the nest, incubating, brooding or feeding the chicks.

If females tend to avoid nests close to occupied nests, it would be advantageous for a male to space his nests as far from each other as possible, this might increase his chance of multiple mating.

Height above ground level appears to have been one factor influencing the females choice of nest site. Nests above 2m. might not have been chosen for a variety of reasons. For example, predators might be able to see the female returning to the nest after foraging excursions more easily above the dense ground cover; or the distance above the ground could be too great for the newly fledged young to fly back into the nest.

A polygamous male Wren may be able to leave more offspring than a monogamous bird both during one season and during his lifetime. Von Haartman (1956) found that a polygamous male Pied Flycatcher (Ficedula hypoleuca Linn.)could father as many offspring in three years as a monogamous male could in six. He suggested (1950) that two types of polygamy exist .

1. 'successive'
2. 'simultaneous'

Male Wrens' polygamy normally falls into the first catagory (Armstrong 1955), in that first one female is mated and then another but not all males are polygamous. 'Simultaneous' polygamy occurs when a male has more than one mate at the same time, and in the Wren population I studied male m2 had two different females laying eggs and incubating at the same time. On the other hand,male m10 had two females which laid in different nests 15 days apart.

This would be considered as 'successive'polygamy even though the second female had laid the first egg before the first female hatched her clutch. However, because the females were not individually marked the first female may have re-nested, because her clutch was predated, in the second nest and only one female was in fact concerned.

The period of approximately three weeks in which the female feed the fledgelings after they leave the nest may prevent her from laying a second clutch if her first clutch was laid late in the breeding season. Yet males often courted females with fledgelings and attempted to mate with them.

It seems unimportant whether the male Wren is successively or simultaneously polygamous provided that he fathers the maximum output of young within a breeding season. Since the male does not assist the female by incubating or, feeding the chicks, either pre- or post-fledging, simultaneous polygamy places no greater strain on his energy resources in foraging than successive polygamy. Where the food supply is less abundant, in the island habitats of the Wrens of St. Kilda, Shetland and the Outer Hebrides, the males are normally monogamous and assist the females in feeding the young (Harrisson and Buchan 1934; Armstrong 1953d)

The chances of a male becoming polygamous depends on the number of suitable nests built and his success in attracting females to the nests. If all nests built are advertised until occupied by a female, then simultaneous polygamy can occur if two females are attracted to different nests at the same time within the breeding season.

Polygamy will maximise the reproductive output of a single territorial male only if there is no difference in survival between the offspring of polygamous and monogamous males. Since the male Wren takes no part in the rearing of young, polygamous males should be more productive.

(V) FINAL DISCUSSION

(V) Final discussion.

The Wren population has shown a rapid increase since the severe winter of 1962-63. Common Bird Censuses have shown a ten-fold increase in the number of males holding territories on farmland since then (Batten and Marchant 1976). Wrens thus have the ability to re-establish population levels quickly after a severe decrease in number. This is possible because Wrens have a high reproductive output, the result of large clutch sizes and the possibility of several broods from each female in a season.

Polygamy does not assist this situation but provides more offspring for a particular male, but because the sex ratio in Wrens is assumed to be equal (Kluijver _et al_ 1940) some males fail to obtain a mate. Sexual selection of males by females will operate. The male with the greatest number of well advertised suitable nests will have a higher probability of attracting a female. As the population of birds increases, more and more males will be forced into unsuitable habitats. If the sex ratio remains the same, since the females will be attracted to the better habitat, there will be an increase in the chance of polygamy for the males in these habitats.(The females will make maximum use of the better habitats because of the possibility of reduced success in producing fledged young in unsuitable areas.)

The quality of the habitat may be dependant upon the density of the food supply. Harrisson and Buchan (1934) have shown that both male and female St. Kilda Wrens forage to feed their young, but even then there is a greater chance of chick starvation than in the mainland habitats. However, the habitat is apparently not bleak enough to produce significant increases in the time necessary for foraging (Bagenal 1958). Cody (1974) has shown a strong relationship between territory size and food density for the island Wrens; the less abundant the food supply the larger their territory. But Cody has given little indication as to when the territory size was measured and whether foraging for island Wrens is resticted to the territory. Further support for a link between territory and food density came from Nicholson (1927) who considered that amongst insectivorous species with weak flight, such as Warblers (Muscicapidae spps.), there may be food territories, since such species would have greater difficulty in obtaining their food requirements than swift flying species such as House Martins (Delichon urbica Linn.). This claim is far from proved (Lack and Lack 1933), and 'weak' or 'strong' flight is a very subjective classification, especially if one considers the Wren as an apparently weak flier which nevertheless has colonised remote islands.

Howard (1920) claims that territory insures ' ample food for the young in close proximity to the nest'. It could be presence or absence of a suitable feeding area around the nest that attracts a female Wren to a particular nest. However, Lack and Lack (1933) point out that if the food supply is to be exclusive to the female, interspecific as well as intraspecific exclusion must occur of birds with similar food requirements. There is no evidence of this in the Wren although the niche overlap with other birds is not great, according to Cody (1974).

Armstrong (1955) found a correlation between territory size and reproductive 'vigour', indicated by the fact that polygamous male Wrens generally defended larger territories than monogamous males. However, one polygamous male of Hollinside Wood had one of the smallest territories (0.58ha.), a result inconsistant with Armstrong's claim. Reproductive'vigour' is defined by Armstrong as ' the number of nests built and the number and volume of songs produced', and was, he believed, dependant upon food supply. With an increase in the number of nests and how well they were advertised there would possibly be an increase in mating success. But 'vigour' may be dependant upon the level of testosterone present more than on the food supply.

Fig 46 shows relationships between song output, increase in territory and breeding success, . The relationship shows that an increase in territory size will make available a greater foraging area, but, perhaps more important, more suitable nesting sites are included within the territorial limits.

The male Wren is extremely catholic in its selection of suitable nest sites and any increase in territory size would undoubtedly include more nest sites. The more nests available increases the chance that a female will select one. If the territory increases until social interaction prevents further expansion one might assume that the object of defence is the nest or the potential nest site.

Von Haartman (1956) considers the breeding system of the Pied Flycatcher as 'polyterritory' where each nest hole is defended and the majority of males have more than one nest hole. The upper limit to the population density of the Pied Flycatcher is set by the number of nesting holes. One might consider that the same situation applies to Wrens, because they defend a large number of nests and each nest is exclusive to the male that built it. However, there is no shortage of suitable sites for nest building so the population cannot be limited in the same way as the Pied Flycatcher.

The size of the male Wren's territory is much larger than that of other small passerines. The Reed Warbler (Acrocephalus scirpaceus Herm.) defends an area of approximately 500 square yards (0.04ha) (Brown 1946); blackcaps (Sylvia atricapilla atricapilla Linn.) and garden warblers (Sylvia borin Bodd.) 0.5 acre (0.2ha.) (Raines 1945); willow warblers (Phylloscopus trochilus trochilus Linn.) 0.3 acre (0.12ha.) (May 1947) and Redstarts (Phoenicurus phoenicurus phoenicurus Linn.) 1 acre (0.4ha.) (Buxton 1950). However, of these only the male garden warbler is known to build 'cocks' nests (Witherby et al 1945), a practice common in the male Wren. The larger territory in the male Wren might be because of the multiple nest building habit. However, as the density increases the average size of the territory may decrease. This situation is found in the House Wren (Troglodytes aedon Linn.) (Kendeight 1941).

An unsuitable habitat might have a lower density of male Wrens and a suitable habitat a high density of males. The only indication of suitability of habitat might be given from the amount of ground cover available when the territories were established

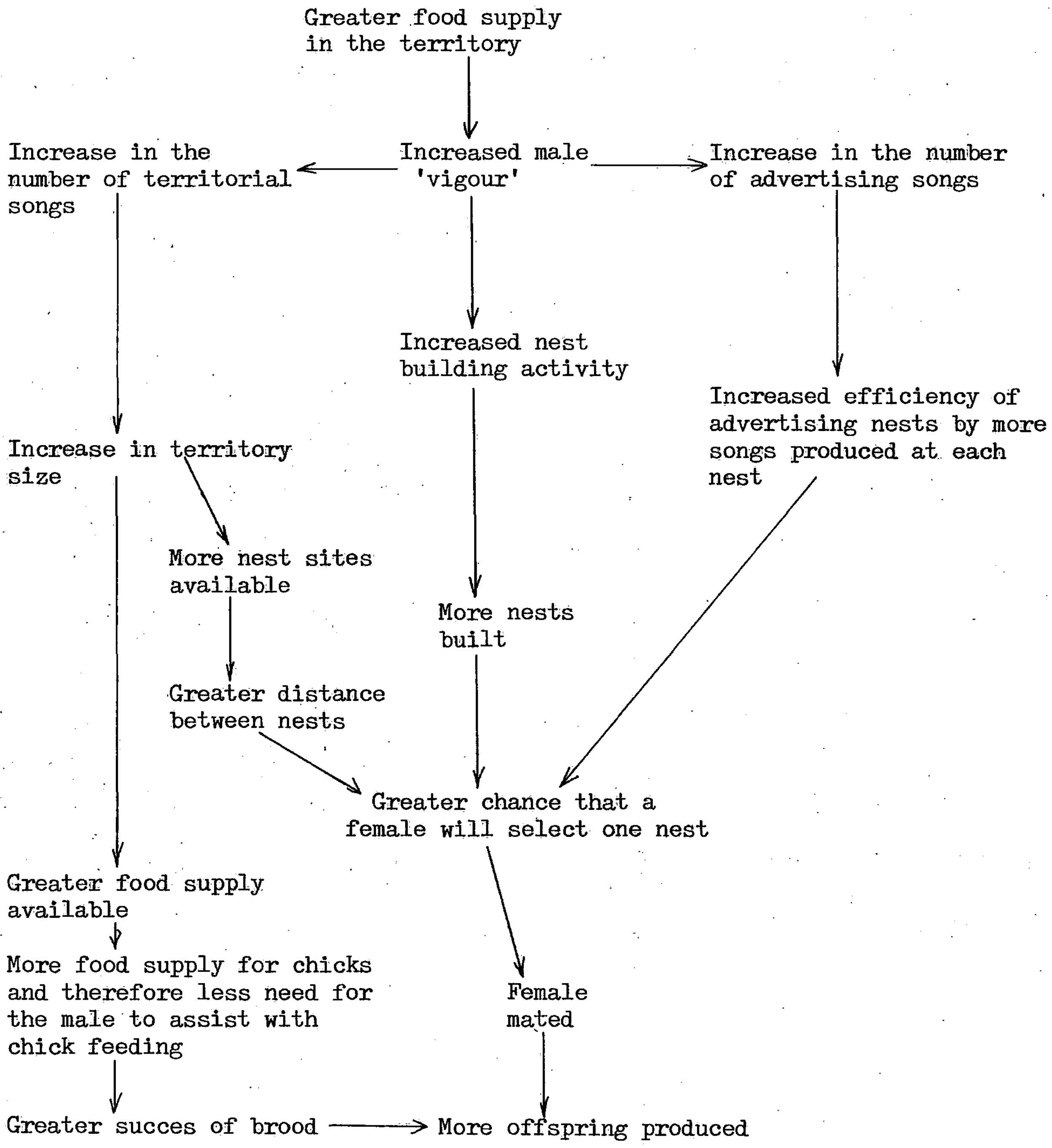
That the population is still increasing rapidly (Batten and Marchant 1976) would imply that the maximum density of many areas has not yet been attained. Expansion of the territories to increase the number of nest sites can still take place where the density of Wrens is low and not all the available ground cover is utilised. One may speculate that the higher the initial density of males, the smaller the increase will be in territory size from May to July, until at some maximum density there may be no increase at all. However, even the minimum territory size could allow every male to build more than one nest. One would expect the maximum density of male Wrens for a woodland to be reached and then expulsion of male Wrens to unsuitable habitats. Williamson (1969) has shown that Wrens prefer certain habitats. The 'reserve' group of males in unsuitable habitats could replace,at any time of the year, any male which died while holding a territory within the woodland. This would ensure a stable density within the wood. That'reserve' males of other bird species replace males that held territories has been shown by Hensely and Cope (1951); Stewart and Aldrich (1951) and Krebs (1976). Therefore the build up of a population of non-breeding 'reserve' males would always mean that a maximum use of the suitable habitat is made as a breeding area.

The male Wren is able to maximize its reproductive potential at different densities by increasing the number of nest sites when the density is low or maintaining a high density in the suitable areas when the population is large. The use of the territory limits the density of a suitable habitat so that the resources are not stretched to an extreme and new suitable habitats are constantly sought after by the unproductive male population.

If a territory is by Noble's (1939) definition 'any defended area' and implies 'any excluded area' (Ricklefs 1973) the only territory for the male Wren is the nest site, The arrangement of nests forms the more usual Wren territory studied. Song is a very difficult defence mechanism to understand, for example, the distance of penetration; the effect of an increase in volume, and a greater knowledge of 'song distance ' as a quantitative measure is needed before defence by song is fully understood.

FIG. 46

Inter-relationships established between territory size, song output and breeding success.



(VI) APPENDIX

(VI) Appendix

Results of the Common Bird Censuses for the Wren population of Hollinside Wood and the Field Station are given in Table.13.

The estimation of the number of territory holding male Wrens from the censuses was much lower than the actual population found after intensive study.

The shape of the territory could have caused some errors in the estimation of the number of male Wrens. Long, narrow territories, for example along stream banks and hedges, could lead to a higher estimation of the number of male Wrens. A male could sing at one end of the territory and then move to the other, but out of sight of the observer, to sing again. Repetition of this several times could confuse the observer into thinking that there were two, not one, male Wrens at this site.

The possible effect of the climate in reducing song output could lead to an underestimation of the number of male Wrens present.

Other possible sources of error that could have arisen are from the actual time that the survey was taken (Slagsvold 1973); the difference between morning and evening song production peaks (Hogstad 1967), and the song depressing effect of rain and wind (Hogstad 1967). The most accurate methods of estimating the size of the population are those of Pough (1947), Odum and Kuenzler (1955) and Weins (1969) but are not applicable to every situation and for every species of bird and are time consuming. The recommendations made by the International Bird Census Committee (1969); Svensson (1970) and Robbins (1970) should be adhered to as far as possible to obtain consistent reliable results.

Table 14.

Number of male Wrens estimated by Common Bird Censuses in Hollinside Wood and the Field Station.

Date	Number of Wrens (male)	Time of census
20/4/76	6	Morning
21/4/76	5	Morning
22/4/76	7	Morning
23/4/76	4	Morning
24/4/76	6	Morning
25/4/76	6	Morning
26/4/76	7	Morning
27/4/76	5	Evening
28/4/76	8	Morning
29/4/76	3	Evening
30/4/76	8	Morning
mean=	5.9 Wrens	

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