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THE ECOLOGY AND BEHAVIOUR OF CLOSELY RELATED SPECIES IN GIBRALTAR (WITH SPECIAL REFERENCE TO SWIFTS AND WARBLERS).

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The Ecology and Behaviour of closely related species in Gibraltar (with special reference to Swifts and Warblers).

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ABSTRACT

Bird communities at Gibraltar are examined and the ecology and behaviour of two species pairs which dominate numerically, the Blackcap Sylvia atricapilla and the Sardinian Warbler S.melanocephala in Matorral, and the Swift Apus apus and the Pallid Swift A.pallidus in the air,are compared.

The communities exhibit seasonal changes in species and biomass probably due to habitat seasonality and geographical location. The latter in part produces the large migrant element in the communities. Largest seasonal fluctuations occured in the simplest habitats. The number of species which potentially interacted with the two species pairs studied changed with season. The communities at Gibraltar differ from those studied by others elsewhere in the Mediterranean Basin.

The Blackcap and the Sardinian Warbler are resident and exhibit morphological deviations from other known forms. The local Blackcap population is intermediate morphologically between the Sardinian Warbler and the nominate Blackcap population, which arrives at Gibraltar in winter. The life cycle of the residents is related to climatic conditions, food supply and the presence of migrants. The two species overlap extensively in resource use but the Sardinian Warbler is broader-niched. Interspecific aggression and territoriality spaces individuals all year. Resident warblers accumulated fat during favourable periods. Mortality was high in both species. Northern Blackcaps returned in successive winters.

Swifts exploited seasonal resources and left in autumn. Life histories are modified accordingly. Overlaps in resource use are high but there is spacing out of groups. Pallid Swifts are less specialised than Swifts and remain longer at Gibraltar, raising two broods instead of one. Pallid Swift mortality is low but higher than for Swift.

The two pairs studied may not be in equilibrium and behavioural interactions maintain resources partitioned. The question is raised as to whether territoriality is related to competition or to interference.

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CHAPTER 1

AN INTRODUCTION

" As species of the same genus, have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera."

Charles Darwin 1859, The Origin of Species.

1.1. THE BIOLOGICAL PROBLEM

Our present knowledge of competition and its consequences to community structure (for historical surveys see Lack 1971, Cody 1974) is due mainly to the pioneer work of Hutchinson (1958), MacArthur (1958), and of those following their line of thinking (Cody & Diamond 1975). In general terms, their studies have revolved around attempting to quantify competition coefficients (α) based on the classical Lotka-Volterra equations of the form

$$\frac{dN_i}{dt} = r_i N_i \frac{\left(K_i - N_i \sum_{j \neq i}^{n} \alpha_{ij} N_j \right)}{K_i}$$

Since the actual coefficients are difficult to estimate, and can only be done so by performing population removal experiments (Pianka 1974, May 1975), most of the work which has been carried out has been based on determining estimates of overlap between species and relating these to the competition coefficients (MacArthur 1972, Cody 1974). Unfortunately, most of this work has involved limited and very brief amounts of data collecting in the field (Cody & Walter 1976, Cody 1978). Most data have, in the case of birds, only been gathered during the breeding season.

The behaviour of individuals and of entire communities can change from one season to the next, in

some cases from one day to the next. Surprisingly little is known of seasonal changes in community structure and of corresponding changes in the response of the components of such communities. Karr (1976) has pointed out that " Further advances in the analysis of avian community structure will be made by persons who evaluate the substructure of avian communities using perspectives of guild configuration (or other subcommunity sets) in the light of substrate availability, physical environment and food resource seasonality, and historical factors and perhaps others. "

The descriptive treatments of seasonal changes in bird communities are of some use in this respect (Blondel 1969, Frochot 1971). Nevertheless treatment of the ecology and behaviour of the community components is usually minimal.

The importance of changes in the competitive environment, especially in areas where sudden changes due to influxes of migrating birds can produce an unpredictable flux (on a day-to-day basis) of species through a community, has been largely ignored (but see Rappole & Warner 1976).This is so despite some interesting predictions from competition theory about the effect of changes in the number of competing species in a community (O'Connor et al. 1975).

It is the aim of this work to examine the seasonal changes which take place in some scrub communities at Gibraltar and to compare the corresponding changes in ecology and behaviour of some of the more important species numerically. Two species pairs have been chosen for

close study, a pair of resident Sylvia warblers and a pair of Apus swifts.

i. Two species of the genus Sylvia, the Blackcap S.atricapilla and the Sardinian Warbler S.melanocephala occur in the same habitats at high densities throughout the year at Gibraltar. In addition, large numbers of Blackcaps from northern Europe spend the winter at Gibraltar and they are separable from the local Blackcaps in the hand. Many other insectivorous species, especially warblers, occur with these two species at various times of year. For example, in spring there are 15 other warbler species (Sylviidae) at Gibraltar, including 6 in the genus Sylvia. This situation provides a convenient opportunity for studying two species which interact with each other under conditions of a marked annual cycle of physical and biotic conditions.

ii. Two very similar species of swifts (Apodidae), the Pallid Swift A.pallidus and the Swift A.apus, nest side by side, occasionally in mixed colonies, at very high densities at Gibraltar. A third species, a hirundine, the Crag Martin Hirundo rupestris, spends the winter in Gibraltar in large numbers at a time when swifts have migrated for tropical Africa. They are the only species of aerial foragers of which a high proportion remain in Europe all winter. By examining the diet of the martins in winter, it is possible to obtain

some idea as to why the swifts leave in the autumn.

This study is divided into five chapters. The rest of this first chapter is devoted to describing the physical environment and the habitats at Gibraltar. The second chapter looks at the bird communities of Gibraltar and examines the effects of a seasonal environment. In chapters 3 and 4 I look at the ecology and behaviour of the Sylvia warblers and the Apus swifts. The last chapter is a general discussion of the results.

1.2. GEOGRAPHICAL LOCATION

Gibraltar is a small peninsula, about 6 kilometres long (from north to south) and 1 kilometre across, at the southern extremity of Iberia (Fig.1.1a). It is situated on the north-eastern corner of the Strait of Gibraltar (Fig. 1. 1b). Its east-facing coastline borders the Mediterranean Sea and on the west it overlooks the Bay of Gibraltar. The Rock (a term which will be used synonymously with Gibraltar) is therefore geographically situated at the meeting point of two continents, Europe and Africa, and of two large bodies of water, the Mediterranean Sea and the Atlantic Ocean.

The Strait (defined in the present context as the stretch of sea encircled by a line from Gibraltar to Ceuta in the east, and from Cape Trafalgar to Cape Spartel in the west, Fig.1.1b) is about 56 kilometres long. It is narrowest between the Spanish town of Tarifa and the Moroccan coast near Jebel Musa, at which point it is only

FIGURE 1.1. Gibraltar - Geographical location.



15 kilometres across.

1.3. TOPOGRAPHY

The Rock itself is an isolated massif of Jurassic limestone, towering above the surrounding countryside. It is linked in the north to the mainland by a narrow sandy isthmus. To the south of this it widens and rises to a maximum altitude of 426 metres (Fig.12). Its eastern and northern sides consist of sheer cliffs which drop right down to the sea in places (Fig.12b), or which break into gentler slopes in others.

The peak lies towards the southern end of Gibraltar and from there a series of slopes and terraces lead southwards towards the sea at Europa Point (Fig.12). The drop along the western side is gentler (Fig.12b), a series of Wild Olive-covered slopes leading down to the town which lies by the Bay of Gibraltar (Fig.11).

The extent and location of the habitats present on the Rock is to a large extent dictated by relief. The sheer east- and north-facing cliffs hold little soil and hence little vegetation. Some soil accumulates at the base of cliffs and low vegetation (steppe or garigue) habitats develop. Dense maquis covers the west-facing slopes which are not so steep and which have a better layer of soil than the steeper slopes.

1.4. HABITATS

The habitats found in Gibraltar are typical

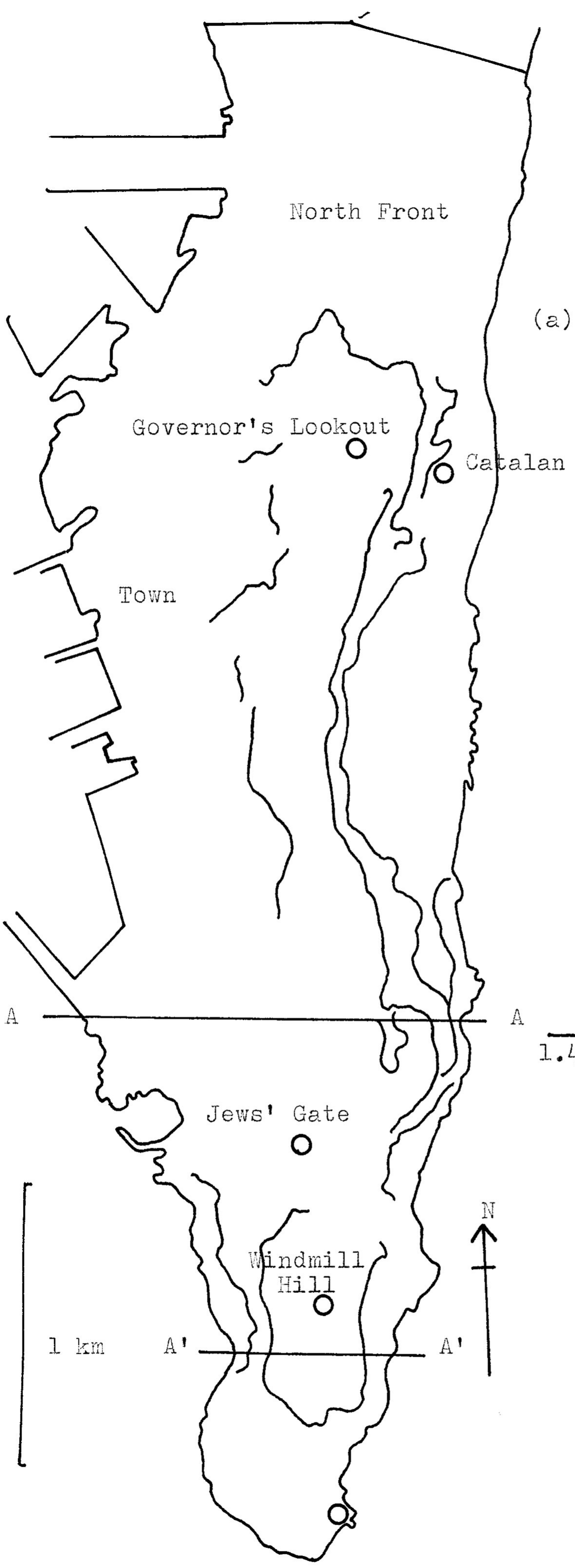


FIGURE 1.2. Gibraltar Main topographical features and places in text.

of most Mediterranean areas (Mooney et al. 1974) but have features which make them unique in the area around Gibraltar (J.Cortes pers.comm.). This is so because most of the soils on the Spanish hinterland are acid whereas on the Rock they are alkaline, since the parent rock is limestone. The soils on the eastern side of Gibraltar are mostly sandy as most of the slopes at the bases of the cliffs have been formed from windblown sand (Fig.1.3). The soils on the western slopes are of the typical Mediterranean Rendzina-like form, and may have the appearance of ' terra rosa ' or ' terra fusca ' depending on the humus content and on the degree of oxidation (Cortes 1978**a**).

Various habitat classifications are possible for Gibraltar (Cortes 1979) but here I have chosen one based on features, such as vegetation height and density, floral composition, which are most likely to be of relevance to birds choosing them.

Matorral is the name given to much of the scrub found in the Mediterranean area (Polunin & Smythies 1973). For Gibraltar, Cortes (1979) has subdivided the matorral into High Maquis, Low Maquis, Maquio-garigue, and Garigue. I omit Maquio-garigue for several reasons. It describes a very localised portion of the vegetation which may quite adequately be ascribed to either Garigue or Low Maquis for present purposes. As far as habitat selection by birds is concerned, the distinction is probably unecessary. The Maquio-garigue is a stage in the succession of the vegetation from Steppe through to the climax Maquis. Other in-between stages could probably be recognised. The

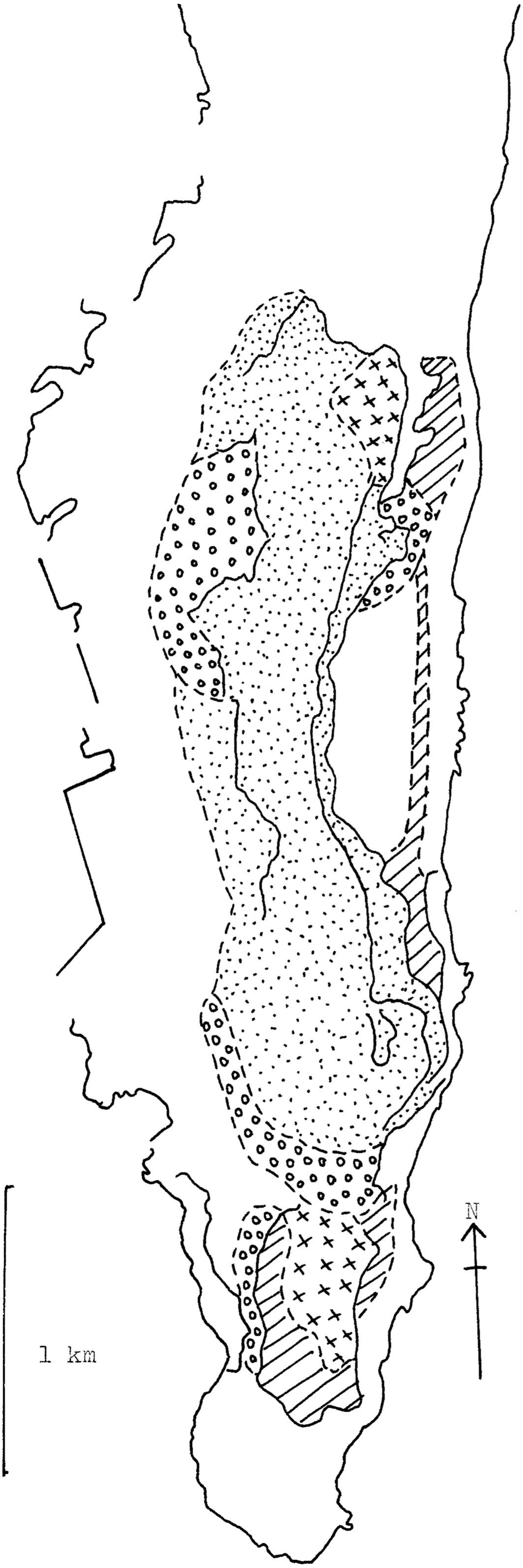


FIGURE 1.3. Gibraltar Distribution of main habitats.

characteristics of the main habitats used by land birds at Gibraltar are given in Table 1.1., and their distribution in Figure 1.3.

There is a growing body of evidence which indicates that most of the vegetation at Gibraltar a century ago consisted of steppe and garigue and that this was kept from developing by goats, sheep and cattle which were grazed on the Rock (Landsdowne in litt.). The dominant vegetation at present is High Maquis (Fig.1.4.) and this may well be the local climax community (Polunin & Huxley 1974). Some areas of High Maquis contain Stone Pines Pinus pinea and Aleppo Pines P.halepensis but they occur in small patches and have a limited distribution within Gibraltar. Cortes (1978a, 1979) lumps pines into High Maquis.

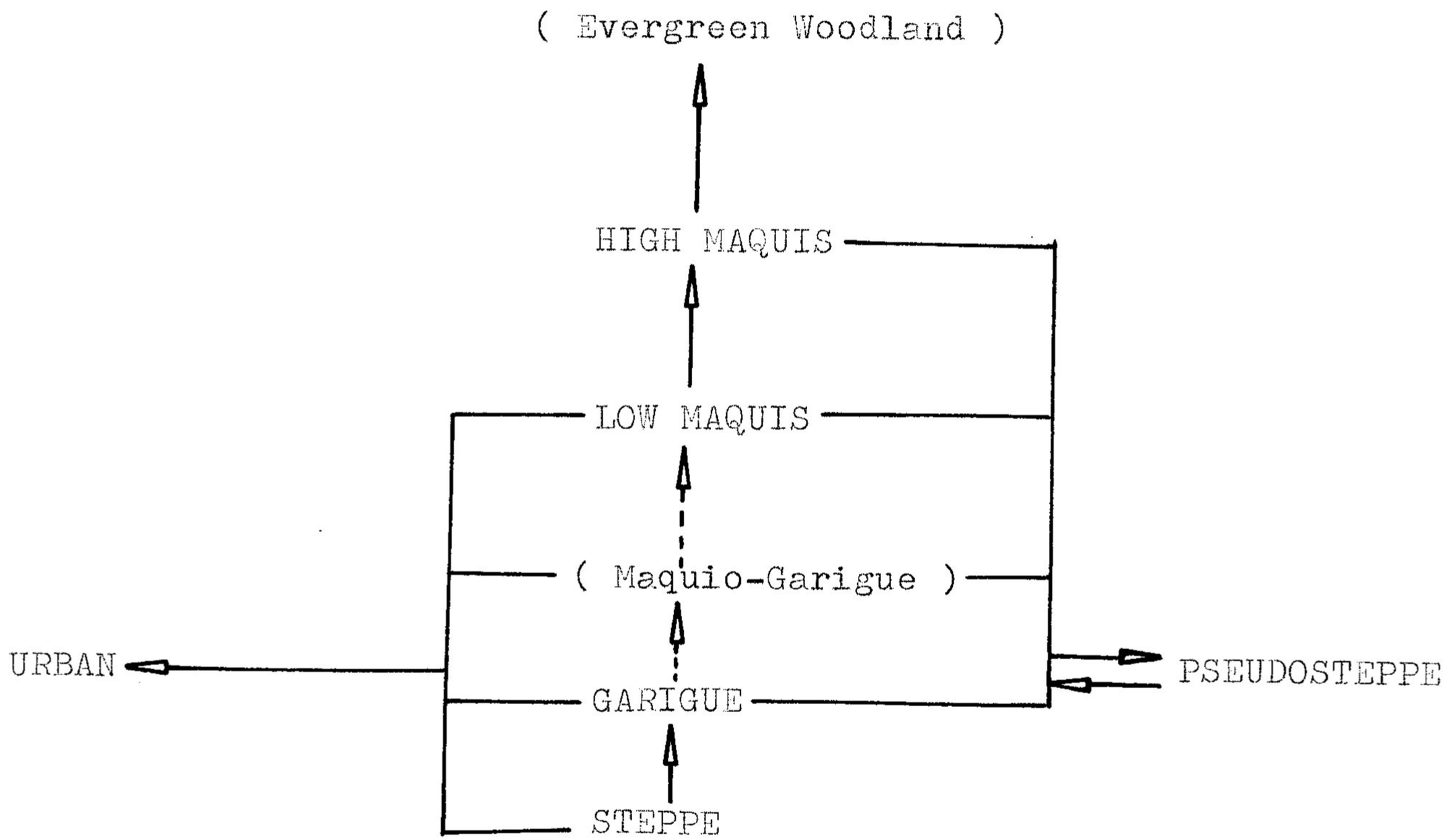
Steppe has nowadays a very limited range in Gibraltar, and it is found mainly on the southern terraces (Fig.1.3.). Some areas within the maquis are regularly cleared by Man and have a pseudosteppe vegetation community (Fig.1.4.). Garigue is also rather limited in extent and occurs chiefly on the lower portions of the Rock. Most of the vegetation is maquis, and the majority is High Maquis (Fig.1.3.). Some low Maquis is found at intermediate altitudes and represents a seral stage between Garigue and High Maquis (Fig.1.4.).

The only other natural or semi-natural habitat available to birds at Gibraltar is cliff (Fig.1.3.). As far as the present study extends, cliffs are relatively unimportant except for their use by some aerial foragers

TABLE 1.1 Characteristics of the habitats occupied by bird species of relevance to this study at Gibraltar.

Habitat Name	Main plant species	Maximum Height (m)	Extent (ha)
High Maquis	Olea europaea, Pistacia lentiscus, Rhamnus alaternus, Osyris lanceolata, Acanthus mollis, Clematis cirrhosa, Smilax aspera, Lonicera implexa, Pinus pinea, P.halepensis, Asparagus albus.	7	95
Low Maquis	Olea europaea, Pistacia lentiscus, P.terebinthus, Rubia peregrina, Rhamnus alaternus, Osyris lanceolata, Acanthus mollis, Ferula tingitana, Foeniculum vulgare, Asparagus albus, Calicotome villosa, Teline linifolia, Coronilla valentina, Oxalis pes-caprae, grasses.	4	21
Garigue	Inula viscosa, Calicotome villosa, Foeniculum vulgare, Smilax aspera, Pistacia lentiscus, grasses.	1	23
Steppe	Narcissus papyraceus, Scilla peruviana, Lotus spp., Lobularia marina, Asteriscus maritimus, Iris spp., grasses.	0.25	18

FIGURE 1.4. Seral stages in vegetation succession at Gibraltar.



at various times of the year. The rest of Gibraltar consists of the town, with scattered gardens which attract many birds. The town is also the main breeding ground of the swifts.

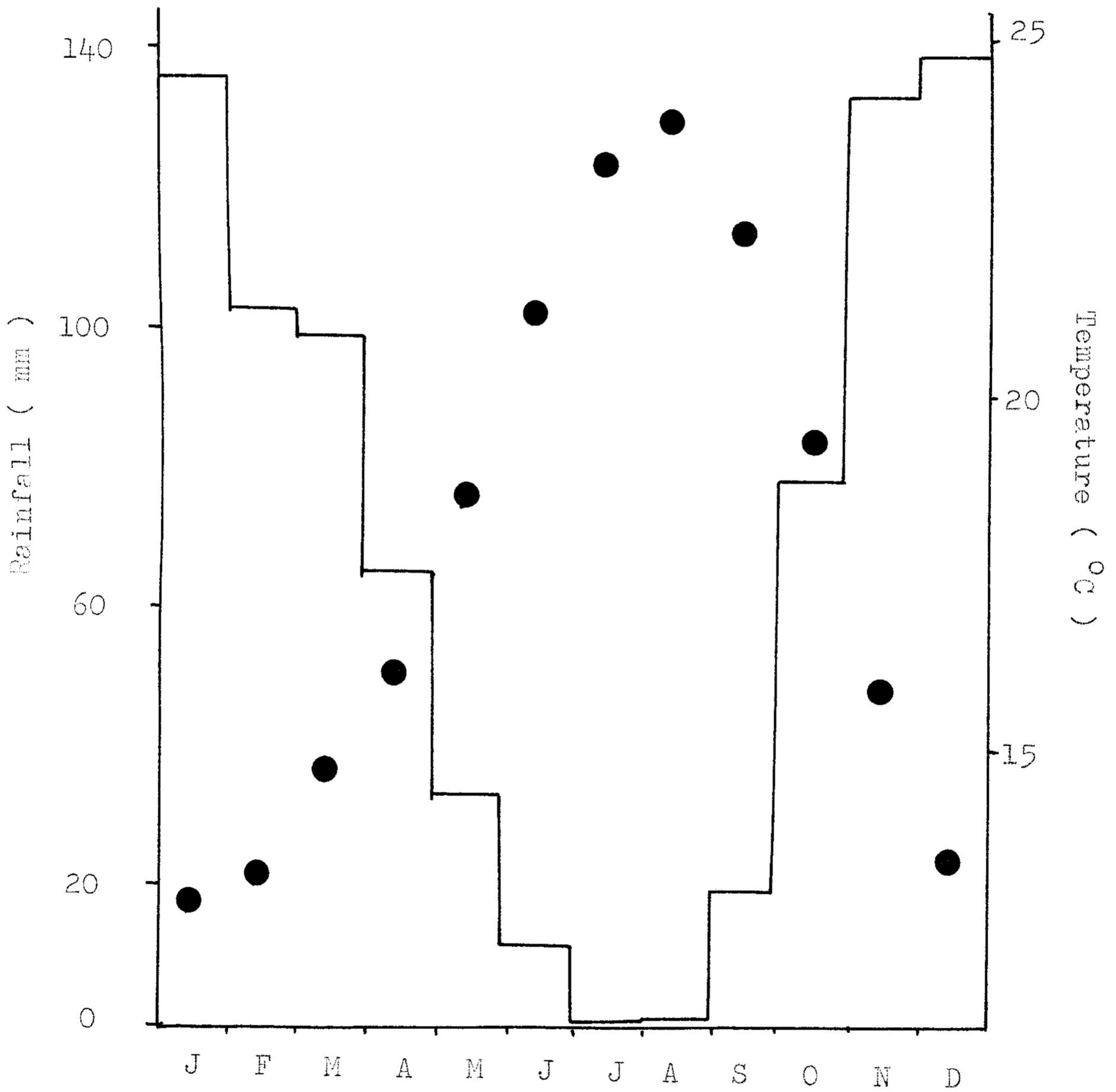
1.5. CLIMATE

Gibraltar has a Mediterranean climate (Mooney et al. 1974). Summers are dry and hot and winters are mild and wet (Fig.1.5.). Average daily mean temperatures range from 12.8°C in January to 23.9°C in August. Total annual rainfall averages 810 mm, and the average monthly rainfall ranges from 0.3 mm in July to 139.2 mm in December. Snow and frost are very rare.

Winds throughout the year blow from the east and west sectors and this must at least be partly due to the local effect produced by the east to west orientation of the Strait itself (Fig.1.1.). In summer, easterlies predominate. These winds gather moisture over the sea and are then forced upwards against the eastern cliffs (Fig.1.2b) producing a dense cloud cap over the Rock which is known as the Levante cloud. Although this cloud produces little rain, the humidity which it carries is thought to partly alleviate the extreme summer drought for some organisms although there is no direct evidence for this. It is unlikely to have much effect on the vegetation as most plants in summer are inactive (Mooney et al. 1974). In winter, westerlies dominate due to the influence of the many depressions which pass nearby.

Although it is useful to consider average conditions, it must be noted that the climate is very variable at

FIGURE 1.5. Mean monthly rainfall (bars) and mean daily temperature (points) at Gibraltar *.



* data for years 1930 - 1971

Gibraltar on a year to year basis (Table 1.2.). This table summarises the climate during the periods of study at Gibraltar.

1.6. THE STUDY PERIOD

The bulk of the work which is presented in this thesis was collected while in possession of the David Lack Studentship from the British Ornithologists' Union between 1976 and 1979. The periods of field study at Gibraltar during this time were : December 1976 - December 1977, March 1978 - December 1978, and March 1979 - July 1979. In addition, some field data was gathered, while an undergraduate, during short intervals in 1973, 1974 and 1975. If thought relevant such data have been included.

1.7. FOOD SAMPLING

Arthropod availability was determined by recording the number of individuals observed in a bush during 1 minute periods. Different bushes could be sampled quickly and so biases due to different weather conditions when sampling, could be made minimal. The method also allowed large samples to be taken within reasonable time limits. The ground was sampled similarly. Sampling was always done about 4 hours after sunrise on calm mornings. Fruit were also sampled in this way, that is the number of fruit counted per bush in one minute. The ratio of ripe to unripe berries was also recorded. Total food per bush was calculated as food per unit time X size of food (length or weight) X bush volume.

TABLE 1.2. Rainfall and temperature deviations from average during September 1973 to July 1975 and December 1976 to December 1978.

Month		Year 1973	1974	1975	1976	1977	1978
January	R		-101.3	-1.8		+142.5	-82.9
	T		+1.3	+1.3		+0.5	+0.4
February	R		-14.2	+32.8		-32.5	+34.2
	T		+0.3	+1.1		+0.8	+1.6
March	R		-79.9	+8.7		-91.5	-54.6
	T		+2.4	-0.7		+1.1	+0.7
April	R		+71.2	-6.8		-64.9	-4.6
	T		-1.6	-0.3		+1.5	-0.1
May	R		-26.9	-7.6		-30.9	+8.9
	T		-0.2	-0.9		-0.2	-1.5
June	R		-2.3	-8.5		+29.3	+5.9
	T		0	-0.5		-1.1	-1.6
July	R		-0.3	-0.3		+7.7	-0.3
	T		+0.3	+0.4		-1.4	0
August	R		-1.9			-1.2	-1.5
	T		+0.5			-5.4	+0.8
September	R	-19.2	-19.2			-19.2	-17.6
	T	+0.7	+0.3			-0.4	+0.6
October	R	-63.7	+25.3			-1.6	-29.9
	T	-0.5	-1.2			-0.1	+0.1
November	R	-15.7	-125.4			0	-91.7
	T	+0.8	+0.1			+0.5	+1.1
December	R	+27.7	-138.5		+152.2	-12.0	+46.1
	T	-0.3	+1.3		+0.7	+1.7	+1.9

Rainfall (R) in mm, Temperature (T) in ^{o}C.

CHAPTER 2

THE ECOLOGY OF SOME BIRD COMMUNITIES AT GIBRALTAR

" Since the seasonal pattern of resource availability seems to be a key factor in the evolution of community diversity, and variation in the nature of exploitation of different resources results in diversities which vary among subsets of consumers, it seems advisable to consider subsets of the avifaunas in evaluating the effects of seasonality."

Karr, 1976 a.

2.1. INTRODUCTION

A knowledge of the structure (Pianka 1973) and of the seasonal changes which take place in any community of organisms is essential before a detailed study of the interrelationships of its components is possible (Karr 1976 a). Although interactions are likely to be greatest within a species, then between congeners, less-related forms may also have an effect on each other particularly in highly competitive environments. The extent of such interactions will probably vary seasonally. Many species, each having a small effect on the competition coefficient (α)of another species, may affect this species as much as just one species which competes more extensively with it. This effect has been termed diffuse competition (MacArthur 1972).

When considering the ecology of the two pairs of species which form the main studies of this thesis, a background knowledge of the bird communities in which they live will be required. For example, the Blackcap and the Sardinian Warbler may interact more at certain times of the year when they overlap more in habitat than during less critical periods, or they may do so when the range of available resources is reduced. They may also interact extensively when the number of species sharing the habitat increases.

The following questions are asked in this chapter.

1. Does the bird community structure in Matorral and in the air change during the year ?
2. Do the number of species which potentially interact with the Blackcap and the Sardinian Warbler in the

Matorral, and with the Swift and the Pallid Swift in the air, change seasonally ?

3. Which species utilise these habitats most and how important are the habitats to them ?

4. How characteristic are these bird communities of the Mediterranean area ?

2.2. METHODS

2.2.1. Censusing techniques

The densities of birds outside the breeding season are currently measured in a number of ways (Emlen 1971, Nilsson 1974, Franzreb 1976). All involve walking repeatedly through an area of vegetation and recording the birds seen and heard. Many such studies have ignored or probably underestimated (Cox & Ricklefs 1977) the proportion of non-resident birds in the communities. This overlooking is probably so because non-resident birds, especially migrants on passage, often skulk and are silent, and thus go by undetected. Yet, as will become apparent, passage birds may be important in communities (2.3.). Other recent studies have also pointed to the importance of transit species in communities (Rappole & Warner 1976, Alerstam & Enckell 1979, Abramsky & Safriel in prep.).

Underestimation of some species is also likely in censusing communities with a proportion of wintering residents (Britton 1974). Underestimation is most probable in communities in dense vegetation and which contain a large proportion of skulking species (Franzreb 1976). For example,

at Gibraltar, the Dunnock Prunella modularis was overlooked in the past (Lathbury 1970). It has since been mist-netted frequently in winter and is now considered a regular element in the Maquis communities, though it is rarely seen.

In the dense Maquis at Gibraltar no method appears to give an adequate measure of species densities outside the breeding season. Mist-netting has shown that some species which were thought to be rare at Gibraltar are in fact regular and abundant (Finlayson 1976). Many other species were under-represented, especially passage birds (Cortes et al. in press).

Of 37 passerines regularly trapped at the Jews' Gate study site in low Maquis, six were never observed, and eight others on fewer than five occasions each. All these species are thick vegetation skulkers (e.g. Reed Warbler Acrocephalus scirpaceus, Garden Warbler Sylvia borin, Nightingale Luscinia megarhynchos). All the species seen were regularly trapped.

In Garigue, the vegetation is very open and low and birds could not be mist-netted systematically as very often the nets were detected and avoided them. However, even extreme skulkers, e.g. Garden Warbler, were regularly detected by line transect and this method appeared to be the more reliable technique of the two in Garigue.

Thus mist-netting was preferred for censusing in low Maquis and transects (Emlen 1971) in Garigue. Care therefore has to be taken in comparing results since different methods have been used. Since most of the discussion to follow will be centred around the importance of species and strategies (Morse 1971) within communities, the main

result which is required is the proportion of each species in the community. The results presented are minima and do not indicate the absolute density in the habitat. For eaxmple, the numbers of, say, Garden Warblers in low Maquis must be greater than the number caught in mist nets, and so their absolute density in the habitat must be higher than the figures given (Appendix 1). If it is assumed that each species is being trapped relative to its abundance in the habitat, then the proportions of each species in the community calculated from the numbers trapped are probably accurate.

Since the same number of censuses were not carried out each month, the density estimates given are birds per hectare per day. In other words, the numbers of birds caught or seen were divided by the area covered (constant) and by the number of days censused.

Low Maquis and Garigue were censused from January 1977 to December 1977 and from March 1978 to December 1978. In addition, some data collected in low Maquis from 1973 to 1976 were also incorporated.

2.2.2. Diversity Indices

Much of the literature dealing with species diversity refers to the Shannon-Weaver Index of species diversity (Lloyd & Ghelardi 1964, MacArthur 1965, Tramer 1969, Kricher 1972). The Shannon-Weaver equation is

$$H' = -\sum_{i}^{s} p_i \log p_i$$

where p_i is the proportion of the total number of individuals contributed by the $_i$th species and s is the number of

species. More recently the Simpson Index of diversity has been used in preference (MacArthur 1972) since the relationship with the alpha matrix is more complicated in the Shannon-Weaver equation. The Simpson Index is therefore more realistic biologically (MacArthur 1972) and it has been used throughout this thesis. The Simpson Index is based on the equation

$$S' = \frac{1}{\sum_{i}^{s} p_i^2}$$

where p_i and s are as in the Shannon-Weaver equation.

2.2.3. Biomass

Only birds which were weighed during the early morning have been used in the biomass analysis in order to avoid variation due to diurnal weight changes. Biomass was taken simply as weight and was measured on a pesola balance to the nearest 0.1 g. Consumer biomass was taken as mean weight raised to the power of 0.7 ($wt^{0.7}$) so as to take the birds' metabolism into account (Salt 1957).

2.2.4. Diet and Foraging methods

In later chapters, a detailed account of the diet and feeding methods of the main species under study is presented. In this chapter, broad diet categories have been determined primarily by observation of where birds were observed feeding and what they were eating, and partly by information in the literature (Blondel 1969, Herrera 1978a, Cody & Mooney 1978). Each species has been categorised in

groups according to the main method of foraging used and the type of food eaten (seeds, insects, etc.). Although the method and the measures are crude, they give a good general impression of the main types of strategies which occur in the habitats being studied (Appendix 2).

2.3. RESULTS

2.3.1. Matorral Communities

Low Maquis and Garigue/Steppe habitats were studied and an analysis of these is given below. High Maquis was examined briefly and is discussed and compared with the two other habitats where relevant.

Low Maquis

46 passerine species were recorded at Jews' Gate; some non-passerines were also present but were relatively insignificant in numbers. The most frequent among these were four migrant species, Turtle Dove, Scops Owl, Hoopoe, and Wryneck.

In Low Maquis, the months with highest species diversity were April and May (Fig.2.2.). There was a second, lower, peak in October. In winter diversity was lower than during the passage periods, but it was higher than in summer. The spring increase in diversity was due to a sudden influx of many species which were passing northwards through the area. Very few of these remained to breed. Although the number of species in the habitat in August and September was high (Fig.2.2.), diversity remained low. This was because only one or two species foraged regularly within the Maquis while migrating south, so that many of the species were represented only by a small number of individuals. As

FIGURE 2.1. Densities of species in low Maquis at Jews' Gate.
1mm thickness = 1 bird/ha

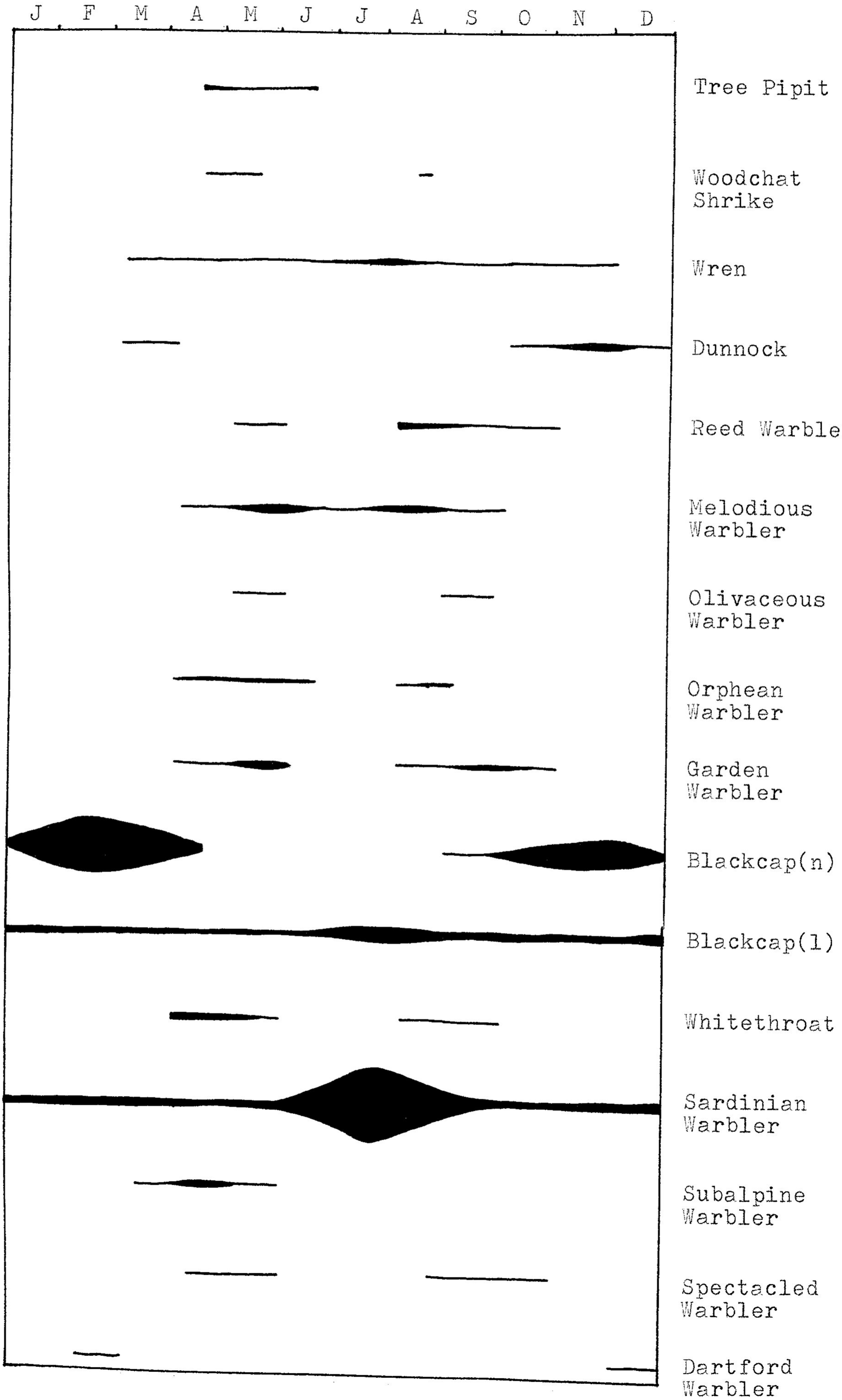


FIGURE 2.1. continued

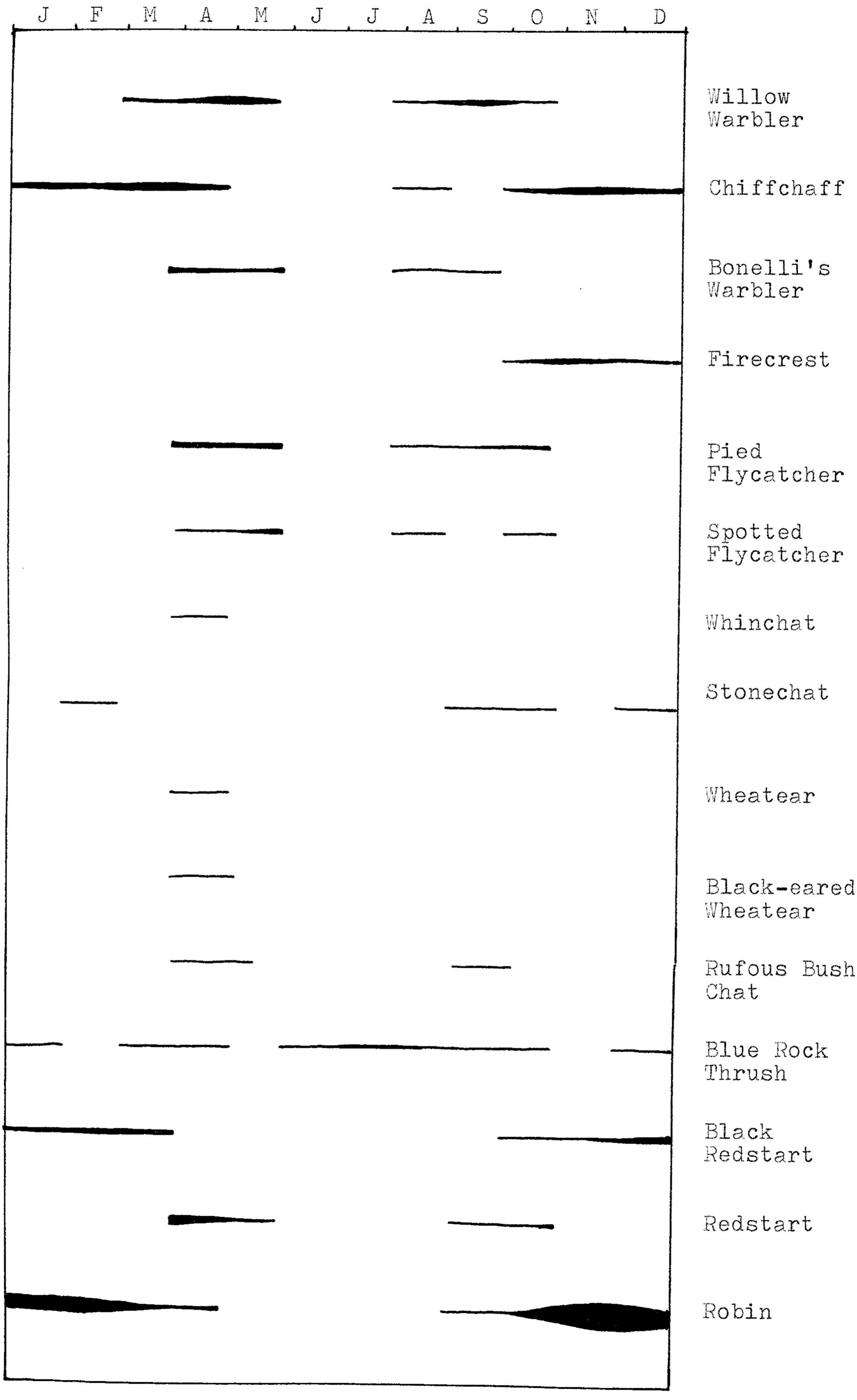
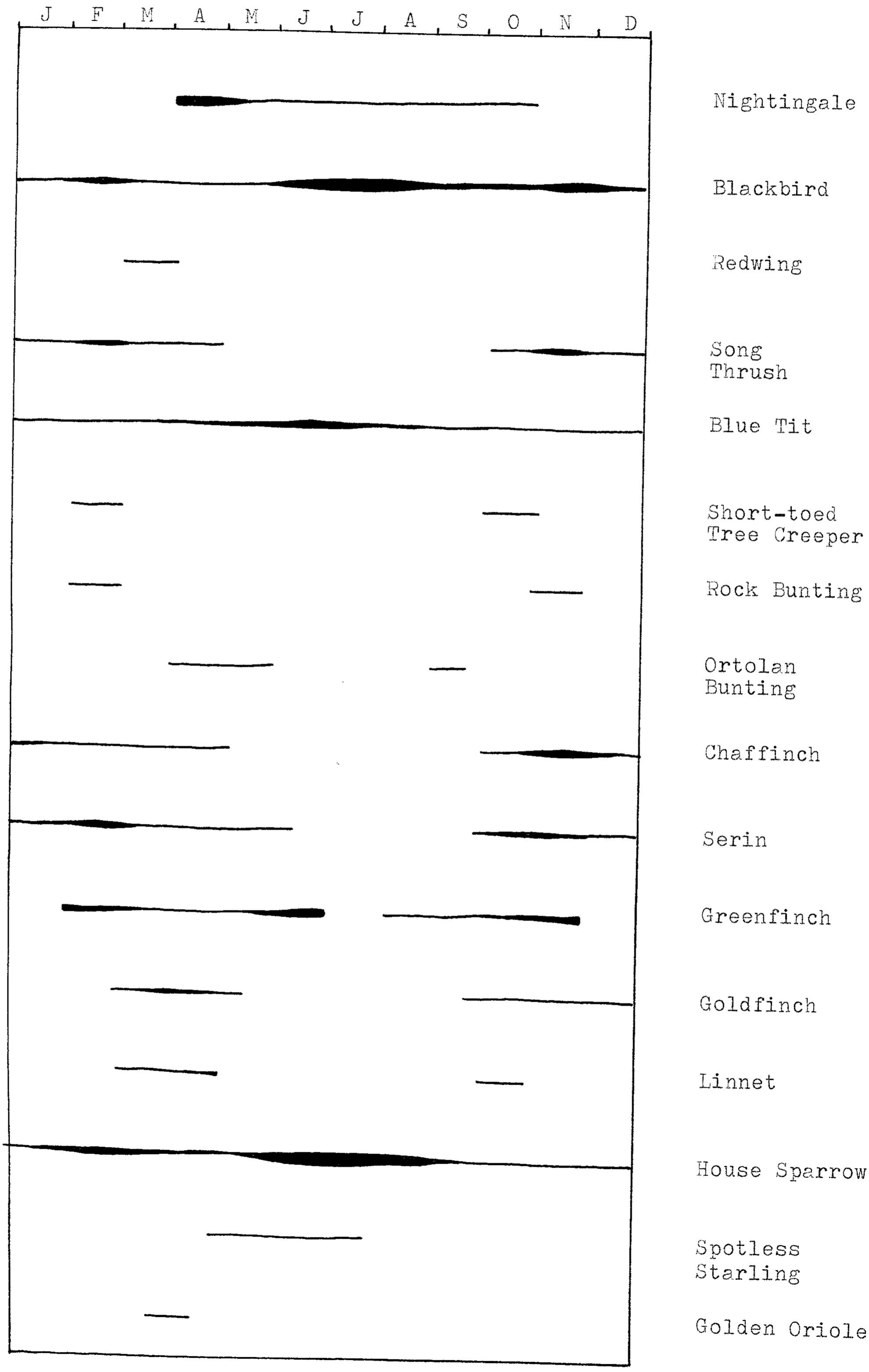


FIGURE 2.1.


J
F
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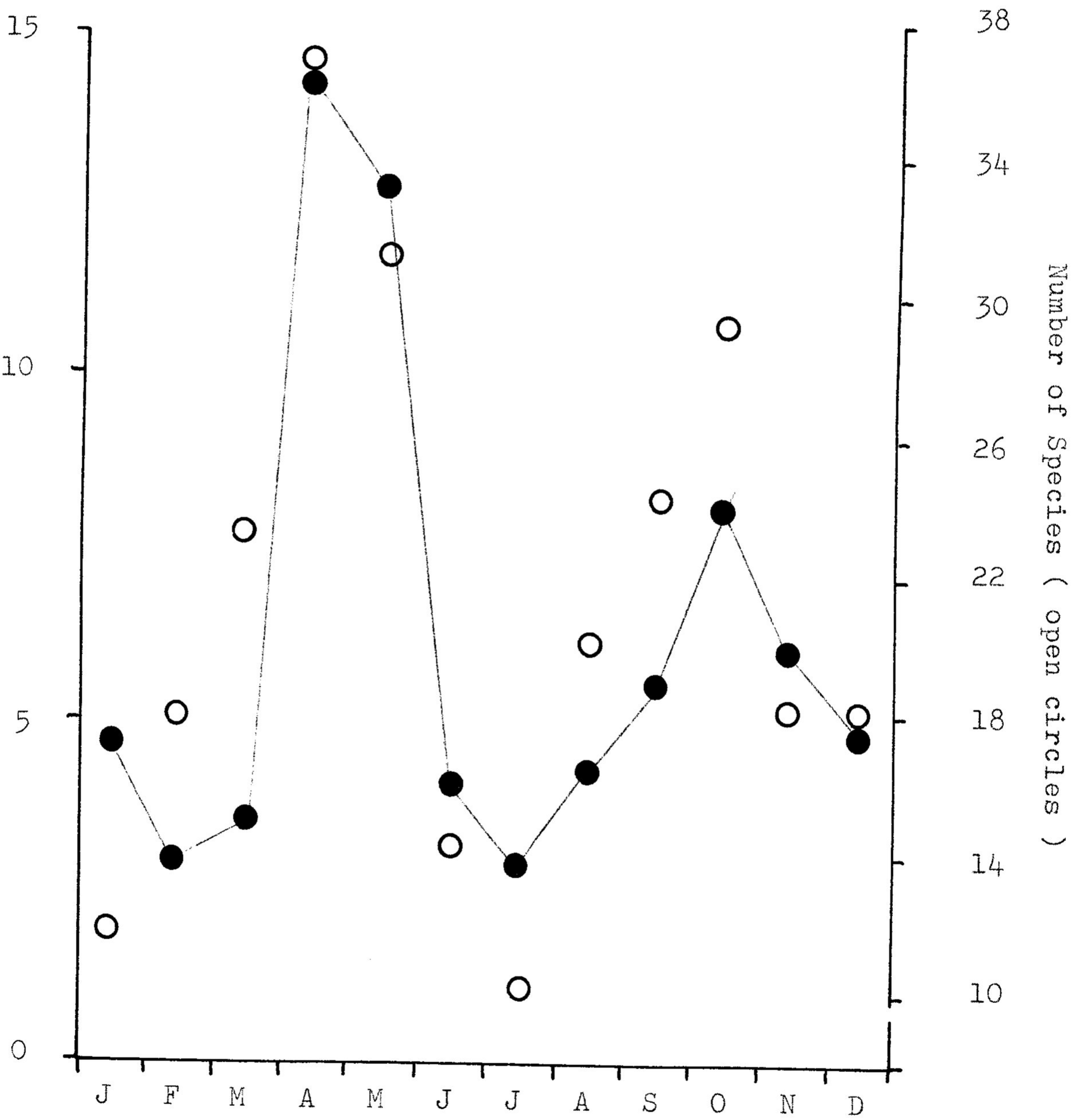
Nightingale
Blackbird
Redwing
Song Thrush
Blue Tit
Short-toed Tree Creeper
Rock Bunting
Ortolan Bunting
Chaffinch
Serin
Greenfinch
Goldfinch
Linnet
House Sparrow
Spotless Starling
Golden Oriole

FIGURE 2.2. Species Diversity and Number of Species in low Maquis at Jews' Gate.



Unless otherwise stated, all diagrams are composed of data from all years lumped.

there is little food for most kinds of migrants in the Gibraltar area (Appendix 3) in early autumn, as throughout most of the Mediterranean Basin (Moreau & Dolp 1970), because the rains arrive in October, very few migrants descend to feed. More migrants stop to forage in the habitat after the rains. By October most trans-Saharan migrants have passed and it is those species which winter in the Mediterranean Basin which enter the community. Although diversity increases in October, it is not as high as in spring. The wet and mild winters enable the habitat to sustain a more diverse community than in summer. Even though the number of species in the habitat increased from January to February, diversity was low in the latter month. This was due to an immense passage of Blackcaps which dominated the bird community numerically.

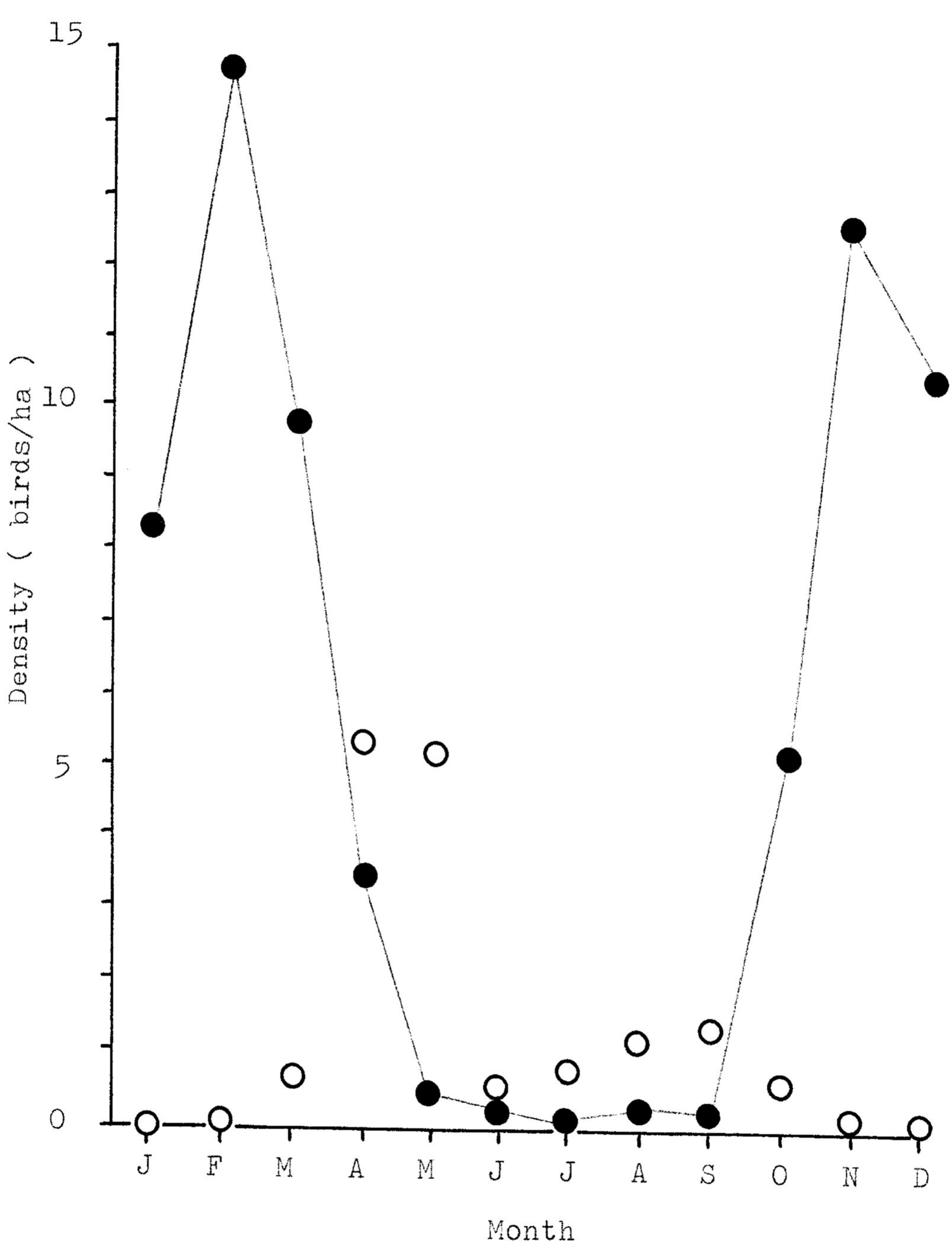
The term migrant is used to describe any species or population which is not resident in the habitat all year. The term therefore includes passage migrants, winter residents and summer residents, and it is equivalent to the ' non-residents ' in other studies (Herrera 1978 a). Migrants occuring at Gibraltar may be grouped under two headings, trans-Saharan migrants and Mediterranean-wintering migrants. The former are birds which breed in Europe and winter in Africa, south of the Sahara Desert (Moreau 1961, Bernis 1962). At Gibraltar they occur mainly while on passage but a few breed in small numbers (with the exception of swifts which breed in large numbers on Gibraltar). Mediterranean-wintering migrants are birds which breed in Europe and which winter along the shores of the Mediterranean Sea

(Bernis 1962). At Gibraltar they occur as passage migrants and as winter residents. Some species, such as the Chiffchaff Phylloscopus collybita winter mostly in the Mediterranean area but have populations which enter tropical Africa (Moreau 1972). Such birds are counted as Mediterranean-wintering migrants as it is not possible to distinguish between the different populations.

Mediterranean-wintering migrants are most abundant in low Maquis in early spring and late autumn (Fig.2.3.). The main species are Blackcap, Chiffchaff, Black Redstart Phoenicurus ochruros, Robin Erithacus rubecula, and Song Thrush Turdus philomelos . They are absent during the summer months but are abundant in winter.

Trans-Saharan migrants never reach the densities of the Mediterranean-wintering migrants (Fig.2.3.). In spring they pass later and in autumn earlier than the Mediterranean-wintering species. The spring peak coincides with the maximum recorded diversity in the community but in the autumn they are scarce and contribute little to the total diversity. The main species are Reed Warbler Acrocephalus scirpaceus, Melodious Warbler Hippolais polyglotta, Orphean Warbler Sylvia hortensis, Garden Warbler S.borin, Whitethroat S.communis, Subalpine Warbler S.cantillans, Willow Warbler Phylloscopus trochilus, Bonelli's Warbler P.bonelli, Pied Flycatcher Ficedula hypoleuca, Spotted Flycatcher Muscicapa striata, Redstart Phoenicurus phoenicurus, Nightingale Luscinia megarhynchos and Ortolan Bunting Emberiza hortulana. They are therefore mainly insectivores which tap temporary food sources during the spring and summer in Europe, and which depart rapidly in the autumn.

FIGURE 2.3. Densities of Major Migrant Groupings in low Maquis at Jews' Gate.



Mediterranean-wintering migrants (solid circles)
Trans-Saharan migrants (open circles)

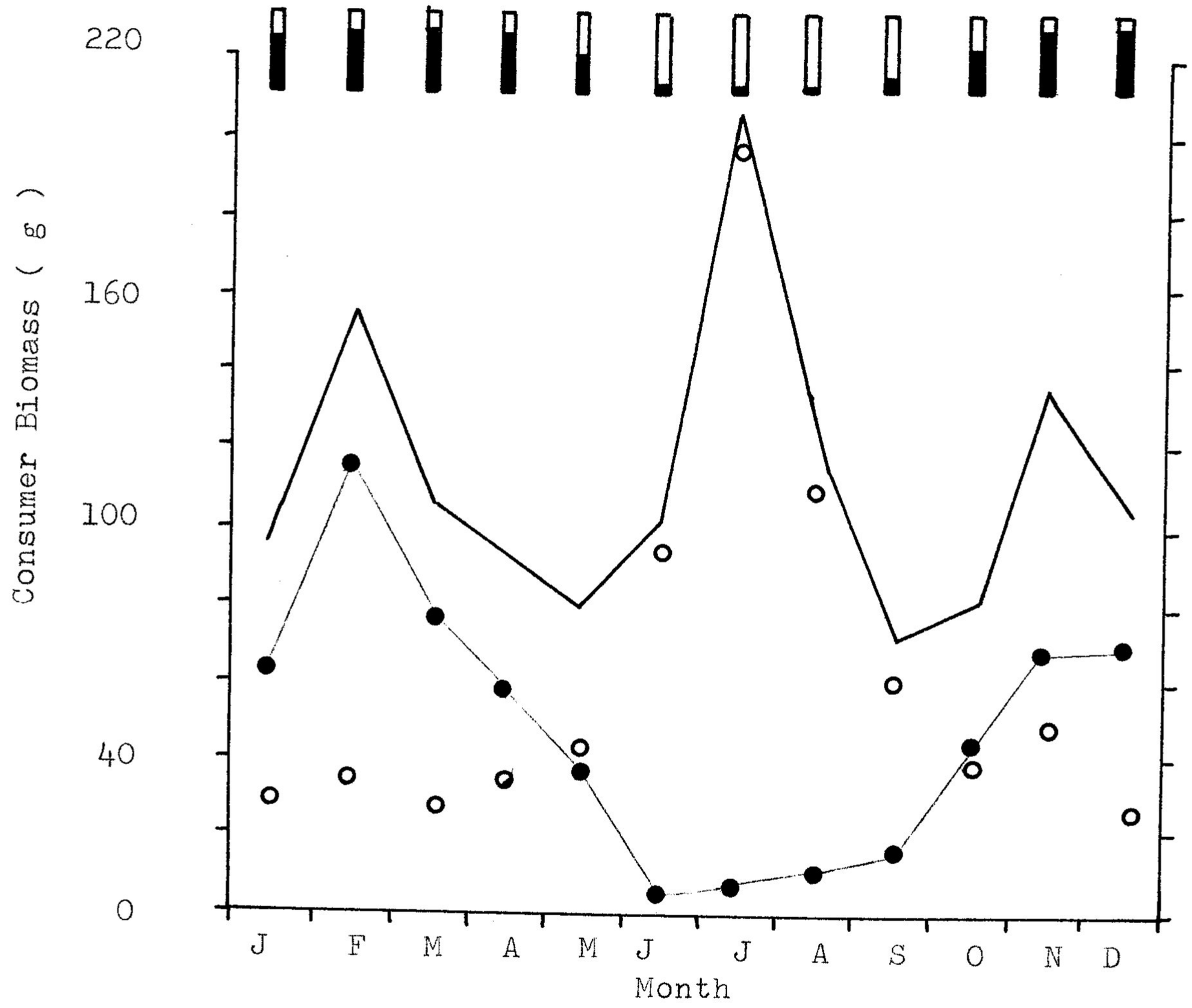
There are three biomass peaks in low Maquis (Fig.2.4.). The main peak is in July and is due to the emergence of many young birds of the resident species (for estimation of number of juveniles, see 3.3.1.), particularly Blackbird Turdus merula, Sardinian Warbler Sylvia melanocephala and Blackcap. The other peaks are in February and in November and are as a result of the large passages of Mediterranean-wintering migrants during these months (especially February). The winter biomass is high and this is to a large extent due to the winter residents. Consumer biomass is lowest in September at the height of the drought, when there are few migrants using low Maquis and when the number of resident individuals is at its lowest (probably as a result of a high juvenile mortality at this time). The other minimum, in May, is due to a low in the number of resident individuals prior to the emergence of the year's offspring. At this time also, the number of trans-Saharan migrants present in low Maquis is small and they add little to the consumer biomass.

Resource exploitation in low Maquis

(a) Ground Insectivores

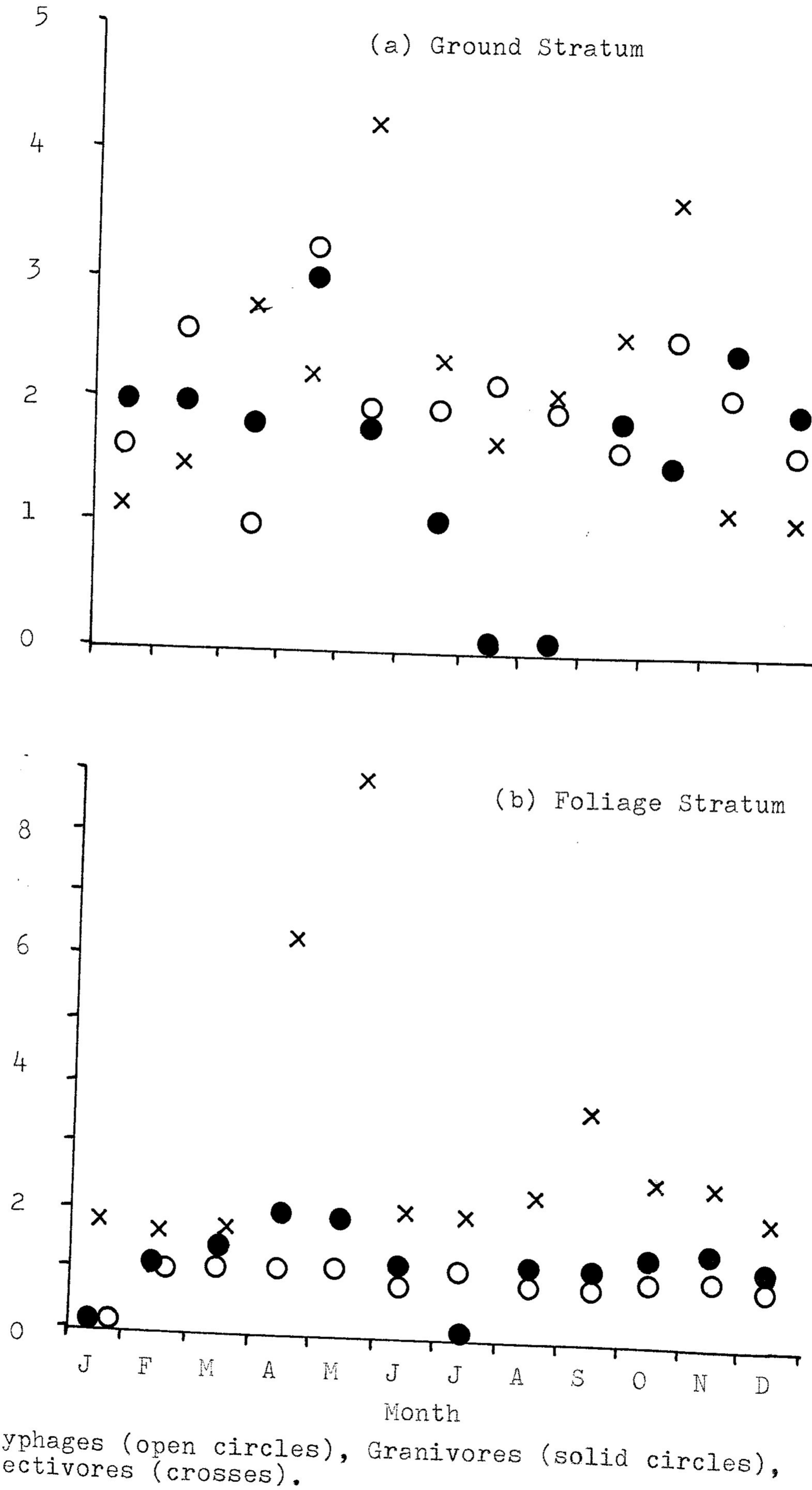
Diversity is generally low except in May and in October (Fig.2.5.). In May the main ground insectivores are trans-Saharan migrants such as the Woodchat Shrike Lanius senator or the Tree Pipit Anthus trivialis but in October it is Mediterranean-wintering migrants, such as Black Redstart or Dunnock Prunella modularis, which are dominant numerically and by biomass. Ground insectivores are never abundant in low Maquis, even though there is a small biomass

FIGURE 2.4. Seasonal Changes in Consumer Biomass in low Maquis at Jews' Gate.



Migrants (solid circles), Residents (open circles), Total (line)
Bar diagrams indicate migrant proportion by biomass (%) - area filled

FIGURE 2.5. Diversity of Main Foraging Groups in low Maquis at Jews' Gate.



Polyphages (open circles), Granivores (solid circles), Insectivores (crosses).

peak in April which is due mainly to migrating Nightingales (Fig.2.6.).

(b) Ground Granivores

Outside the period June to August, the ground granivore element in low Maquis is diverse (Fig.2.5.) but it is never significant in biomass (Fig.2.6.).

(c) Ground Polyphages

The ground polyphage sub-community is diverse and is also important by biomass (Figs.2.5., 2.6.). In summer the most important biomass contribution is from the residents, e.g. Blackbird and Blue Rock Thrush Monticola solitarius, but others such as the Song Thrush contribute substantially to the increases in the period November to February (Fig.2.6.).

(d) Foliage Insectivores

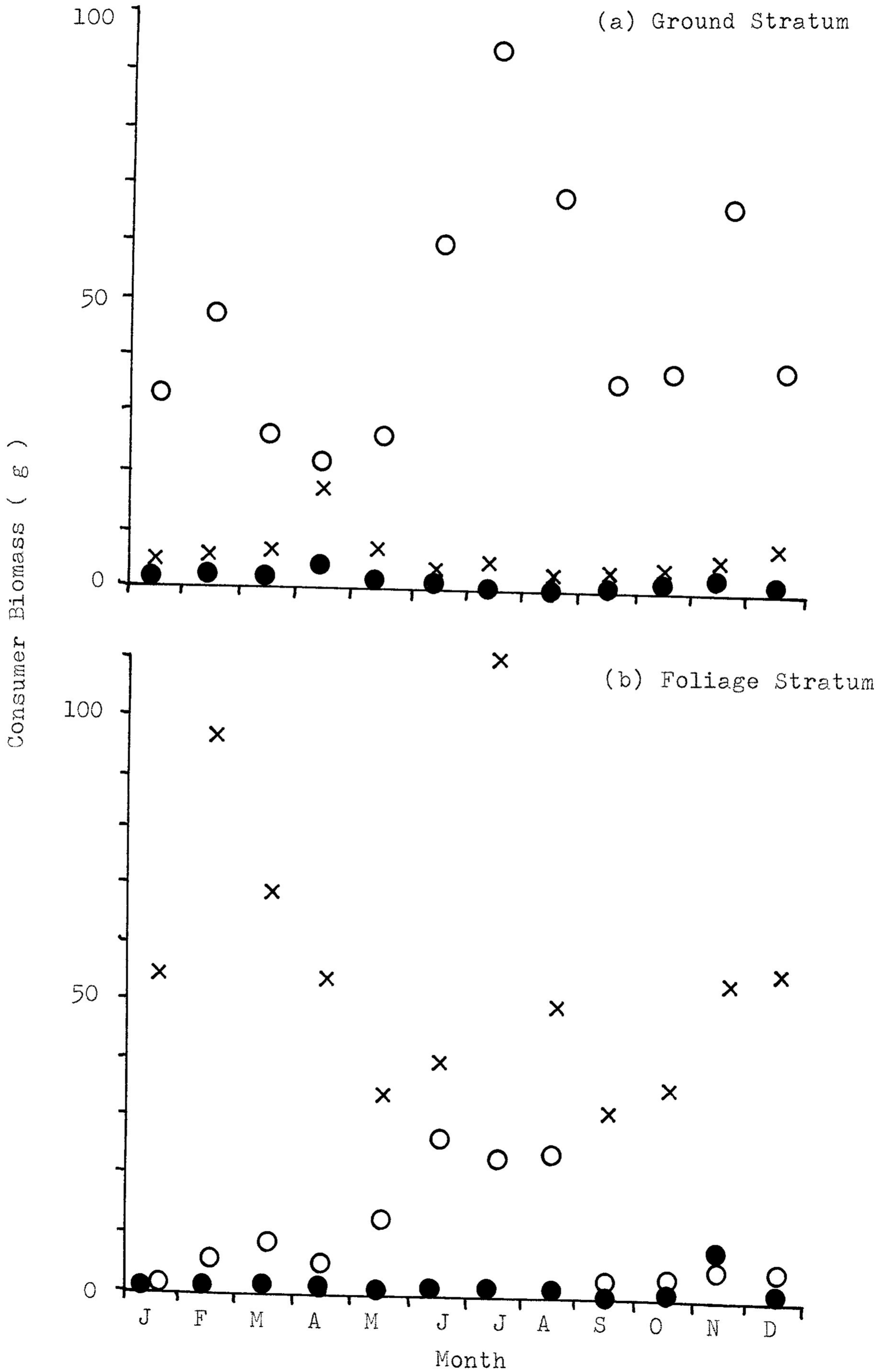
In low Maquis, foliage insectivores dominate numerically and by biomass. As many species are trans-Saharan migrants, an April-May peak in diversity is expected, as is a lower one in September (Fig.2.5.). However, they contribute little to the total biomass which peaks in February (due to migrating Blackcaps) and in July (due to fledgling Blackcaps and Sardinian Warblers, 3.3.1.). The winter biomass is high because many foliage insectivores are in the community at that time.

(e) Foliage Granivores

The habitat appears to be poor for granivores and, although there are peaks in diversity in spring and autumn (Fig. 2.5.), their biomass is insignificant (Fig.2.6.).

(f) Foliage Polyphages

FIGURE 2.6. Impact of main Foraging Strategies in low Maquis at Jews' Gate.



Polyphages (open circles), Granivores (solid circles), Insectivores (crosses)

Polyphages are not as important in foliage as they are on the ground and their diversity in foliage is low. A small biomass increase in the summer probably results from the emergence of young birds (Fig.2.6.).

(g) General Remarks

Five species are resident in low Maquis. Two are abundant foliage insectivores, the Blackcap and the Sardinian Warbler, and both are capable of switching their diet to other food sources in times of insect shortage (3.4.9.). A third foliage insectivore, the Blue Tit, is scarcer and only uses the habitat for foraging. The two other species are ground foragers and both are polyphagous. The Blackbird takes a wide range of foods and the House Sparrow, though at times mainly a granivore, also takes arthropods, fruit, nectar, etc.

Very few other species breed in low Maquis and none of these are common. The Wren, though strictly a resident, appears to be absent from low Maquis in winter (Fig.2.1.). Similar phenomena elsewhere have been attributed to inter-habitat movements by others, even though the evidence is no stronger than that presented here (Frochot 1971, Herrera 1978 a). The Nightingale is a summer visitor and one or two pairs breed in low Maquis.

Several species enter the habitat in winter. Two are abundant, the Chiffchaff, a foliage insectivore which becomes essentially a nectarivore at the height of the winter (3.4.10), and the Robin which is a ground polyphage. There are several other species in smaller numbers in this habitat in winter, Dunnock, Firecrest, Black Redstart, and Song Thrush. The Blackcap population is augmented by many individuals from further north (3.3.3.). All other

species occur in transit.

The dominant species, numerically and by biomass, in low Maquis are indicated in Figs.2.7., 2.8. Foliage insectivores/ frugivores and ground polyphages are dominant. The first category may also be considered omnivorous. This situation also occurs in the other habitats at Gibraltar and appears to be related to the spring/summer peak in foliage insect abundance (Appendix 3) and with the relative abundance of ground arthropods in winter (Appendix 3). The few species which are resident are plastic (Morse 1971), some generalists and others specialists. The two ground feeders have a varied diet and can easily cope with the summer drought, whilst the foliage insectivores change to alternative foods to insects in winter. A small number of species enter the community in winter but these are more specialised and have to leave in summer. The densities of the few resident species are very high (5.3., Appendix 1). It appears that many other summer visitors which could utilise the habitat cannot settle there because of the numerical (McNaughton & Wolf 1970) and social (Morse 1974) dominance of the residents. Examples of such species are Subalpine Warbler, Melodious Warbler, and Rufous Bush Chat.

Garigue/Steppe Complex

56 species are regular annually in this habitat at Gibraltar. In addition, there are a few non-passerines of importance, notably Barbary Partridge Alectoris barbara, Little Owl Athene noctua, Hoopie and Wryneck.

The months with highest species diversity in Garigue were March, April, October and November (Fig.2.9.). The autumn

FIGURE 2.7. Dominant Species by Numbers in low Maquis at Jews' Gate.

Melodious Warbler (mw), Garden Warbler (gw), Blackcap nominate (bc), Blackcap local (bc'), Sardinian Warbler (sw), Willow Warbler (ww), Chiffchaff (ch), Black Redstart (br), Robin (r), Nightingale (n), Blackbird (bb), House Sparrow (hs).

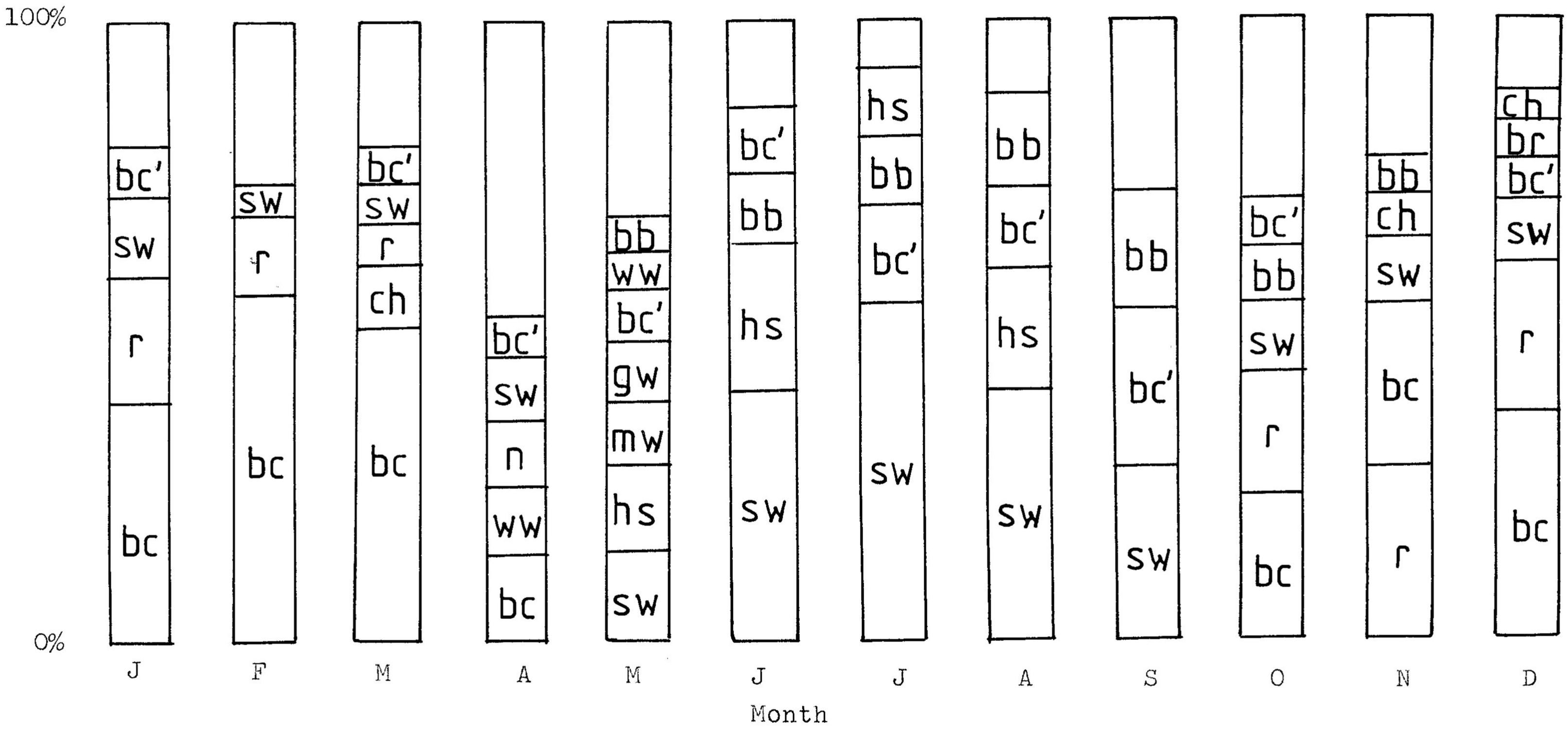


FIGURE 2.8. Dominant Species by biomass in low Maquis at Jews' Gate.

legend as in Fig.2.7.

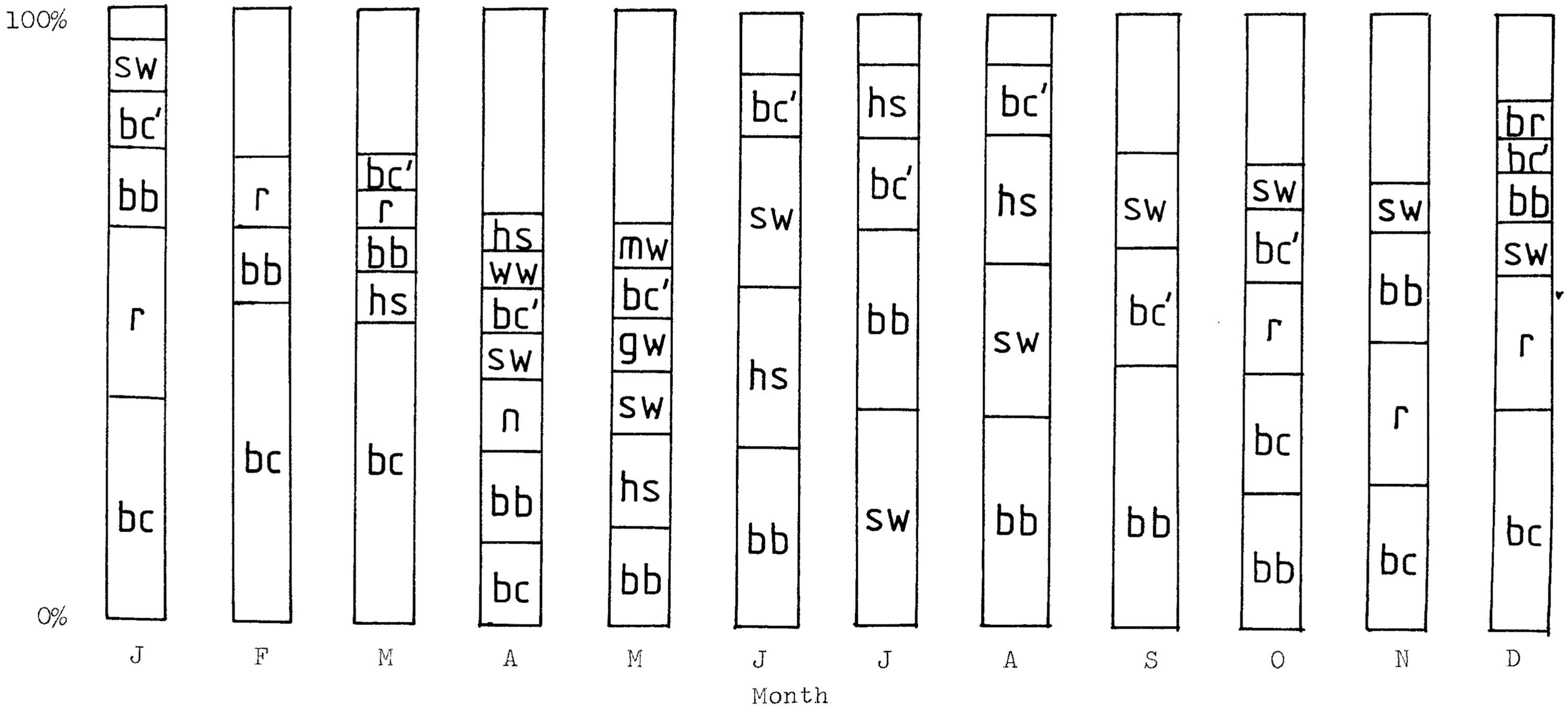
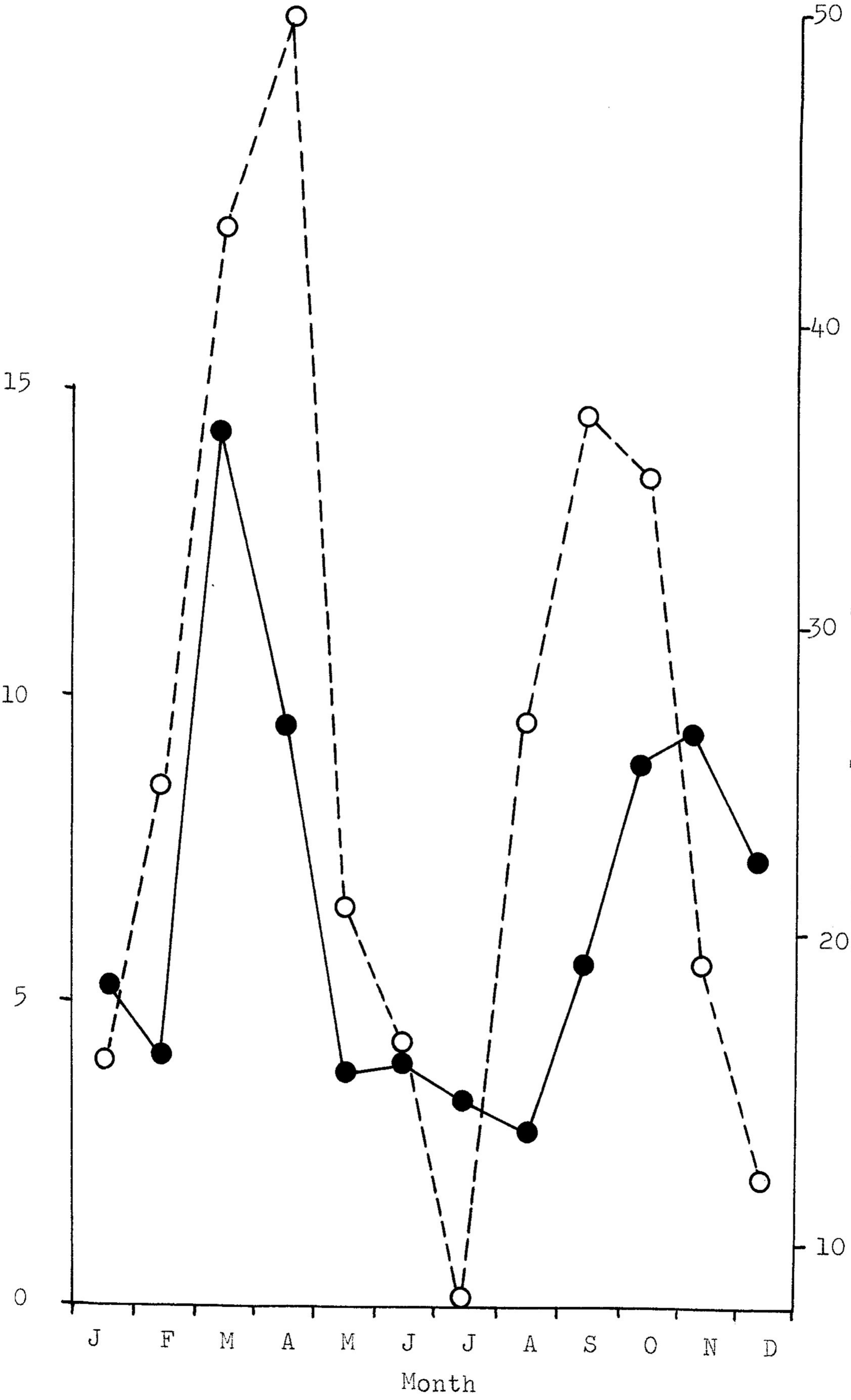


FIGURE 2.9. Species Diversity and Number of Species in Garigue at Windmill Hill.



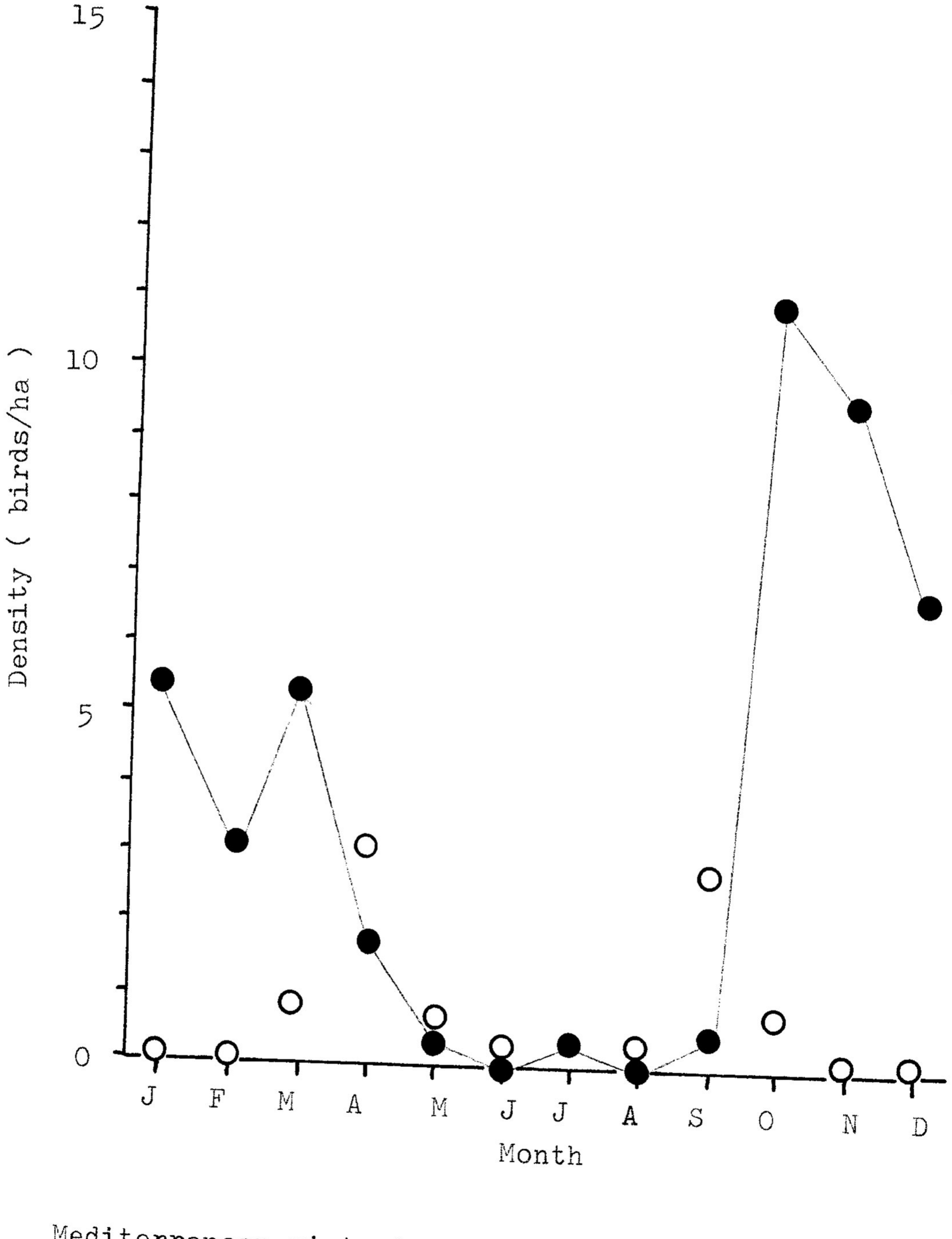
peak remains lower than the spring one, as in low Maquis, but the difference between the two peaks is less pronounced than in low Maquis. The community is diverse in winter, especially in December, but it is poor during the summer months, with a minimum in August at the height of the drought (Fig.1.5.). The pattern is therefore essentially as in low Maquis although there are differences which will be dealt with later.

Mediterranean-wintering migrants are most abundant in October (Fig.2.10.). There is then a gradual decline in density through the winter and there is only a small increase in March. The density in winter is high. Between April and September density is low or zero. Trans-Saharan migrants peak in spring and in autumn, after and before the Mediterranean-wintering migrants respectively (Fig.2.10.). The spring peak is in April and the autumn one is in September. Densities are always low in comparison with those of the Mediterranean-wintering migrants.

The main species of Mediterranean-wintering migrants in Garigue are Skylark Alauda arvensis, Crested Lark Galerida cristata, Song Thrush, Black Redstart, Stonechat Saxicola torquata, Dartford Warbler Sylvia undata, Meadow Pipit Anthus pratensis, Goldfinch Carduelis carduelis, Greenfinch C.chloris, Serin Serinus serinus, Linnet Acanthis cannabina, and Corn Bunting Emberiza calandra.

The main trans-Saharan migrants are Hoopoe, Short-toed Lark Calandrella cinerea, Wheatear Oenanthe oenanthe, Black-eared Wheatear O.hispanica, Redstart, Whinchat Saxicola rubetra, Whitethroat Sylvia communis, Spectacled

FIGURE 2.10. Densities of Major Migrant Groups in Garigue at Windmill Hill.



Mediterranean-wintering Migrants (solid circles)
Trans-Saharan Migrants (open circles)

Warbler S.conspicillata, Rufous Bush Chat Cercotrichas galactotes, Willow Warbler, Melodious Warbler, Tree Pipit Anthus trivialis, Tawny Pipit A.campestris, Woodchat Shrike, and Ortolan Bunting.

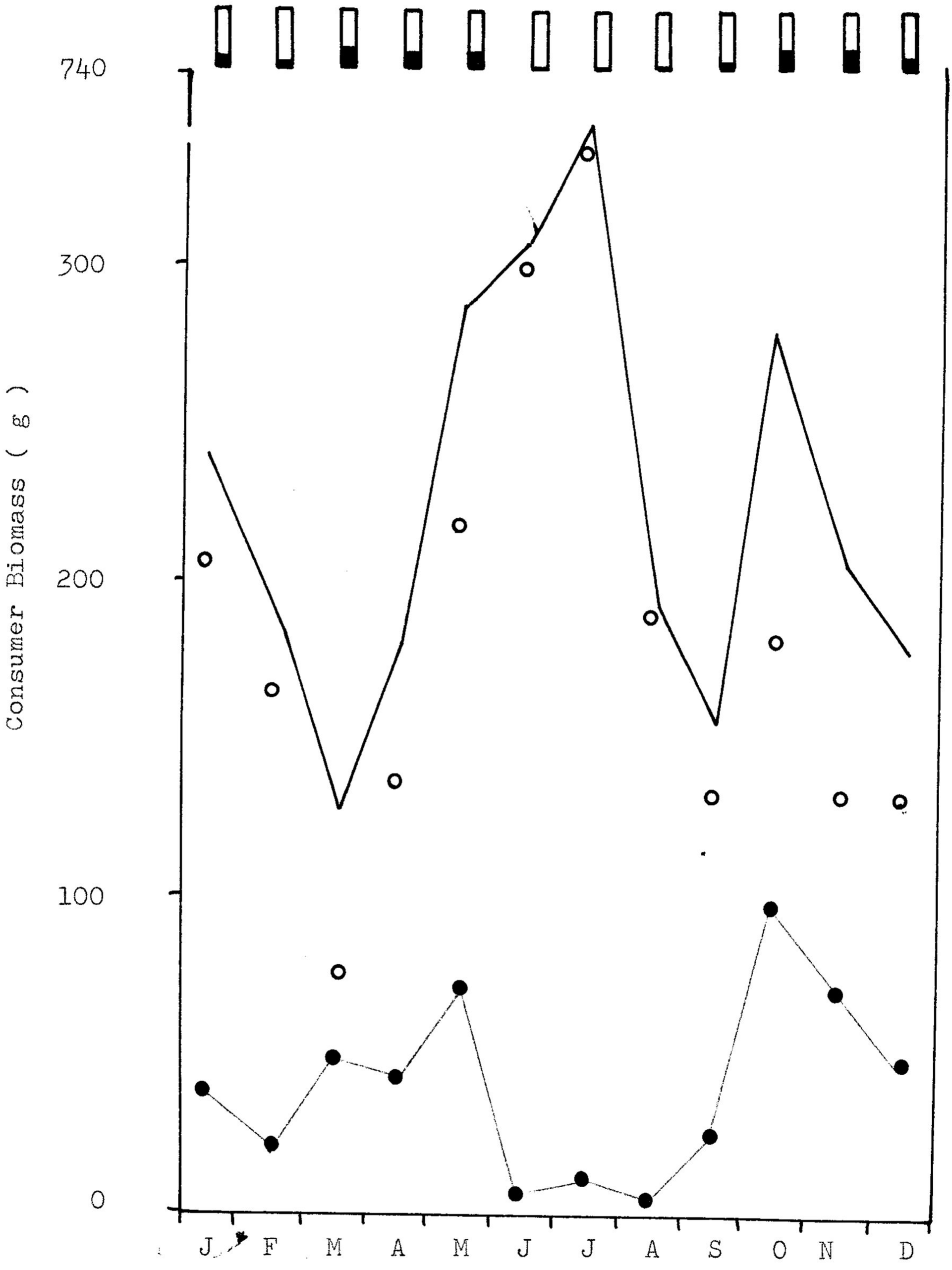
The main peak in biomass in Garigue occurs in July (Fig.2.11.). This, as in low Maquis, is due to the emergence of many young birds from the nests, especially Spotless Starlings and Blackbirds. There are other peaks in October and in January due mainly to Mediterranean-wintering migrants. Biomass is lowest in March when there is a resident low and there are few large migrants present.

Resource exploitation in Garigue

(a) Ground Insectivores

Diversity is low in mid-summer (Fig.2.12.) when the ground is dry and in mid-winter when few insects are active. There are two main peaks in diversity, in May and in September, and both are due to trans-Saharan migrants on passage. The increase in September is as a result of some species, such as Wheatear and Redstart, which do not seem to overfly the area as much as other trans-Saharan migrants at this time. As ground arthropods were not as scarce as foliage arthropods at this time,it could be that these species were able to stop to feed (Appendix 3). In tropical Africa, the ground-foraging trans-Saharan migrants are those which remain right through the dry season (Morel 1968, P.Lack pers.comm.)· There are many other species present in small numbers in September. Further on towards

FIGURE 2.11. Seasonal Changes in Consumer Biomass in Garigue at Windmill Hill.



Migrants (solid circles), Residents (open circles), Total (line) Bar diagrams indicate migrant proportion by biomass (%) - area filled

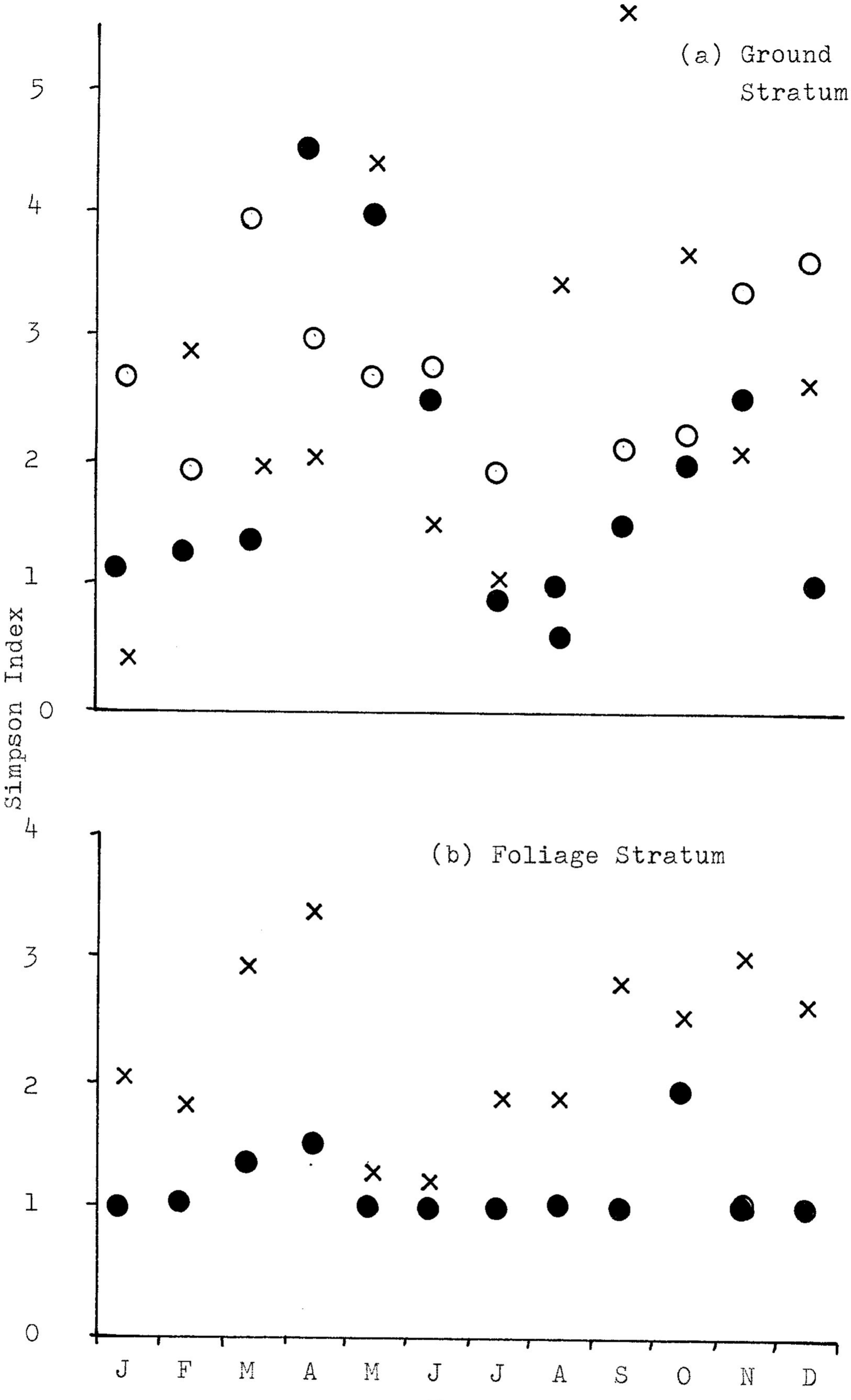


FIGURE 2.12. Diversity of main foraging strategies in Garigue at Windmill Hill.
Polyphages (open circles), Insectivores (crosses), Granivores (solid circles).

winter, there are just a few, abundant, species and so diversity is low. In biomass terms, however, there are no such peaks excepting a small increase in winter biomass and a low in summer (Fig.2.15.).

(b) Ground Granivores

The changes in ground granivore diversity are similar to those of the ground insectivores except that the spring peak occurs earlier and is higher than the autumn peak which is in November (Fig.2.12). In both cases the peaks are due to migrating finches and buntings, especially Linnet, Serin, Goldfinch and Corn Bunting. There is no biomass peak in spring but there is one in summer, due to the hatching of young Barbary Partridges, the only ground granivore species present regularly in this habitat at this time. There is a second, lower, peak in October due to the finches (Fig.2.13.).

(c) Ground Polyphages

The ground polyphage community is very diverse especially in winter and early spring, but diversity is very low in August when only a small number of species is present (Fig.2.12.). The biomass pattern is the opposite of this (Fig.2.13.). Ground polyphages dominate by biomass all year but the peak coincides with the emergence of young birds in July. The main species are Spotless Starling, Blackbird and House Sparrow. There follows a sharp decline, probably due to habitat emigration and to mortality (Fig.2.13.).

(d) Foliage Insectivores

The foliage insectivore community is diverse and fluctuates less than the ground insectivore community (Fig.2.12.).

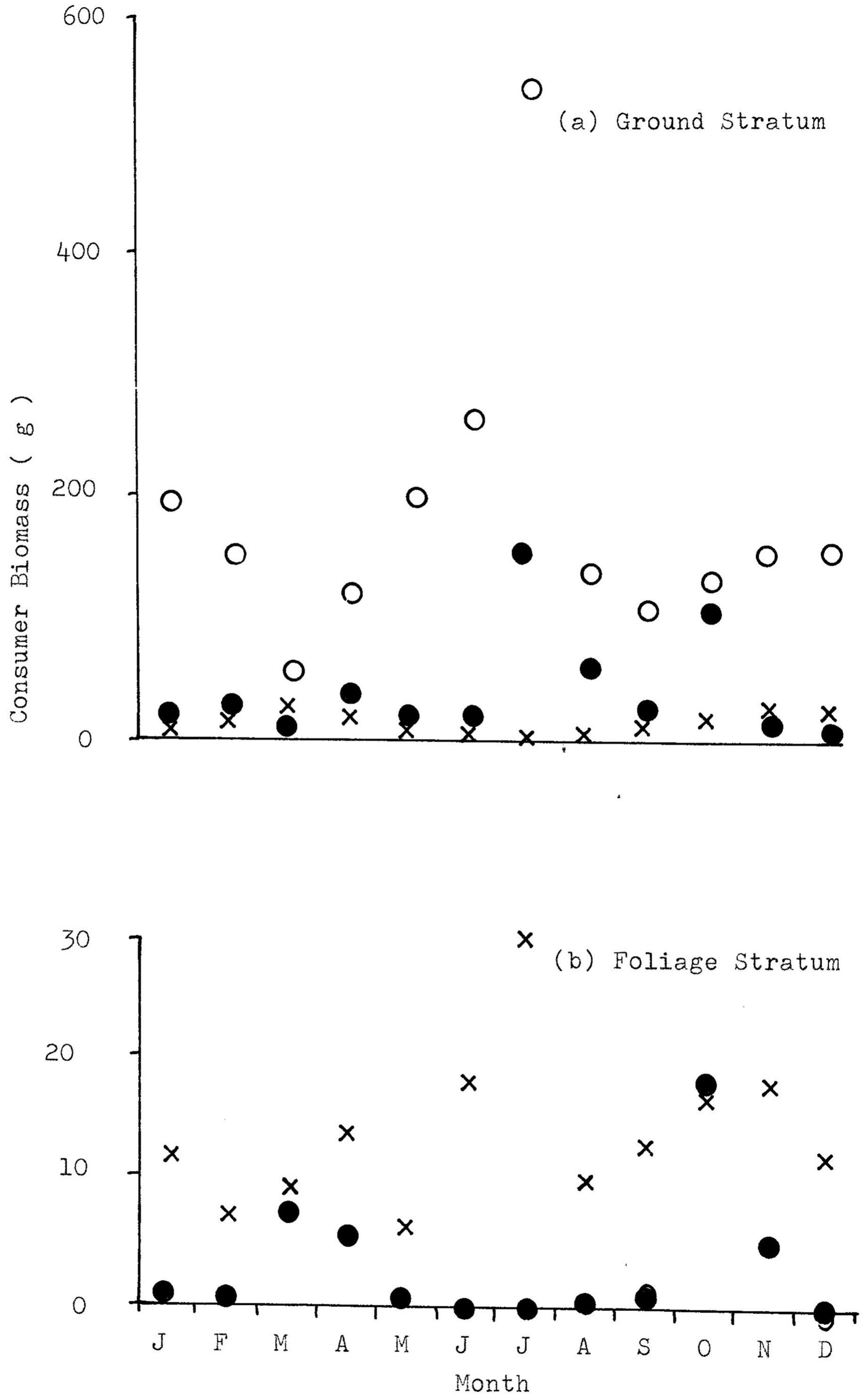


FIGURE 2.13. Impact of Main Foraging Strategies in Garigue at Windmill Hill.
Legend as Fig.2.12.

The main peak is in April with the passage of a wide range of trans-Saharan warblers. After the summer drop, there is a gradual rise towards a more diverse winter community but there is no autumn peak. The biomass peak occurs in July with the hatching of Sardinian Warblers (Fig.2.13.). Overall, foliage insectivores are insignificant in this habitat when compared to ground polyphages.

(e) Foliage Granivores

There are only a few foliage granivores in this habitat and there is only a slight peak in diversity, in October due to finches which are on passage (Fig.2.12.). Foliage granivores contribute little biomass but there are two recognisable peaks, one in spring and the other in autumn (Fig.2.13.).

(f) General Remarks

Six species are resident in Garigue. Four are ground polyphages, the Spotless Starling, the Blackbird, the Blue Rock Thrush and the House Sparrow. They all have versatile diets. At least two of these species can move from one habitat to another to forage. There is only one resident foliage insectivore, the Sardinian Warbler. The other resident is a ground granivore, the Barbary Partridge, which could also be classed as a polyphage as it regularly eats shoots, roots and other vegetable matter. The Garigue residents are thus mainly ground foragers.

No other species breed in Garigue although some, like Fan-tailed Warbler Cisticola juncidis, Spectacled Warbler and Corn Bunting attempt to do so in some years. There are some species which enter the community in winter and some

of these may be important numerically or by biomass (Figs. 2.14., 2.15.). These species are Skylark, Meadow Pipit, Stonechat, Black Redstart, Robin, Song Thrush, Corn Bunting, Crested Lark, Fan-tailed Warbler, and Chiffchaff.

2.3.2. A comparison of Matorral Communities

Species Diversity

The overall pattern of seasonal changes in species diversity is the same in low Maquis and in Garigue (Figs.2.2., 2.9.). There is nevertheless a greater species turnover in Garigue. If High Maquis is also included (Fig.2.16.) then this habitat has least species turnover of the three. It seems probable that the more-open habitats are more seasonal than the more-complex ones, and cannot support as many resident species (Cody 1974, Karr 1976 a, Alerstam & Enckell 1979).

The summer low in Garigue extends over a longer period than in low Maquis (Figs.2.2., 2.9.) supporting the view that this habitat is more seasonal than the Maquis habitats. Winter diversity is similar in both habitats but low Maquis holds more species than Garigue. The peaks in diversity during the migratory periods are similar in the two habitats but Garigue can sustain many more species than low Maquis. The diversity peaks do not coincide exactly in the two habitats and come earlier in spring and later in autumn in Garigue than in low Maquis. This confirms that Garigue is more seasonal and has a longer, harsher summer than low Maquis. This summer extends into late spring and early autumn in Garigue. Therefore, despite

FIGURE 2.14. Dominant Species by Numbers in Garigue at Windmill Hill.

Sardinian Warbler (sw), Spotless Starling (Sp), House Sparrow (hs), Blackbird (bb), Black Redstart (br), Serin (s), Stonechat (st), Meadow Pipit (mp), Goldfinch (g), Barbary Partridge (bp), Linnet (l), Greenfinch (gr), Chiffchaff (ch), Robin (r), Skylark (sk).

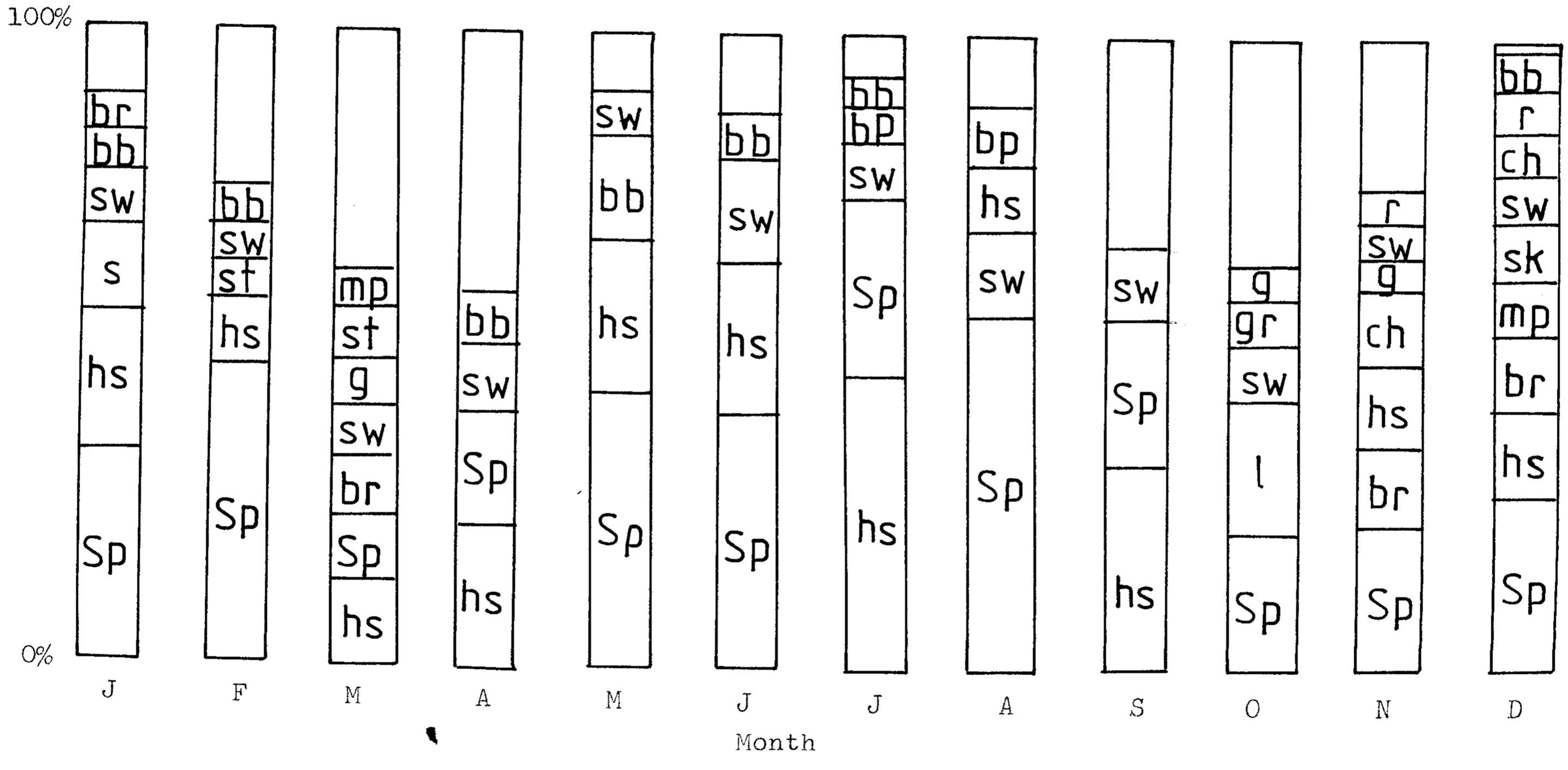
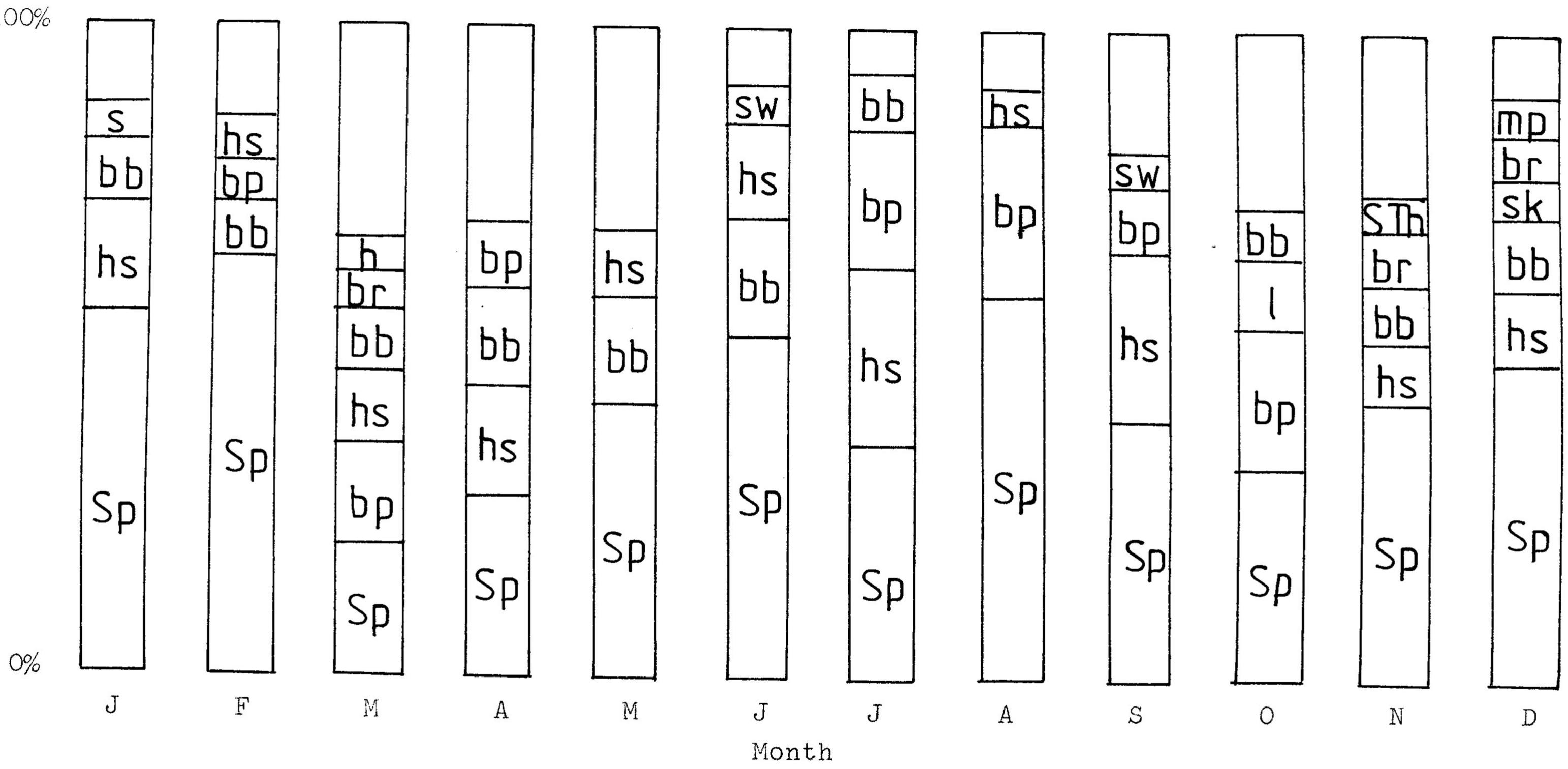


FIGURE 2.15. Dominant Species by biomass in Garigue at Windmill Hill.

legend as Fig.2.14. Hoopoe (h), Song Thrush (STh)



the presence of many migrant species in May and September, diversity is then very low as few species use the Garigue. It is only in March, October and November that transit birds can utilise the Garigue for foraging. In low Maquis, diversity remains high into May and there is then a sharp drop in June (Fig.2.2.). In the autumn the increase in diversity is less abrupt than in Garigue.

Migrants

Mediterranean-wintering migrants always reach higher densities than trans-Saharan migrants in the two habitats (Figs.2.3., 2.10.). In low Maquis, Mediterranean-wintering migrants reach a peak in density in February and another in November, and in Garigue in October and in March. In low Maquis, the spring peak is greater than the autumn one, but in Garigue the autumn one is more important than the spring one. This is difficult to explain and a further knowledge of the nature of the migrants using these habitats will be required before the question can be finally resolved. However, the Garigue pattern is more consistent with that of an arrival of birds for the winter, whereas in low Maquis the pattern has clear-cut peaks due to passage birds. Thus, Blackcaps and Chiffchaffs produce the peaks in low Maquis and it could be that these birds are less common in autumn because low Maquis is less productive then than in spring, or because many are aiming for a rapid entry to the wintering grounds further to the south. In both spring and autumn, Mediterranean-wintering migrants reach higher densities in low Maquis than in Garigue. The summer low extends over a similar period in the two habitats.

In low Maquis, the spring peak for trans-Saharan migrants is also more pronounced than the autumn peak but the two peaks are more or less the same in Garigue. Many of the trans-Saharan migrants which use low Maquis are foliage insectivores with restricted Mediterranean breeding ranges. Many of these are known to overfly the Mediterranean shores in the autumn, e.g. Subalpine Warbler and Orphean Warbler (Moreau 1972). Many of the trans-Saharan migrants which use Garigue are ground insectivores which extend further north into Europe than the foliage insectivores. They probably have to stage their journey in several flights and may not be in as good a position to overfly the Mediterranean shores (Langslow 1976, Smith 1979). This could also partly explain why many of the trans-Saharan migrants in Garigue, e.g. Whinchat, Redstart or Wheatear are as common in autumn as they are in spring.

Consumer Biomass

Consumer biomass is always higher in Garigue than in low Maquis (Figs.2.4., 2.11.). This is so because the dominant species numerically in the habitat are larger than the dominant species in low Maquis, e.g. Spotless Starling and Blackbird. The pattern is otherwise very similar in both habitats, with a main peak in July which coincides with the emergence of young birds. There is an autumn peak in the two habitats which in low Maquis is due exclusively to migrants but which in Garigue is also partly as a result of resident species. For example, Spotless Starlings congregate in flocks in Garigue in the autumn where they forage on the ground.

In Garigue, migrant biomass never exceeds resident biomass (Fig.2.11.) but in low Maquis migrant biomass exceeds resident biomass from October to April (Fig.2.4.). There is a small mid-winter peak in Garigue which does not occur in low Maquis. In both habitats migrant biomass is lowest in the summer.

Resource exploitation

(a) Ground Insectivores

Both habitats have diverse ground insectivore communities (Fig.2.5., 2.12.) with peaks in spring and autumn. In low Maquis the greatest diversity is in May and in Garigue it is in September. In the two habitats diversity is lowest in winter and in summer. Ground insectivore consumer biomass is insignificant in both habitats (Figs.2.6., 2.13.).

(b) Ground Granivores

Ground granivores form a diverse community at all times except in mid-summer. In mid-summer there are no species in low Maquis and only one in Garigue. Small peaks occur during the passage periods but the only one of note is that produced by finches and buntings in Garigue during April and May. The ground insectivore biomass is negligible in low Maquis but is considerable in Garigue in July and in October.

(c) Ground Polyphages

Polyphages are, by definition, diet generalists and as such they are successful in highly seasonal environments (Morse 1971). In Garigue and in low Maquis, the summer drought produces a dry and unproductive ground stratum and so only species which can have a varied diet can

remain to breed. Ground polyphages form a diverse community in both habitats and the seasonal changes in diversity are small, indicating that the community is a stable one. Other strata or foods may be temporary and may be invaded by non-residents but ground polyphages are capable of exploiting many opportunities which become available at different times of year, so they can be resident.Polyphages dominate the ground stratum by biomass all year(Figs. 2.6., 2.13.). In Garigue, ground polyphage biomass dominates the community all year. In low Maquis ground polyphages dominate by biomass in June and from August to November (Fig.2.6.).

(d) Foliage Insectivores

In Garigue foliage insectivore diversity is similar to that of ground insectivores except that there is no peak in the autumn and that the spring peak is a month earlier (Fig.2.12.). In low Maquis diversity is generally higher than in Garigue especially in April and in May when the habitat has a wide range of foliage insectivores (Fig. 2.5.). Foliage insectivores are thus much more important in the denser vegetation than in the simpler habitats.

(e) Foliage Granivores

In both habitats foliage granivores are insignificant (Figs.2.5., 2.6., 2.12., 2.13.).

(f) Foliage Polyphages

There are no foliage polyphages in Garigue and in low Maquis they are insignificant.

General Comments

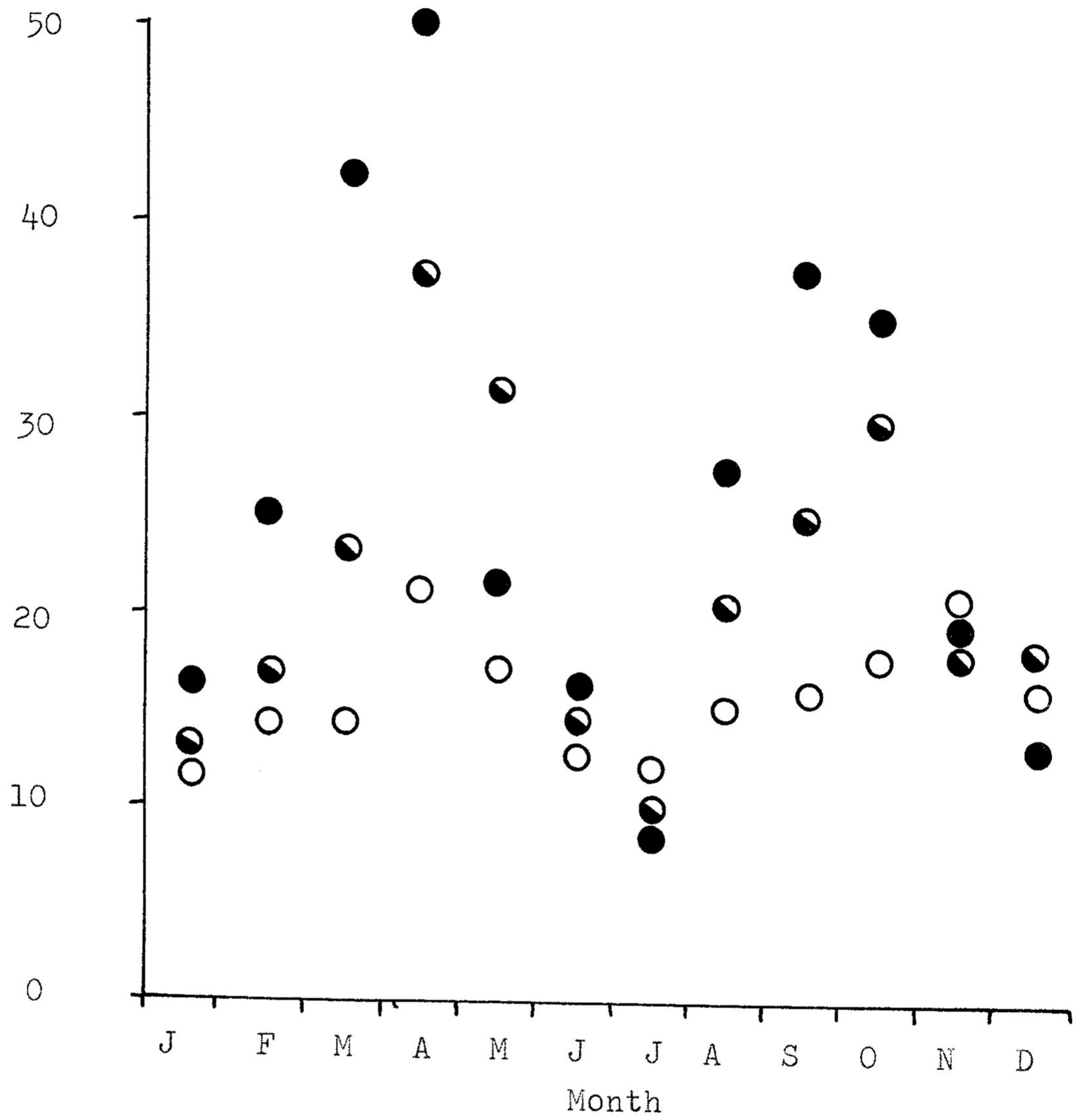
Several general trends emerge from the above comparisons

and descriptions. The environment at Gibraltar is a highly seasonal one and its communities reflect this, usually being poor in the summer and richer in winter. The communities are most diverse during spring and autumn as a result of the wide range of species which utilise the habitats while on migration. The nature of the migrants which use these habitats will be dicussed next in this chapter. There are inter-habitat variations in the pattern described above, habitats with simplest vegetation structure having the greatest species turnover. In Garigue there is a difference of 42 species between the month with the highest number of species and that with the lowest number of species. In low Maquis the difference is only 27 species, and in High Maquis it is 9.

Consumer biomass shows a different pattern. The greatest biomass values are achieved in July and they are much higher in Garigue than in low Maquis. Passage birds contribute to spring and autumn biomass peaks, but mainly so in low Maquis. Thus, although many migrants use Garigue, few produce a great impact (in terms of consumer biomass) and the habitat is dominated by a few resident species. In low Maquis migrants may exceed residents in biomass at certain times of year.

Plastic species (Morse 1971) are dominant in both habitats and it is these which are resident (Cody 1974, Herrera 1978 a & b). In low Maquis foliage foragers are more important than in Garigue which is dominated by ground foragers. Granivores are mostly unimportant except the Barbary Partridge in Garigue, and finches and buntings in

FIGURE 2.16. Seasonal Changes in the Number of Species occupying three scrub habitats at Gibraltar.



High Maquis (open circles), low Maquis (half-solid circles), Garigue (solid circles).

the same habitat during the autumn. Insectivores are important in spring and summer but in winter it is those species which can switch to other foods which remain.

Of the species which are dominant numerically or by biomass (i.e. those which contribute over 5% by numbers or biomass to the community) in low Maquis, 6 are warblers which feed mainly on foliage insects, 2 are ground insectivores, and 3 are ground polyphages. In Garigue, only 2 insectivorous warblers are dominant, but there are 5 species of ground polyphages, 4 of ground insectivores, 3 of ground granivores, and 2 of foliage granivores.

2.3.3. The Migrants

Migrants contribute substantially in numbers and biomass to the communities. A discussion of these birds is therefore necessary. For simplicity, migrants passing Gibraltar have been divided into Mediterranean-wintering migrants and trans-Saharan migrants.

It has been known for some time that even though many passerine migrants are capable of crossing the Mediterranean Sea on a broad front (Casement 1966), large numbers seem to concentrate along particular routes (Bernis 1962). The Strait of Gibraltar is such an area and the high density of night migrants flying over the Strait drops almost to zero west of Cape Trafalgar (Nisbet et al. 1961).

It seems that in spring many migrants are following the West Moroccan coastline northwards and are getting

channeled into the Strait. Blondel (1969) suggests that the concentrations may be due to birds using the coasts near the Strait as leading lines. Although some concentrations may occur in the Strait in autumn as well as in spring (Bernis 1962), many trans-Saharan migrants totally avoid southren Iberia between late July and late September during the drought (Moreau 1961). Instead, autumn migrants appear to lay down fat in the wetter north-west (Hope Jones et al. 1977) or even the west (Thomas 1979) of Iberia, before flying straight to Africa south of the Sahara. The migrants which winter in the Mediterranean Basin move south through Gibraltar later than the trans-Saharan species, once the rains have arrived to southern Iberia in October, and they are then more abundant in the south-east of the peninsula than in the north-west (Bernis).

The trans-Saharan migrants which pass through the Gibraltar area are mostly from Western Europe and they winter in tropical West Africa (Bernis 1962, Finlayson 1977, 1978a). In autumn they are about to cross the Sahara Desert and the Gibraltar area must be one of the last sources of food before the crossing. Since most trans-Saharan migrants pass south in August and September they must find little food even there. Many therefore overfly the area after having fattened further north (Moreau 1961). This is most likely in birds which breed along the Mediterranean shores because they can accumulate fat in the breeding grounds and from there fly straight south into Africa.

In spring the situation is reversed as the trans-Saharan migrants have just crossed the desert and many are emaciated (Ash 1969). At this time food is abundant in the Gibraltar area and there is an opportunity to recover. Most trans-Saharan migrants grounded at Gibraltar in autumn are heavier and carry more fat than in spring (Tables 2.1., 2.2.) and so the need to land will be less then. In spring, trans-Saharan migrants stopping at Gibraltar were heavier than those which had finished crossing the Sahara but they were lighter than those preparing to cross the desert in spring (Table 2.3.). This suggests that they can regain some weight in Gibraltar before continuing further north. In autumn, birds stopping at Gibraltar were much heavier than those at the end of the crossing of the Sahara in West Africa (Fry et al. 1970). They were nevertheless lighter than birds about to cross the desert northwards in spring (Table 2.3.). This suggests that birds cannot lay down as much fat as possible in autumn at Gibraltar and that the fat they carry has probably been deposited north of Gibraltar. The desert crossing will be easier in autumn (Moreau 1972). Very few trans-Saharan migrants stay for long periods at Gibraltar when grounded especially in autumn (Table 2.4.). This is expected in an area with little food (Rappole & Warner 1976).

Many of the Mediterranean-wintering migrants which pass over Gibraltar in autumn will only have a short flight left to the wintering grounds. They are therefore likely to be light. They arrive with the rains and so can

TABLE 2.1. Weights of trans-Saharan and Mediterranean-wintering migrants trapped at Gibraltar in spring and autumn.

Species	Spring			Autumn		
	Mean	s.d.	N	Mean	s.d.	N
Trans-Saharan						
Woodchat Shrike	29.3	3.26	17	36.3	2.75	3
Reed Warbler	10.9	1.47	7	13.7	1.88	11
Garden Warbler	16.5	1.60	48	19.9	3.27	45
Orphean Warbler	20.0	2.11	24	22.3	2.69	3
Whitethroat	14.1	2.24	26	16.4	2.43	6
Spectacled Warbler	8.1	0.25	3	10.8	0.79	8
Melodious Warbler	10.9	0.95	54	11.7	1.85	20
Willow Warbler	7.9	0.96	82	9.4	1.47	61
Bonelli's Warbler	7.0	0.63	34	8.4	1.36	3
Pied Flycatcher	11.4	0.92	28	14.1	0.28	21
Spotted Flycatcher	14.2	1.32	20	17.6	1.56	6
Redstart	13.9	1.38	24	15.0	0.35	13
Whinchat	15.9	1.94	10	18.5	1.98	2
Nightingale	20.1	2.11	55	23.9	2.17	18
Mediterranean-wintering						
Blackcap	17.8	1.67	40	18.5	1.25	40
Chiffchaff	7.1	1.07	88	7.2	0.88	76
Black Redstart	17.0	1.43	16	15.4	0.15	30
Robin	16.6	1.44	28	15.6	0.15	62
Stonechat	15.1	0.71	2	16.5	1.94	31

All weights in grammes. No birds caught six hours after sunrise have been included.

TABLE 2.2. Fat Levels of migrants trapped at Gibraltar in spring and autumn

	Fat Score					
Season/Group	0	1	2	3	4	Totals
Trans-Saharan						
spring	4	25	32	29	23	113
autumn	2	3	8	21	49	83
Mediterranean-wintering						
spring	4	14	10	10	10	48
autumn	41	73	55	50	17	236

$X^2_9 = 129.83 \quad p < 0.001$

Blackcaps are analysed separately (Fig.3.36) since their numbers are so high that they would bias the samples in their favour if all the data were lumped together.

TABLE 2.3. Mean Weights of some trans-Saharan migrants trapped at Gibraltar and at other points during the migration.

(a) Spring (northward) Migration

Species	Locality				
	Chad[1]	Defilia[2]	Kafiene[3]	Gibraltar	Britain[4]
Woodchat Shrike		29.2		29.3	
Reed Warbler	11.9			10.9	11.9
Blackcap	20.9	14.1	17.9	17.8	16.9
Garden Warbler	22.2	16.3	17.1	16.5	16.6
Whitethroat	15.1	13.7		14.1	13.0
Subalpine Warbler	11.2	8.3		9.4	
Willow Warbler	9.7	7.9	8.9	7.9	
Chiffchaff		6.3		7.1	
Bonelli's Warbler		7.2		7.0	
Pied Flycatcher	16.7	11.6		11.4	11.8
Spotted Flycatcher	22.7			14.2	14.6
Redstart	14.7	13.1		13.9	13.9
Whinchat				15.9	16.1
Nightingale	29.1	18.3		20.1	21.3

(b) Autumn (southward) Migration

Species	Locality	
	Gibraltar	Chad[1]
Reed Warbler	13.7	10.4
Garden Warbler	19.9	17.4
Whitethroat	16.4	14.3
Willow Warbler	9.4	8.0
Pied Flycatcher	14.1	11.6
Spotted Flycatcher	17.6	14.0
Redstart	15.0	14.7
Nightingale	23.9	19.4

Data from: 1. Fry et al. (1970) 2. Ash (1969) 3. Smith (1979) 4. Smith (1966)
All weights in grammes.

TABLE 2.4. Number of Migrants trapped more than once on the same site within seven days.

	Spring		Autumn	
	Trans-S	Med^n-W	Trans-S	Med^n-W
Observed	17	71	3	38
Expected	25	48	8	48

$X^2_3 = 18.72 \quad p < 0.001$

Expected values calculated from the total number of birds captured in each category.

Of 673 trans-Saharan migrants captured, only 20 (3% ? were subsequently retrapped the same season. Of 1,823 Mediterranean-wintering migrants caught, 109 (6%) were subsequently retrapped the same season. $X^2_1 = 8.6 \quad p < 0.01$.

recover quickly. In spring they will be fattening for the journey north and so they have higher weights and fat scores (Tables 2.1., 2.2.). In spring this increase is only shown by some species but other effects may have masked similar gains in other migrants, e.g. Chiffchaff or Blackcap. Some individuals of these species passing in spring may have crossed the Sahara and so would be lean (Ash 1969), lowering the mean weight of the sample. In spring, Mediterranean-wintering migrants commenced to move early and they spent longer fattening at Gibraltar (Table 2.4.). In autumn they continued into Morocco, but as they did not require much fat for this, they proceeded rapidly (Table 2.4.).

Gibraltar's habitats are therefore important for some migrant species. In autumn they are poor for trans-Saharan migrants and most avoid the area then. With the rains in October many Mediterranean-wintering migrants arrive and use the habitats. Many of these move quickly south into Morocco but others gradually accumulate for the winter. In spring there is a massive movement of Mediterranean-wintering migrants which forage extensively throughout the vegetation. Later in the spring many trans-Saharan migrants pass through quickly but use the habitats for regaining some of the energy lost while flying over the Sahara Desert.

2.3.4. Conclusions

The questions raised in 2.1. with respect to Matorral

communities can now be looked at once more.

1. It is clear from the preceding descriptions that the Matorral communities, especially the Garigue community, change considerably between months. These changes involve species composition and diversity, species density and biomass. These changes can be attributed to the seasonal nature of the habitats, to their geographical location, and to the effects of Man's activities (5.2.).

The structure within the community is also subject to change, with various classes or foraging types differing in importance in the habitats during the course of the year. The number of transit birds in the habitats is probably exceptionally high for a habitat in such an area (Fig.2.17.).

2. The Blackcap and the Sardinian Warbler are essentially foliage insectivores although at certain times of year they forage on the ground or take vegetable matter for food. For the present discussion foliage insectivores will be considered as the most likely species to interact with the resident Sylvia warblers and ground insectivores will be the next group which is most likely to interact.

In low Maquis, the foliage insectivore community is most diverse in April and May (Fig.2.5.), during the residents' breeding season. Several other foliage insectivores, apart from the two resident Sylvia species, are dominant numerically or by biomass in low Maquis. The Chiffchaff is dominant in March, November and December; the Willow Warbler in April and May; the

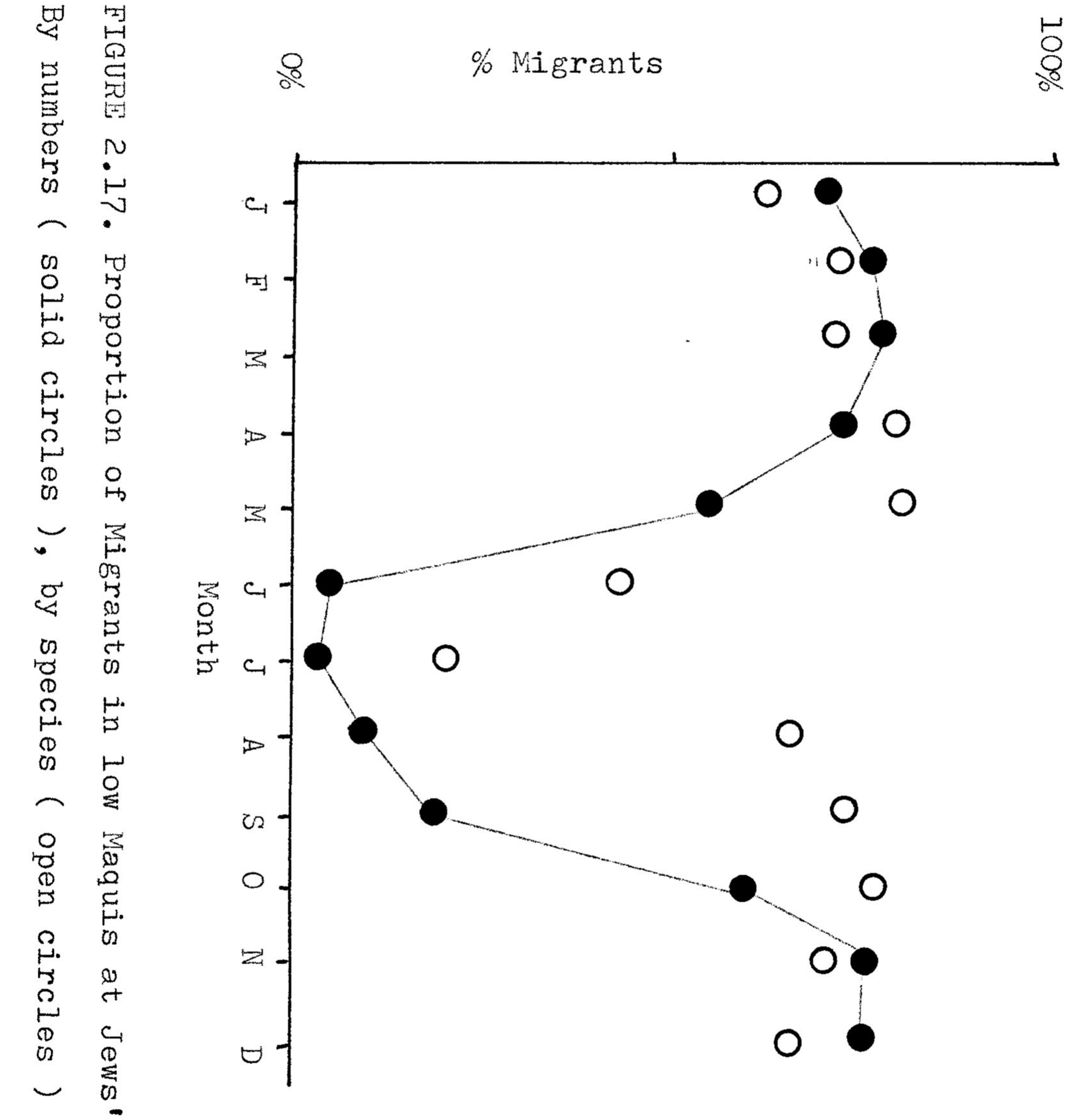


FIGURE 2.17. Proportion of Migrants in low Maquis at Jews' Gate. By numbers (solid circles), by species (open circles)

Garden Warbler in May; the Melodious Warbler in May. In Garigue, where Blackcaps are scarce and do not breed, foliage insectivores are more diverse than in low Maquis all year, but especially in March, April, and from September to December. The only foliage insectivore which is dominant apart from the Sardinian Warbler however, is the Chiffchaff, in November and December.

The ground insectivore is diverse in low Maquis with peaks in May and in October. The most important species are Black Redstart in December; Robin from October to March; and Nightingale in April. These birds are, in fact, polyphagous but they take mostly insects.

The ground insectivore community in Garigue is more diverse than in low Maquis, especially in May and in September. The dominant species are Black Redstart from November to January and in March; Stonechat in February and March; Meadow Pipit in March and December; Robin in November and December.

The resident Sylvia species meet most similar species ecologically in spring when they are breeding, and during the autumn also in Garigue. In late summer there are less similar species than in spring or autumn but food resources are low then.

Despite this, the only other dominant Sylvia species at any time is the Garden Warbler, in May.

3. Species which dominate by overall consumer biomass are considered to cause the greatest impact on the habitats and strata where they forage. In low Maquis

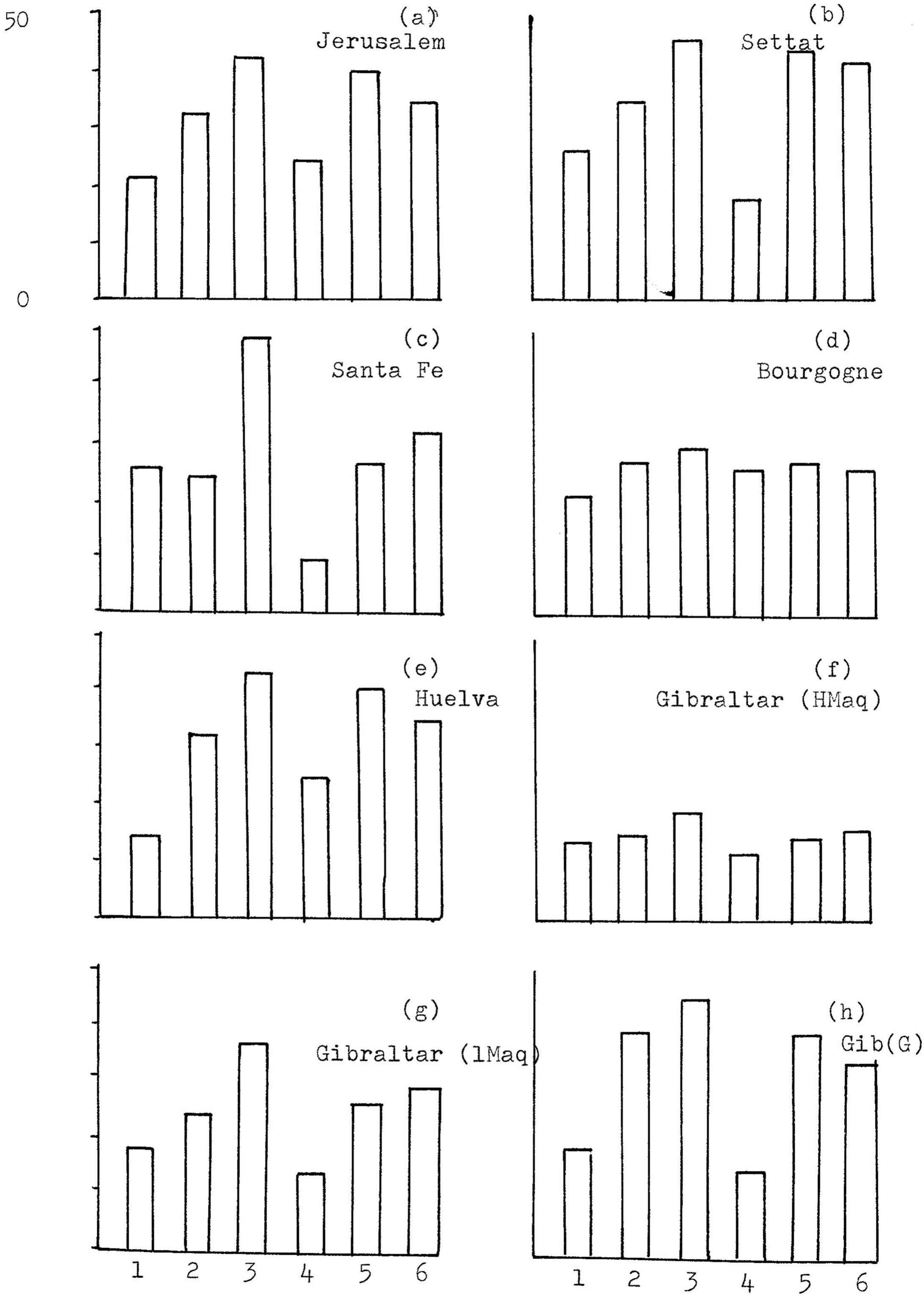
it is the ground polyphages and the foliage insectivores which dominate by biomass. Of these, the nominate Blackcap (see 3.2.2.) and the Robin are the main species between October and March, and the Sardinian Warbler, the Blackbird and the House Sparrow from May until October. Other important species are Garden Warbler, Melodious Warbler, local Blackcap, Willow Warbler, Black Redstart and Nightingale.

The Maquis is the exclusive breeding habitat of the local Blackcap. To other species such as the Blackbird or the Sardinian Warbler it is the main habitat, i.e. that in which they are most abundant. To the migrants low Maquis is important because it has a wider range of foods than Garigue. This habitat is especially important to Blackcaps and Robins in winter as they consume many berries which are only found there.

In Garigue, ground polyphages and foliage insectivores dominate by biomass although the latter group is less significant there than in low Maquis. Ground granivores are important there in summer and autumn. The dominant species by biomass throughout is the Spotless Starling, but Blackbird, House Sparrow and Barbary Partridge are also important. The Sardinian Warbler is not important in Garigue. Important non-resident species are Black Redstart, Serin, Meadow Pipit, Linnet, Skylark, Hoopoe and Song Thrush. This habitat is therefore more important to ground foragers than to foliage foragers.

4. There is very little in the literature regarding seasonal changes in Mediterranean bird communities (Blondel 1969, Thuoy 1976, Herrera 1978 a, Abramsky & Safriel in prep.). What little there is refers to habitats which are not really comparable to those in Gibraltar and so comparisons have to be treated with caution. In addition to the present discussion, the breeding bird community at Jews' Gate is compared to the breeding community in similar scrub at Terrubia, Sardinia (Cody & Mooney 1978) in section 5.3. Seasonal changes in the number of species at several sites are shown in Fig.2.18. The areas selected for comparison are (a) near Jerusalem, Israel (Safriel pers.comm.), (b) Settat, Morocco (Thuoy 1976), (c) Santa Fe, France (Blondel 1969), (d) Bourgogne, France (Frochot 1971), (e) Huelva, Spain (Herrera 1977). None of these areas is dominated by Wild Olives Olea europaea as is Gibraltar. Perhaps the two most similar habitats are the Santa Fe Garigue (Blondel 1969) and the Gibraltar Garigue. All these communities may be divided into two categories, those with most species in spring and least in winter (Fig. 2.18.) and those with most species in spring and least in summer (Fig.2.18.). Gibraltar's communities all have least number of species during the summer and in this respect they resemble the Moroccan site and the Santa Fe Garigue. The more open habitats like Garigue appear to be the most seasonal and show greatest fluctuations in the number of species between seasons, whereas the habitats with taller and denser

FIGURE 2.18. Number of Species in some Mediterranean Bird Communities.



1=winter, 2=early spring, 3=late spring, 4=summer, 5=early autumn, 6=late autumn.

vegetation show less-pronounced fluctuations (MacArthur 1959, Willis 1966, Frochot 1971, Karr 1976 a, Herrera 1978 a & b, Alerstam & Enckell 1979). When compared to any of the bird communities listed above, Gibraltar's communities are unique in several respects.

(i) The Gibraltar low Maquis and Garigue have a very high proportion of transit species of birds at most times of year. The only sites resembling Gibraltar in this way are the Santa Fe Garigue (Blondel 1969) and the site at Settat (Thuoy 1976). The Spanish site (Herrera 1977) contains few migrants despite its proximity to Gibraltar.

(ii) A unique resident community. With the exception of the Santa Fe Garigue (Blondel 1969), the three Matorral communities at Gibraltar contain the lowest number of resident species of all the communities under consideration (see also 5.3.). The most striking feature of the Maquis communities at Gibraltar is the presence of the Blackcap as an abundant resident species. This bird is common in the area around Gibraltar outside the breeding season but it is a rare nester (F.Bernis, C.M.Herrera, J.Pineau, pers.comm.) except on Gibraltar. The other species which appears unique to the Gibraltar communities is the Spotless Starling which does not breed in any of the other areas mentioned.

(iii) Another aspect of interest is the high densities reached by the resident species at Gibraltar (5.3.). The nesting density of Sardinian Warblers is 0.95 birds/ha in High Maquis, 1.18 in low Maquis, and 1.37

in Garigue at Gibraltar (in fact with other censusing methods densities are often much higher, up to 3 pairs/ha, see 3.4.10.). In Santa Fe the Sardinian Warbler breeding density is 0.95 birds/ha, and in Terrubia, Sardinia it is 1.04 birds/ha (Cody & Mooney 1978). The Blackbird density is also high, 1.78 birds/ha in High Maquis, 0.53 in low Maquis (probably underestimated), and 1.13 in Garigue. The density of Spotless Starlings in Garigue, also during the breeding season, is 2.33 birds/ha.

(iv) The absence of a range of parids in the Gibraltar communities is notable. The only species present is the Blue Tit which has a maximum breeding density of 1.16 birds/ha in High Maquis, low compared to the 1.96 birds/ha at the Huelva site (Herrera 1977) during the breeding season.

The reasons for the impoverished nature of the breeding bird communities at Gibraltar are dealt with in 5.3.

2.4. AERIAL BIRD COMMUNITY

Birds which typically feed on ' aerial plankton ' are discussed briefly here. Eight species are regular at Gibraltar, three species of swifts (Apodidae) and five species of hirundines (Hirundinidae). These are Pallid Swift Apus pallidus, Swift A.apus, Alpine Swift A.melba, Swallow Hirundo rustica, Red-rumped Swallow H.daurica, Crag Martin H.rupestris, Sand Martin Riparia riparia, and House Martin Delichon urbica. Other aerial foragers, e.g. flycatchers, have been discussed in the previous sections.

These aerial foragers generally feed over all the vegetated areas around Gibraltar. They range widely and some species, e.g. swifts and the Crag Martin, regularly fly into the Spanish hinterland. Their habits make regular and systematic censusing impossible, especially during the early part of the breeding season when many individuals are nesting and others of the same species are migrating north.

In contrast to the Matorral communities, the aerial foraging community is at its peak during the summer months (Table 2.5.). Aerial arthropods are probably scarcer during the cooler, winter months, and only one species remains, the Crag Martin. Six of the eight species nest on the Rock, the exceptions being Red-rumped Swallow and Sand Martin (although the Swallow is nowadays also a rare nester). Two species are numerous, the Pallid Swift with about 2,000 pairs and the Swift with about 1,100 pairs. Two other species nest in small and restricted colonies, the Alpine Swift with about 30 pairs in two small colonies and the House Martin with about 20 pairs in one colony. A few pairs of Crag Martins nest on the isolated cliffs on the eastern face of the Rock, but their numbers build up to about 3,000 individuals in the middle of the winter (Elkins & Etheridge 1974, Finlayson 1978b). Of the eight species, seven are trans-Saharan migrants, the exception being the Crag Martin which is a Mediterranean-wintering migrant.

Briefly, we can consider the questions raised in 2.1.

1. The structure of the aerial foraging community changes seasonally. The breeding community is dominated

TABLE 2.5. Number of species of aerial foragers present at Gibraltar in different months.

Month	Species
January	1
February	4
March	7
April	8
May	8
June	8
July	6
August	8
September	8
October	4
November	4
December	1

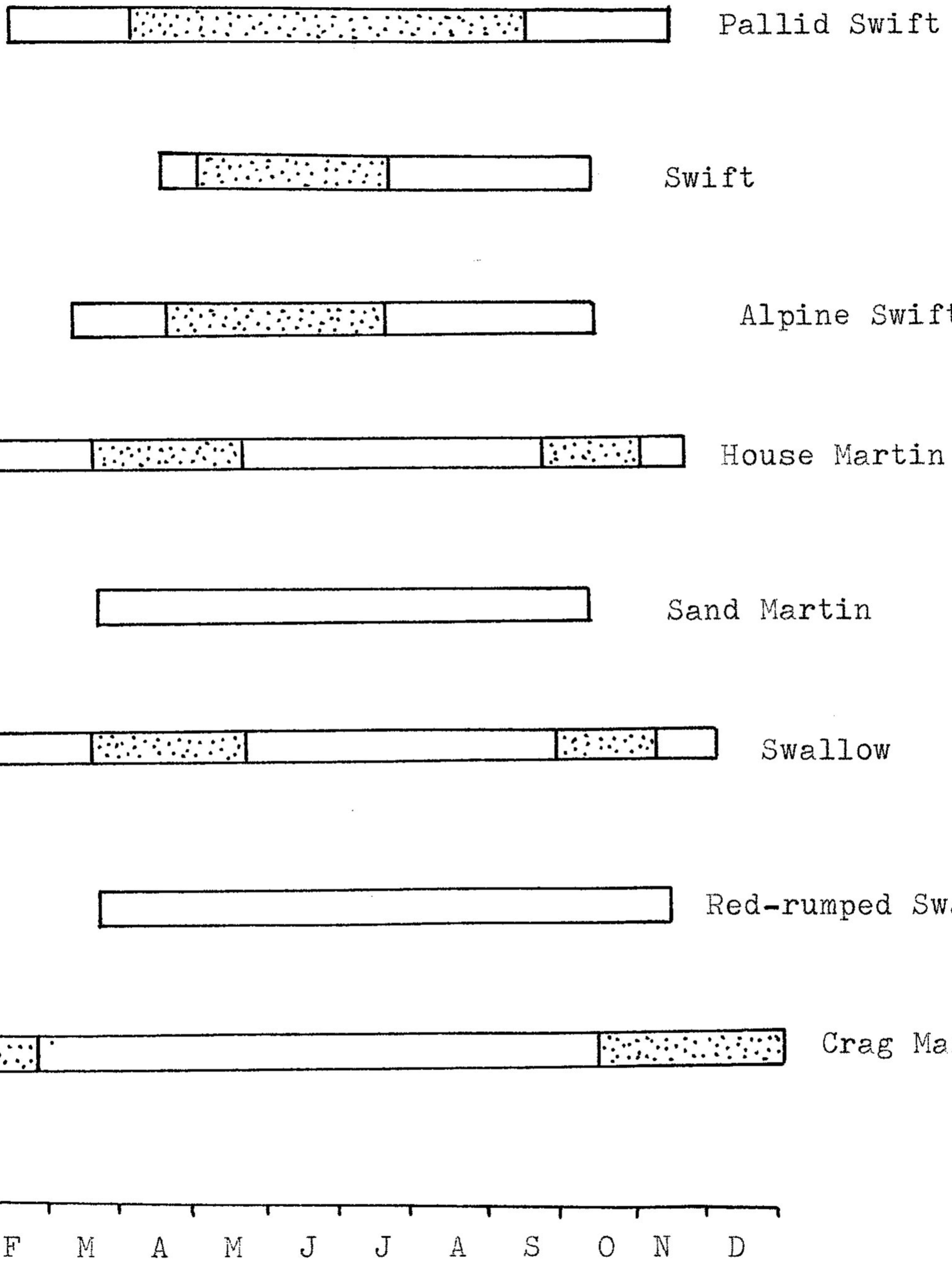
numerically by swifts and hirundines are scarce. In winter the community is essentially monospecific and a hirundine dominates. Peaks in numbers also occur during the passage periods (Fig.2.19.), especially for Swallow and House Martin. However, these birds mostly fly over Gibraltar and forage little so that the impact they cause on the breeding species is probably negligible, certainly less than that of the Matorral migrants on the Matorral residents. The other contrast with the Matorral communities is the lack of residents. The aerial environment is even more seasonal than Garigue or Steppe. Aerial foragers are highly specialized and incapable of changing diet drastically as can a Spotless Starling or a Blackcap, and so they are forced to leave (Morse 1971).

2. The number of species present changes through the year (Fig.2.19.) but none of the species are abundant and probably have little effect on the swifts. The only other abundant aerial forager, the Crag Martin, is isolated temporally from the swifts.

3. This question has been answered indirectly already. Swift and Pallid Swift dominate the air in spring and summer, and Crag Martin in winter. The aerial ' habitat ' is critical for these species as they are unable to forage in any other way or on other foods.

4. The presence of the Crag Martin as an important wintering species appears to be unique in the areas examined (Fig.2.18.). In Settat (Thuoy 1976), three species of swifts are abundant nesters, the

FIGURE 2.19. Seasonal Distribution of Aerial Foragers at Gibraltar.



Peaks stippled

Pallid Swift, the Swift and the House Swift A.affinis. The Alpine Swift is absent. In addition, the Swallow and the House Martin are also abundant breeding birds at Settat but the only other hirundine there is the Sand Martin which is a passage migrant. In Huelva (Herrera 1977), only Swallow and Red-rumped Swallow foraged in summer, but non-passeriformes were excluded from the study. In the Jerusalem area (Safriel pers.comm.) the Swift and the Alpine Swift are resident but there are no Pallid Swifts. The Swallow is also a resident. Additionally, the Red-rumped Swallow is a summer visitor and the Sand Martin and the House Martin are passage migrants. In the Camargue area (Blondel 1969) the Swift is the only nester but the Pallid Swift does nest in the south of France (Affre & Affre 1967). The Swallow and the House Martin occur on passage and breed, and the Sand Martin is a passage migrant.

The many cliffs and old buildings contribute to the large swift breeding population at Gibraltar. They also account for the masses of wintering Crag Martins.

CHAPTER 3

COMPARATIVE ECOLOGY AND BEHAVIOUR OF THE BLACKCAP AND THE SARDINIAN WARBLER IN THE GIBRALTAR MATORRAL

" The Black-headed (= Sardinian) Warbler..... might well be named the Gibraltar Warbler, being the only species which is a regular resident on the Rock. In habits it much resembles the Blackcap. "

Lt.Col.Howard Irby, 1895.

3.1. INTRODUCTION

The Blackcap and the Sardinian Warbler are the main resident foliage-gleaning insectivores at Gibraltar. The Sardinian Warbler is common within its essentially circum-Mediterranean range (Vaurie 1959, Voous 1960). Typically, it is associated with Mediterranean scrub but its habitat and foraging preferences are little known, especially outside the breeding season. As it is a resident, its ecology during the winter months (when most other congeners are in tropical Africa, Moreau 1972) is of particular interest.

The Blackcap is widespread in the Palaearctic but it is mostly associated with mature woodland rather than with Maquis, even within the Mediterranean region (Cody & Walter 1976). Most of the northern populations are migratory, and the main wintering grounds are thought to be in southern Europe and in North Africa (Voous 1960). Blackcaps also winter regularly south of the Sahara Desert (Vaurie 1959 , Moreau 1972). Although the ecology of the Blackcap has been studied in closer detail than that of the Sardinian Warbler (Barlain 1978, Berthold 1978), most work has been carried out in the northern part of the range, and little is known of the ecology of the Blackcap in southern Europe at any time of year.

At Gibraltar, both species occupy Maquis and are often in close contact with each other. This situation, with both species occupying the same habitats

in sympatry, is probably rare. Both species occur at high densities (Table 3.14., 3.4.10). For this reason the approach throughout most of this chapter will be comparative.

The main emphasis in this chapter will be on adaptations which allow these two species to be resident on Gibraltar, and on the mechanisms which promote their coexistence. In addition, the question of why other warblers do not remain to breed at Gibraltar, despite their abundance as passage migrants and the apparent availability of resources for them, will be discussed.

3.2. TAXONOMY

3.2.1. The Sardinian Warbler

Williamson (1974) recognizes four sub-species. The nominate S.m.melanocephala (Gmelin) occurs on the mainland of Mediterranean Europe and in North Africa. It is also found in the Balearic Islands, Corsica, Sardinia, Malta and Sicily. In the Middle East it is replaced by S.m.momus (Hemprich & Ehrenberg). The other two sub-species have very local distributions, S.m.leucogastra (Ledru), considered synonymous with melanocephala by Vaurie (1959), in the Canary Islands and S.m.norrisae (Nicoll) in Egypt. Vaurie (1959) also accepts S.m.pasiphae (Stresemann & Schisbel) from Canea and Crete, but it is omitted by Williamson .

In all aspects except bill length, the Sardinian Warblers which are resident on Gibraltar fall within the range of measurements of S.m.melanocephala

(Table 3.1.). The plumage is also similar. The Sardinian Warblers which are resident on Gibraltar are nevertheless longer-billed than nominate birds (Williamson 1974). A small sample of Sardinian Warbler skins measured conformed with Williamson's data and suggested the difference in bill length to be a real one. The taxonomic position of the Gibraltar Sardinian Warbler population requires re-assessment.

3.2.2. The Blackcap

Throughout the whole of the Palaearctic mainland, the Blackcap is divided into two sub-species, the nominate S.a.atricapilla (Linnaeus) in the west, and S.a.dammholzi (Stresemann) in the east (Vaurie 1959). Several sub-species have been described from islands. Vaurie (1959) recognizes S.a.paulucci (Arrigoni) in Sardinia and S.a.heineken (Jardine) from Madeira (Williamson 1974 adds the Canary Islands). Williamson (1974) also recognizes the form S.a.koenigi (von Jordans) from the Balearic Islands and adds S.a.atlantis (Williamson) from the Azores and Cape Verde Islands. In general, the island forms appear to be darker than those of the mainland and some have shorter wings. In all island forms, the position of the tip of the second primary lies between the tips of primaries 6 and 7, or even between 7 and 8. In the nominate race this is rare and the tip of the second primary is usually in line with the tips of primaries 5 and 6 (Williamson 1974, and pers. obs.).

On the continent there is some evidence of a cline in some characters from west to east

TABLE 3.1. Morphological characteristics of Sardinian Warblers trapped at Gibraltar.

Character	Mean	s.d.	N
Bill length			
Adult male	14.0	0.81	13
Adult female	13.9	0.70	10
Juvenile	13.7	0.77	73
Wing length			
Adult male	58.2	1.09	13
Adult female	58.1	0.74	10
Juvenile	58.1	1.68	140
Tarsus length			
Adult male	19.3	1.31	13
Adult female	20.1	1.74	10
Juvenile	20.5	1.68	73
Tail length			
Adult male	59.4	2.62	13
Adult female	56.3	3.16	8
Juvenile	57.1	2.68	71

All measurements in millimetres

(Vaurie 1959). I have not found any indication of any grading of characters between northern and southern Europe, from skins examined at the British Museum (Natural History).

The resident Blackcap at Gibraltar differs significantly from the nominate sub-species in several characters. Since nominate birds are present in Gibraltar alongside local birds from September to May, a comparative morphological analysis was possible using data gathered by a single observer.

The local form is smaller than the nominate. Weights of 30 local Blackcaps trapped in mid-winter (all during the morning) were lower than for 30 nominate birds trapped under the same conditions (Table 3.2.).

The wing is shorter in the local Blackcap, but bill and tarsus length are similar to the nominate (Table 3.2.). The tail appears to be slightly longer in the local form than in the nominate but the difference is not significant. The wing relative to weight is shorter in the local Blackcap than in the nominate, indicating that the shorter wing is not just due to its smaller size. The Tail:Wing length ratio is higher in the local Blackcap (i.e. the tail is longer in relation to the wing) but this may be due to the reduction in wing length. The index of roundness (as defined by Gaston 1974) shows that the wing is more rounded in the local form than in the nominate (Table 3.2.).

TABLE 3.2. Morphological characteristics of local and nominate Blackcaps trapped at Gibraltar.

Character	Mean	s.d.	N
Bill length			
local	14.0	0.969	22
nominate	14.2	0.512	14
Wing length			
local	68.6	2.185	30
nominate	74.1	1.874	30
Tarsus length			
local	20.1	1.365	22
nominate	19.8	0.839	14
Tail length			
local	59.1	2.223	22
nominate	57.7	1.917	14
Weight			
local	17.6	0.916	30
nominate	18.6	1.529	30
Bill : $^{3}/_{wt}$			
local	5.383		
nominate	5.398		
Tarsus : $^{3}/_{wt}$			
local	7.728		
nominate	8.077		
$Wing^{2}$: $\log_{10}wt$			
local	3706.9		
nominate	4325.2		
Tail : wing			
local	86.15		
nominate	79.76		
Roundness			
local	80.80	2.477	23
nominate	77.66	1.733	12

All measurements in millimetres and weights in grammes

The wing formula of the local Blackcap differs from that of the nominate in several ways. The wing point is more frequently the fourth primary in the local Blackcap and the third in the nominate sub-species, but this is not exclusive. Primaries 1, 6, 7, 8, 9 and 10, and the first secondary are significantly longer, relative to the length of the wing, in the local Blackcap (Table 3.3.).

In the local Blackcap, the position of the primary 2 tip usually lies between the tips of primaries 6 and 7, very rarely between 5 and 6 which is the rule in the nominate sub-species. In this respect the local Blackcap resembles the island forms.

In the local form the plumage in general is much darker than in the nominate form. The upper parts are dark olive, this extending into the rump. The nape is dark grey, only slightly greyer than the rest of the upper parts in the female, but more conspicuous in the male. The crown is jet Black in the male and reddish-brown in the female. The wings and tail are very dark brown. The underparts are greyer, less white, than in the nominate. The flanks are a uniform dark buffish-olive. The under-tail coverts are like the flanks. The throat and breast are as the flanks though much greyer. The belly is dirty white, with a greyish tinge towards the breast.

The local Blackcaps differ from the island sub-species in several ways. They are more olive, less grey on the upper parts than S.a.paulucci. The range

TABLE 3.3. Relative lengths of flight feathers in local and nominate Blackcaps trapped at Gibraltar.

Primary	Number	Mean	s.d.	N
1.				
	local	35.0	1.988	22
	nominate	37.7	1.932	13
2.				
	local	6.4	0.988	23
	nominate	5.7	1.032	13
3.				
	local	0.2	0.422	23
	nominate	0 = Pt		14
4.				
	local	0 = Pt		23
	nominate	0.1	0.267	14
5.				
	local	1.9	0.733	23
	nominate	2.5	1.330	13
6.				
	local	5.4	0.935	23
	nominate	7.1	1.754	13
7.				
	local	7.5	1.074	22
	nominate	10.5	1.506	13
8.				
	local	9.7	1.265	23
	nominate	12.3	1.357	12
9.				
	local	11.1	1.290	23
	nominate	14.3	1.729	14
10.				
	local	13.1	1.521	22
	nominate	16.4	1.447	14
11. secondary				
	local	16.9	1.670	22
	nominate	19.6	1.447	14

All measurements in millimetres. All are distances from the wing point.

of wing lengths given for this race is 68 to 74 mm (Williamson 1974) and so paulucci includes individuals which have longer wings than the Gibraltar form (maximum recorded wing length = 72 mm). Similarly S.a.heineken (70 - 77 mm) and S.a.atlantis (69 - 78 mm) are also longer-winged than the Gibraltar form. S.a.heineken is even darker than the Gibraltar form. Both S.a.heineken and S.a.atlantis have melanistic forms but no such type has been found in Gibraltar. The separation from S.a.koenigi is not so easy as this sub-species has been identified from only three males. These specimens were examined and measured but conclusions have to be treated with extreme caution due to the smallness of the sample. The main difference could lie in the length of the wing since S.a.koenigi had a mean wing length of 71.3 mm (95% confidence limits = 70.0 - 72.6 mm), see Table 3.2.

As with the Sardinian Warbler (3.2.1.), the taxonomic position of the Gibraltar Blackcap needs to be looked into.

3.2.3. Discussion

The two resident Sylvia species on Gibraltar differ morphologically from other known forms of the species (3.2.1., 3.2.2.). This is the important conclusion which has to be drawn from this section. The Blackcaps which are resident on Gibraltar may resemble some of the island forms but it is unlikely that they share a common ancestor. It is more likely

that these similarities are due to similar selective pressures acting in the different geographical areas. Most of the island forms have shorter, more rounded wings than the migratory forms and this is probably related to their sedentary existence (Gaston 1974).

It is not known if the Gibraltar variants of the Sardinian Warbler and the Blackcap are restricted to the Rock. The Sardinian Warbler is widespread in the area around Gibraltar and there ought to be considerable gene flow between populations in the area, preventing the Gibraltar population from becoming genetically isolated (note however that of over 800 Sardinian Warblers ringed at Gibraltar none were recovered in Spain or Morocco even though over 10 were recovered on the Rock). The Blackcap, on the other hand, is a rare nesting species in the Spanish hinterland and along the Moroccan coastline (F.Bernis, C.M.Herrera, J.Pineau, pers.comm.). The Gibraltar population may therefore be genetically isolated, at least the chances of this being the case must be greater than for the Sardinian Warbler population. Irby (1895) found the Blackcap commonly on the Rock but only a few pairs nested there, mainly in gardens. The Blackcap may have established a foothold recently as a breeding species on the Rock, though alternatively the few seen by Irby may have been remnants of a larger breeding population when Gibraltar was wooded (5.2.).

The main morphological alterations from the nominate sub-species which are evident in the Gibraltar Blackcaps are consistent with the habit of living in

dense, low scrub. A shortening and rounding of the wing, an increase in the wing : tail ratio, and a decrease in size, are modifications consistent with species colonizing denser and lower vegetation than they have previously occupied (Gaston 1974). In this aspect the Blackcap is converging significantly with the Sardinian Warbler which is a typical Maquis inhabitant.

It is not possible to be certain of the reasons for the variations just described. It is likely that the Gibraltar Blackcap has recently invaded the Maquis on the Rock (3.4.11.) and that it has become morphologically adapted to this new breeding habitat. The Sardinian Warbler may not be different from that same species in the neighbourhood of Gibraltar. If it is, then the long beak may be an adaptation to taking a wider range of prey items than normal since the breeding communities at Gibraltar have an impoverished range of Sylvia species. In other words, if the long beak is typical of the Gibraltar population, it could have evolved as a form of character release (Grant 1972).

3.3. COMPARATIVE LIFE HISTORIES

In this section, the general distribution of the main ecological events in the life history of the two warbler species will be described. The first sub-section will compare the breeding period of the two species, the second will compare the ecology immediately

after breeding, and the third will compare dispersal in the autumn and other types of movements.

3.3.1. The Breeding Season

In the dense Maquis there are numerous nest sites available to breeding warblers. Most of the Maquis at Gibraltar consists of an unbroken mass of thick vegetation and much of it is on steep ground. Locating nests in these circumstances is a very laborious procedure and whole days can be spent attempting to find a single nest. During the course of this work, several nests were found and details of clutch size, brood size, and nest location were recorded. The samples were very small for a detailed analysis. In view of this difficulty, nest finding was abandoned altogether.

Since it was easy to trap large numbers of warblers, an approximate estimate of the breeding seasons of the two species was obtained by comparing the relative numbers of unringed juveniles caught at weekly intervals during the late spring and summer.

In the hand, the juveniles of the two species were easily separated from the adults. Young Blackcaps are similar to the females but the brown cap is much less pronounced and lacks rufous pigmentation. The under parts are grey and there is no white on the lower abdomen. Juveniles are, on average, smaller than adults. Young Sardinian Warblers also resemble females but they lack the bright red eye-ring, which is

usually flesh-coloured instead. The head contains varying amounts of brown and there is less contrast between the crown, nape and mantle than in the female. The outer tail feathers are always dirty white or even grey, and the remiges are brown. In the adults the outer tail feathers are pure white and the remiges are grey. However, during the late summer (August and September), many juveniles replaced tail and even some wing feathers (3.3.2.) and the differences between first year birds and adults were then reduced.

The proportion of unringed juvenile Blackcaps trapped at the Jews' Gate site increased during the second week in June (Fig.3.1.). The proportion was obtained by recording the number of unringed juvenile Blackcaps trapped at the site at weekly intervals, commencing 15th May. This figure was then divided by the total number of Blackcaps caught in the same period, thus giving the proportion. Data for the study years have had to be lumped in order to have larger samples, so that year to year variations in the pattern have had to be ignored. Such year to year variations may have been negligible as juveniles appeared around the same dates each year.

New Blackcaps only started to appear in the middle of June (Fig.3.1.) and their numbers gradually rose to a peak around the second week of August. It is likely that this increase was due to fledgling Blackcaps which had hatched near the study site, and so it reflects the time when most young

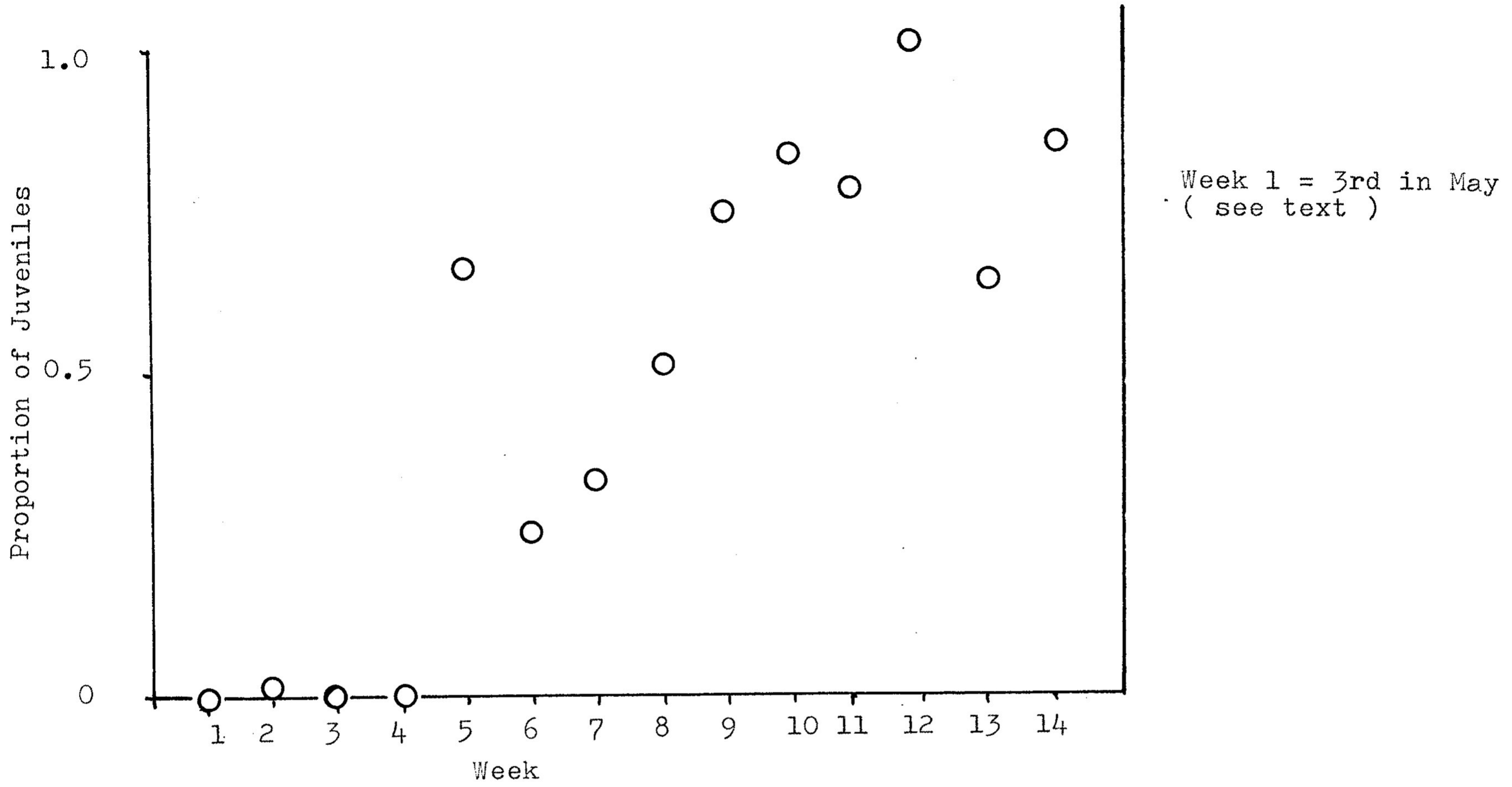


FIGURE 3.1. Proportion of new (unringed juvenile) Blackcaps trapped at Jews' Gate.

Blackcaps emerged from the nests.

New Sardinian Warblers started to appear at the end of May (Fig.3.2.), three weeks before the first Blackcaps. There was a gradual rise in their proportion until the second week of June. After this, the proportion remained high until August when a slow drop commenced (Fig.3.2., Table 3.10 a). In both species the maximum proportion of new birds was similar, at about 0.8 of all the birds trapped (Figs.3.1., 3.2.).

From these data it is possible to work back and calculate, very approximately, the breeding seasons of the two species. The method has several limitations; the proportion of unringed young birds in a sample need not reflect an increase in this component and could even be due to a decrease in the number of retrapped birds (which could result from these birds skulking more than at other times of year). The increase in new birds could also be due to the unringed birds being more mobile than the ringed ones, thus increasing their chances of being trapped. Also, it could represent immigration from another area, even within Gibraltar (Fig.3.8.). All these influences are possible and cannot be isolated, but in approximate terms the increase in unringed birds must be, in part at least, due to new birds leaving the nests. It is also possible that there may be a lag between the time when the young leave the nests and the time when they were first trapped. Many of the young birds were trapped in the

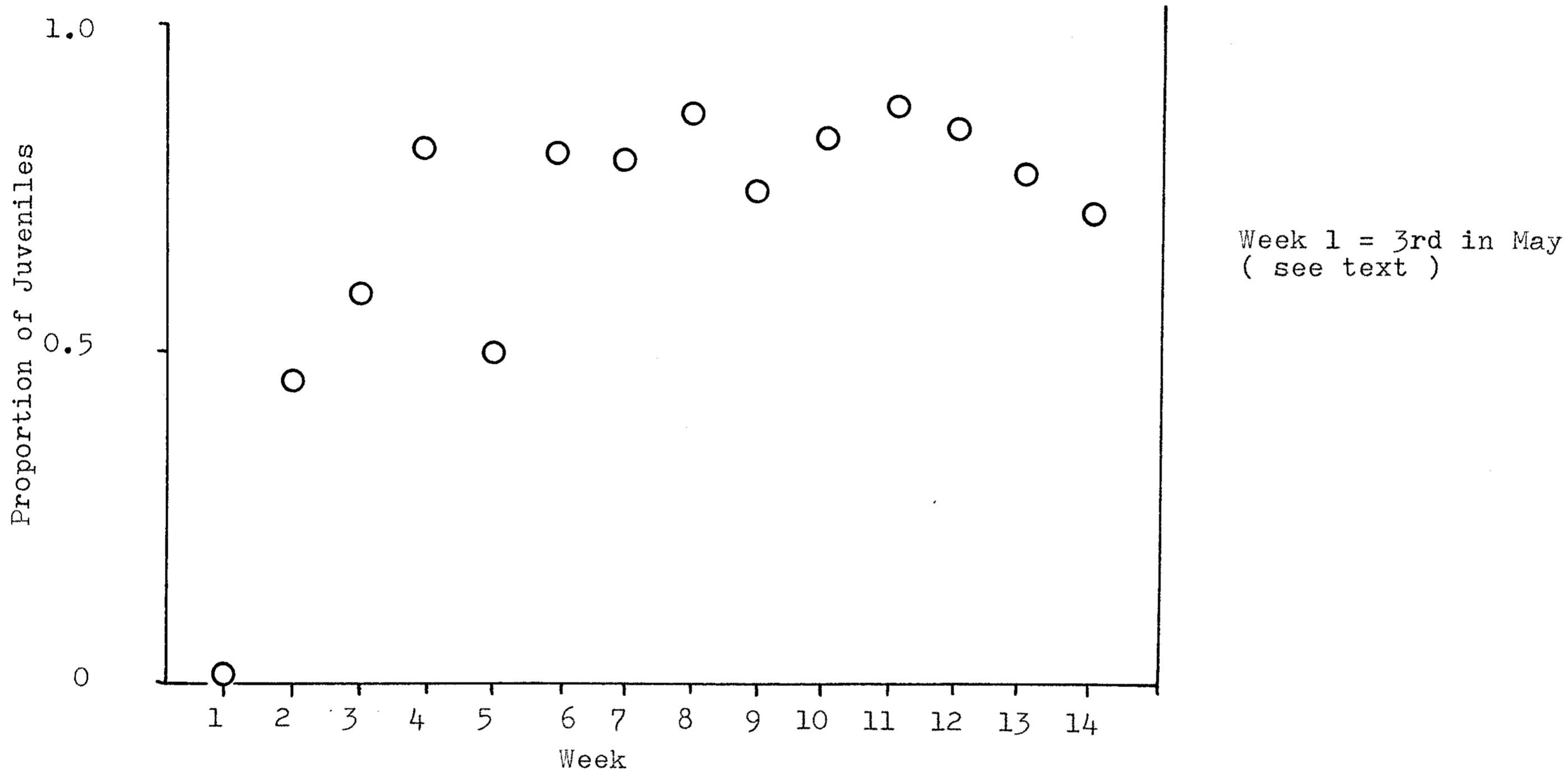


FIGURE 3.2. Proportion of new (unringed juvenile) Sardinian Warblers trapped at Jews' Gate.

company of adults and this suggests they were being caught soon after leaving the nests.

The incubation period of the Sardinian Warbler is 13 to 14 days (Bannerman 1954, vol.3, Harrison 1975) and that of the Blackcap is 10 to 16 days (Mason 1976), usually 12 to 13 (Harrison 1975). The fledging period of the Blackcap is 10 to 14 days (Harrison 1975) though Mason (1976) gives 8 to 14, mean 11 days for the British Isles. The fledging period of the Sardinian Warbler is 11 days (Harrison 1975). As a rough working hypothesis, it can be taken that the period between laying the first egg and leaving the nest in both species will be between 3 and 4 weeks long. Assuming that the juveniles were being trapped fairly soon after they emerged, a rough plan of the breeding seasons of the two warbler species at Gibraltar can be constructed (Fig.3.3.). In this plan data obtained from nests have also been incorporated to increase its accuracy.

The Sardinian Warbler appeared to commence activities earlier than the Blackcap and these spanned a wider time period. Sardinian Warblers are known to lay two clutches (Bannerman 1954 vol.3, Harrison 1975) and it seems very likely that many pairs did so at Gibraltar. The long period of juvenile emergence supports this view (Fig.3.2.). The Blackcap started much later and it is unlikely that more than one brood was raised, even though two broods are known in some parts of the range (Harrison 1975).

The mean laying date of the Blackcap in Britain

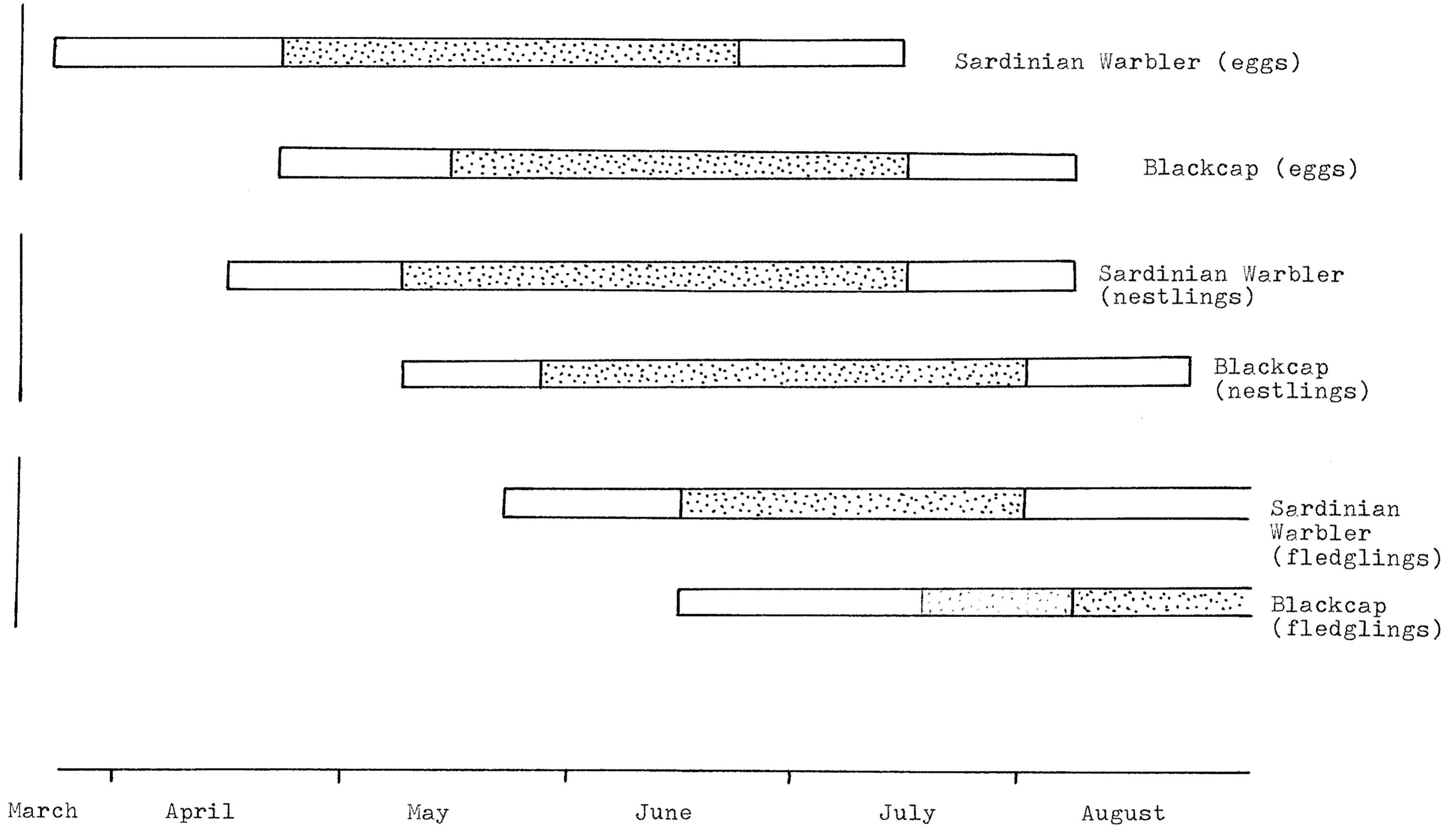


FIGURE 3.3. Main events in the breeding season of Blackcaps and Sardinian Warblers at Gibraltar.

is 18th May (Mason 1976). Harrison (1975) gives late May, rarely late April, but does not specify geographical location. In Gibraltar, mean laying date was probably around the middle of May, although early birds must occasionally start as much as a month earlier (e.g. a brood of three found on 14th May, 1978). Thus Blackcaps commenced laying at Gibraltar at about the same time as in Britain, although some pairs may have done so several weeks earlier.

The mean laying date for Sardinian Warblers was probably a month earlier than for the Blackcap (Fig.3.3.) but some must have commenced in late March since three broods were found in mid-April (one on 9th April, 1977). Harrison (1975) gives mid-March to mid-April for the breeding season of the Sardinian Warbler.

Territorial behaviour commenced early in both species. Some Blackcaps held winter territories (3.4.10.) and sang almost all year. Full song could be heard from the beginning of March. Sardinian Warblers started singing at the end of February but full song, with display flights, commenced at the end of March and reached a peak in the middle of April. During the study period, paired Sardinian Warblers were observed as early as the second week of February. The first pairs of Blackcaps were not observed until the last week of March.

Temporal overlap in the emergence of the young Warblers was estimated from the equation

$$C_{kj} = O_{jk} = \frac{\sum p_{ij}p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where p_{ij} and p_{ik} are the proportions of the $_i$th resource, in this case week of the year, used by the $_j$th and $_k$th species (Pianka 1973). The overlap between Blackcap and Sardinian Warbler was 0.863. A high overlap is expected in a pair of species which are exploiting similar resources in similar ways. The Sardinian Warbler is less specialized than the Blackcap in most dimensions (3.4.11.) and this may enable it to start breeding earlier.

This reduces the overlap in the emergence of the juveniles to some extent. The overlap is nevertheless high. The peak in the resources which both species use must be too concentrated in a short period to allow a complete separation of breeding activities.

3.3.2. The Moult

After breeding, adult Blackcaps and Sardinian Warblers enter a complete moult. The juveniles only undertake a partial moult. Moult was scored in all warblers trapped during the post-breeding periods of 1977 and 1978 in the standard way (Snow 1967). Body moult was scored from 0 to 5, 0 signifying all the plumage to be old (unmoulted) and 5 new and completely moulted. For each bird, the date was recorded and the moult data were converted to percentage completion of

moult. For example, a completely moulted primary tract would score 50 and this would be considered 100% moulted; a primary tract scoring 25 would be 50% moulted, and so on.

Primaries, secondaries, tertials, rectrices and body (head, under parts and upper parts) were scored separately and an average for all five was obtained by adding the stage of moult for each of the five areas and dividing by five. Thus the stage of moult is a compound of the different tracts.

Rate of Moult

Moult scores for all observations were plotted against date and the slope of the regression line indicated the rate of moult, assuming this to be linear (Newton 1966, 1967). The rate of moult in adult Blackcaps was 0.733 $\pm$ 0.250. The difference in slope from zero was significant at the 2% level (Student's t-test). from this result it is estimated that, on average, an adult Blackcap would take 136.4 days to complete the moult. The range ($\pm$ 2 SE) is high, 101.7 to 207.0 days.

The rate for juvenile Blackcaps was 0.238 $\pm$ 0.104, a difference in slope from zero which is significant at the 5% level. If a juvenile were to undertake a full moult at this rate, it would take 420.2 days to complete ($\pm$ 2 SE = 292.4 to 746.3 days). The juvenile Blackcap only moults partially. The maximum proportion of feathers moulted by a juvenile Blackcap at Gibraltar

was 20%. At the above rate it would have taken this bird about 84 days to complete this partial moult. The rate of moult of adult Sardinian Warblers was 0.807 $\pm$ 0.296, and it is significant from zero at the 2% level. The average duration of a full adult moult was therefore 123.9 days ($\pm$ 2 SE = 90.7 to 195.7 days). The rate for the juvenile Sardinian Warbler was 0.536 $\pm$ 0.056, and it is significantly different from zero at the 0.1% level. A young Sardinian Warbler would complete a moult fully in 186.6 days ($\pm$ 2 SE = 168.9 to 208.3 days). Like the juvenile Blackcap, the juvenile Sardinian Warbler does not moult fully. It does moult more feathers than the Blackcap, and individuals were found which moulted over 60% of the plumage.

Discussion

The rate of moult in adult Blackcaps and Sardinian Warblers was slow. From the data collected, the fastest moulting adult would take about three months to change all its feathers. It is well known that birds which have to fit the moult in a limited period, moult very rapidly (Snow 1967). Some passerines such as the Snow Bunting Plectrophenax nivalis moult in 30 to 40 days and become flightless for part of the time (Snow 1967, Green & Summers 1975). As a rule, birds which breed furthest north (and which have to migrate south in autumn) moult fastest (Haukioja 1971). This is even true between sub-species of the same species. For example, migrant races of the Loggerhead

Shrike Lanius ludovicianus have a more rapid moult than resident races, and the moult takes place over a more contracted period of time (Miller 1931). White-crowned Sparrows Zonotrichia leucophrys show similar trends (Mewaldt et al. 1968).

It is to be expected, therefore, that the moult in a southerly latitude will be slow, especially in species which are non-migratory. It would be useful to have moult information from Blackcaps in northern Europe to see if the rate of moult in these is indeed faster. Blackcaps and Sardinian Warblers enter moult at a time when food resources are scarce and it is probably to their advantage to moult slowly.

The average starting date of the adult Blackcap moult, worked out from the regression line, was 4th June ($\pm$ 16 days) and for adult Sardinian Warbler it was 30th May ($\pm$ 13 days). On average, Blackcaps would end moulting around the beginning of October and Sardinian Warblers at the end of August.

The rate of moult of a juvenile bird is expected to be slower than for an adult of the same species since less energy can be devoted to the process by birds which are still growing. Juveniles will also be less likely to be as efficient at feeding than the adults (Davies & Green 1976) and must find the post-fledging period more difficult than the adults. Young Sardinian Warblers moult relatively faster than young Blackcaps and renew more feathering than the Blackcaps. The rate of moult is too slow to enable

them to moult fully. A young Sardinian Warbler fledging in early June and starting to moult by the middle of the month, would be able to moult half its feathers by mid-September. Young from later broods would have to moult fewer feathers. Young Blackcaps emerged later and most probably did not start moulting until the end of June. The regression line gives 30th June ($\pm$ 10 days) for young Blackcaps. These first birds could moult 20% of the plumage in just under three months.

Since young Blackcaps fledge later than young Sardinian Warblers on average, and since they moult more slowly than the Sardinian Warblers, it is to be expected that they shpuld moult less feathers. Juvenile Blackcaps were never observed moulting remiges at Gibraltar in late summer or autumn. Young Sardinian Warblers frequently replaced all the tertials and sometimes even some secondaries or primaries (Table 3.4.). Young Blackcaps did moult the body feathers completely. Young male Blackcaps had complete black caps with no trace of brown by September. Many of the young Blackcaps from northern populations, which arrived at Gibraltar in October and November, had up to half the feathers of the crown unmoulted. Of 32 northern first year Blackcap males trapped in the 1977 and 1978 winters, 23 had brown feathers on the cap. Of 18 local first year males trapped in the same period, none had brown on the cap ($X^2_1 = 38.08$, $p < 0.001$). Since the local Blackcaps do not have to migrate in autumn, it seems

TABLE 3.4. Extent of Wing Moult in juvenile Sardinian Warblers trapped in late summer and autumn at Gibraltar.

Number Moulting/Moulted			
Primaries	Secondaries	Tertials	Number of warblers checked
7	28	73	190
3.68%	14.74%	38.42%	

likely that the reason they can moult further than young Blackcaps from further north is related to their sedentary nature.

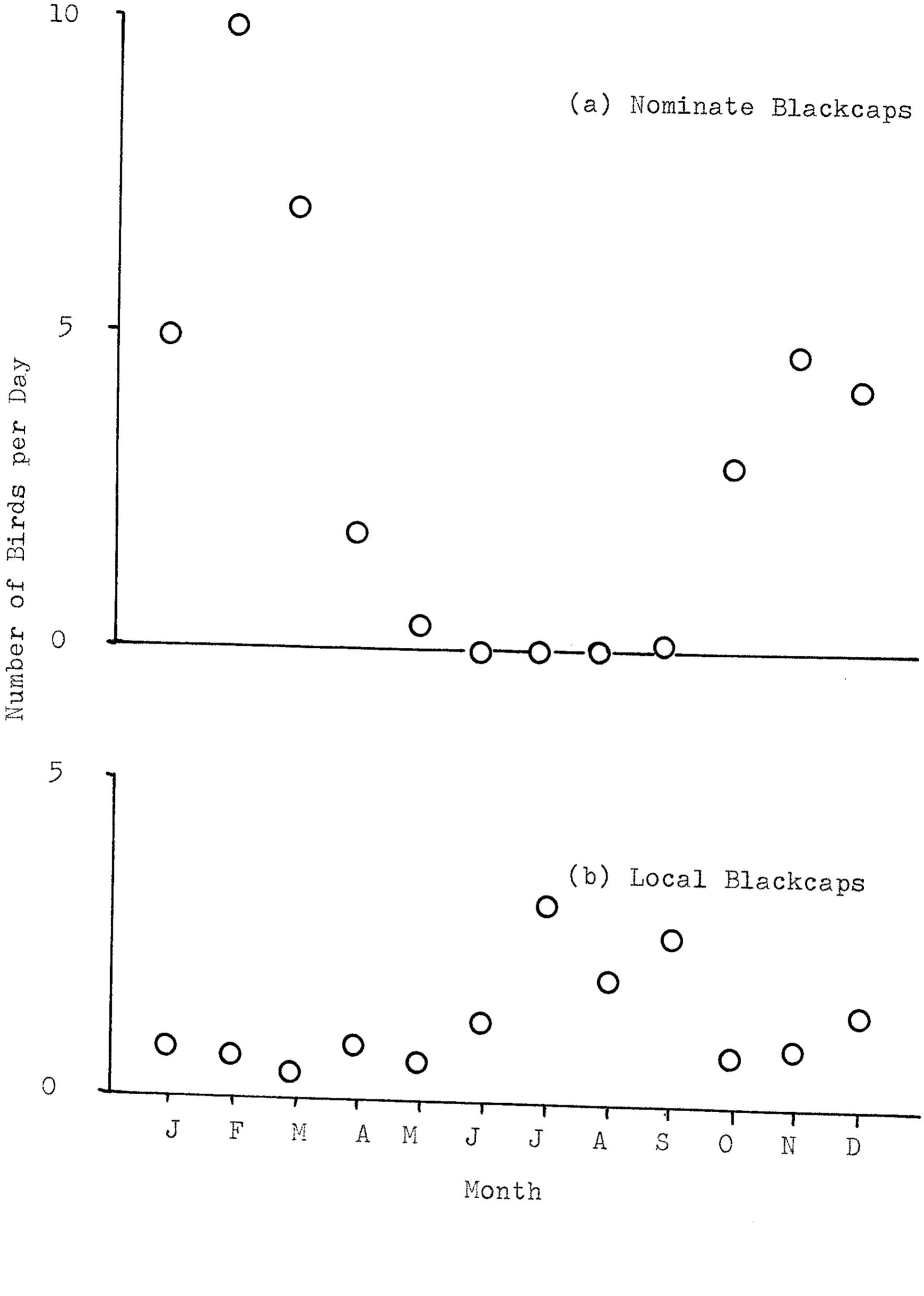
3.3.3. Movements

Between the moult and the next breeding season, Sardinian Warblers and Blackcaps at Gibraltar perform few major energy-demanding activities comparable to breeding or moulting. There are no long-distance recoveries of local Sardinian Warblers or Blackcaps, strengthening the view that these birds are strict residents on Gibraltar. There are, nevertheless, very pronounced spring and autumn passages of Blackcaps through Gibraltar and there is also an indication that there may be a small movement of Sardinian Warblers. Apart from these, there is also evidence of movement by both species on a local scale, within Gibraltar.

Long-distance movements

In the autumn, there was a very pronounced passage of nominate sub-species Blackcaps through Gibraltar during October and November (Fig.3.4.). Many birds remained in Gibraltar for the winter and were frequently retrapped, but others continued into Morocco. There was an even more pronounced spring migration northwards which started as early as February. There was still a small passage into May (Fig.3.4.). The February peak is probably greater than the autumn one because it contained birds which

FIGURE 3.4. Numbers of Blackcaps trapped in Maquis at Gibraltar.



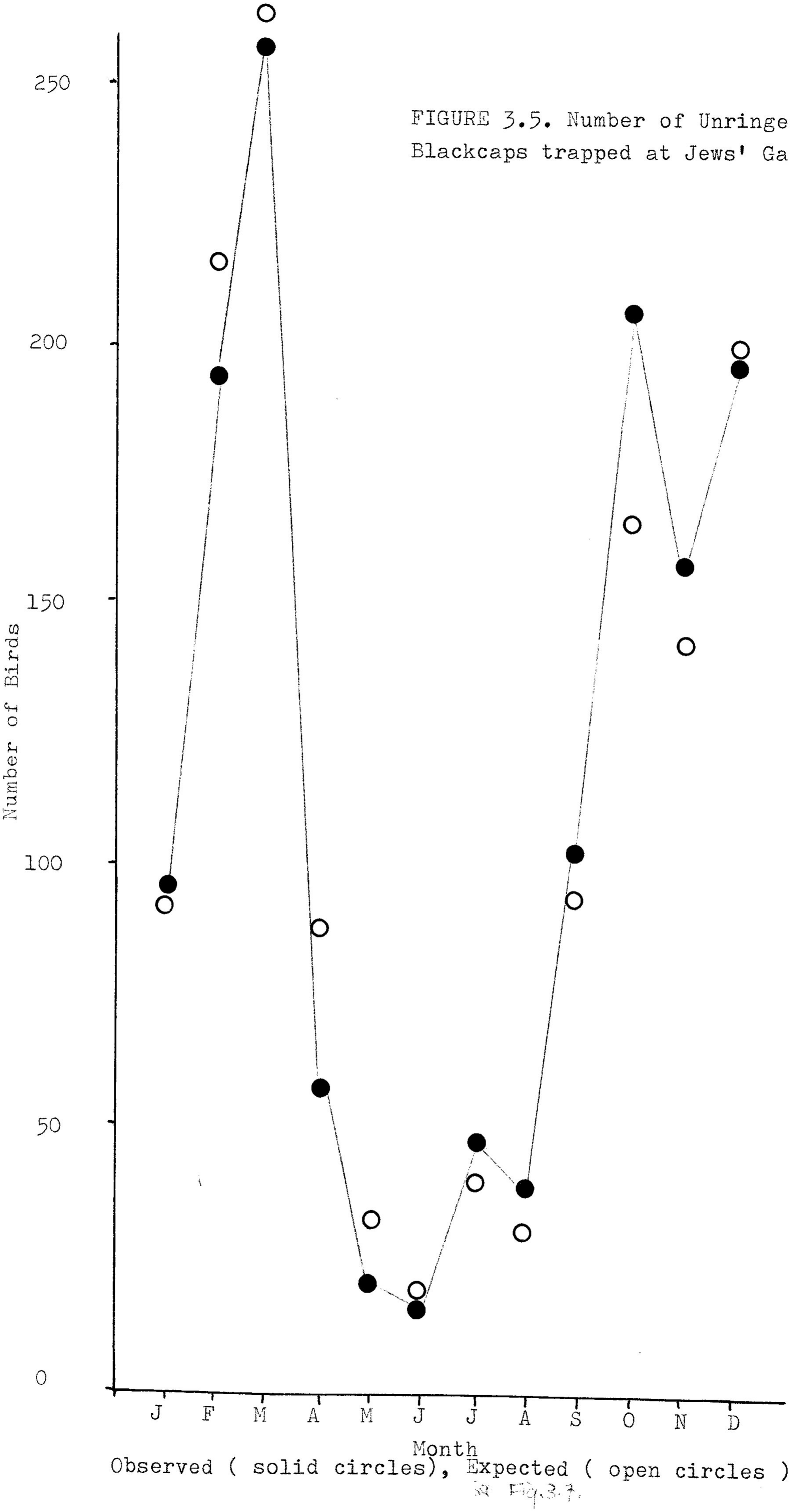
were migrating and others which were winter residents on Gibraltar, and were not ready to leave (the two categories are inseparable). In February, the number of unringed birds trapped was less than expected, indicating that many were winter residents which were being retrapped. In October and November, the number of unringed birds was greater than expected and confirmed that these were migrants that were newly arrived (Fig. 3.5.).

For most of the time that Blackcaps of the nominate sub-species were present at Gibraltar, first-year birds predominated (Table 3.5.). In the autumn and early winter, the ratio of first year Blackcaps to adult Blackcaps was about 1 : 6.88, but towards the spring it dropped to 1 : 1.38. The sex ratio did not depart significantly from 1 : 1 except in February and March when males outnumbered females significantly (Table 3.6.).

With the exception of the first year male Blackcaps, there was no difference in the weights of Blackcaps trapped in spring, autumn or winter (Table 3.7.). First year male Blackcaps were heavier in spring than in winter, but they were not heavier than autumn birds. Despite this, Blackcaps in spring appeared to have greater fat deposits in the tracheal pit than at any other time (Table 3.8.).

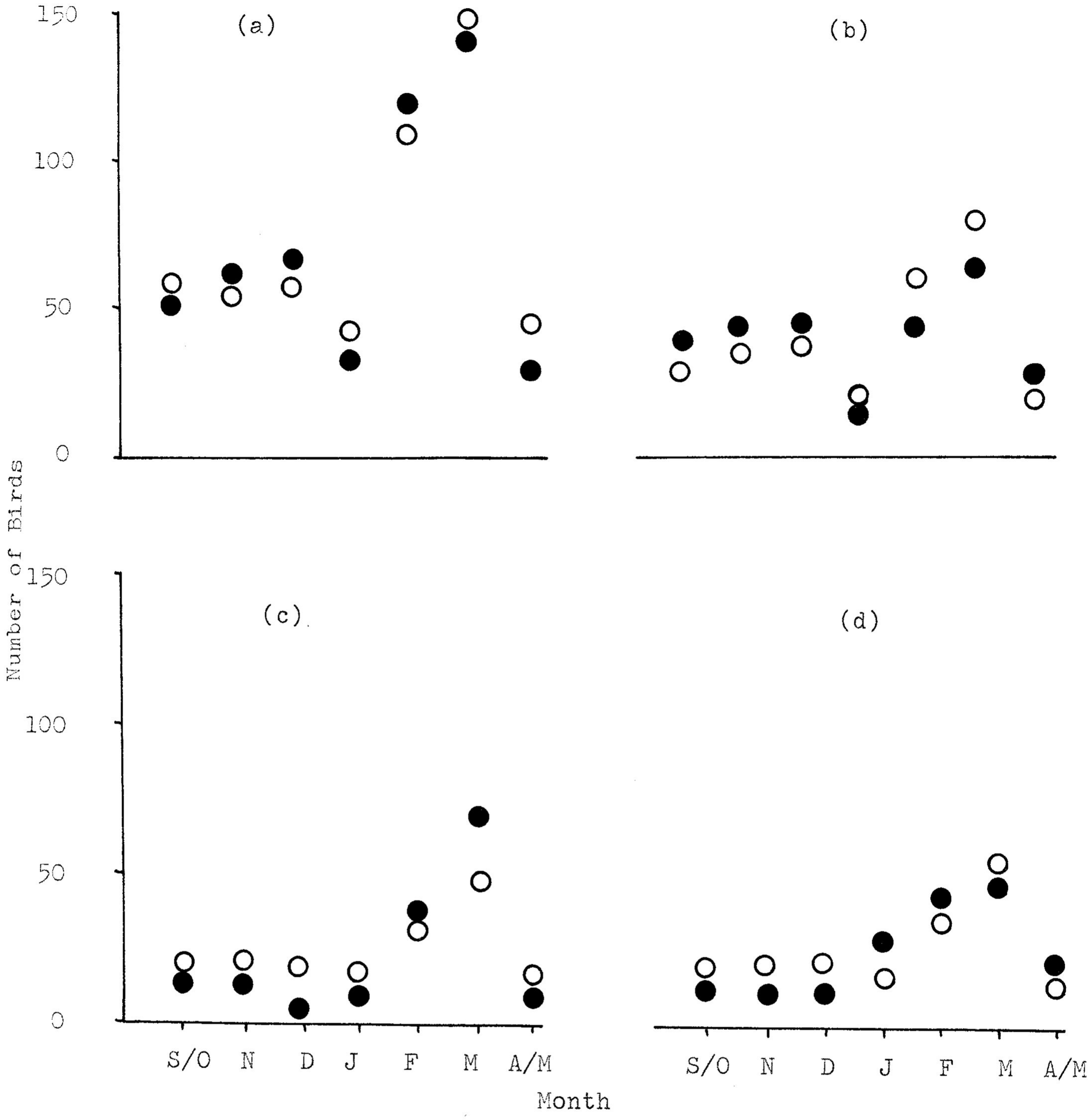
Although Sardinian Warblers are strictly residents in Gibraltar, there appeared to be an increase in the number of unringed individuals trapped at Jews' Gate in November and possibly December. There was also a

FIGURE 3.5. Number of Unringed Blackcaps trapped at Jews' Gate.



Observed (solid circles), Expected (open circles)
& Fig. 3.7.

FIGURE 3.6. Numbers of nominate Blackcaps of different ages and sexes in Maquis at Gibraltar.



(a) First year males (b) First year females
(c) Adult males (d) Adult females
Observed (solid circles), Expected (open circles)

TABLE 3.5. Proportion of first-year Blackcaps at Gibraltar between September and May.

Month	Proportion of First-year birds	N
Sep/Oct	0.758	120
Nov	0.824	125
Dec	0.873	126
Jan	0.565	85
Feb	0.681	238
Mar	0.638	320
Apr/May	0.581	93

All years lumped. $X^2_6 = 48.88$ $p < 0.001$

TABLE 3.6. Sex Ratio in nominate Blackcaps at Gibraltar between September and May.

Month	Male : female	X^2	probability
Sep/Oct	1 : 0.714	3.33	>0.05
Nov	1 : 0.712	3.53	>0.05
Dec	1 : 0.775	2.03	>0.05
Jan	1 : 1.125	2.37	>0.05
Feb	1 : 0.566	18.30	<0.001
Mar	1 : 0.538	28.80	<0.001
Apr/May	1 : 1.214	0.87	>0.05

All years lumped. All X^2 values to 1 degree of freedom

TABLE 3.7. Weights of nominate Blackcaps trapped at Gibraltar in autumn, winter, and spring.

Age/Sex	Mean	± 2 SE	N
(a) Autumn			
Adult male	18.5	17.9-19.1	24
Adult female	18.1	17.6-18.5	21
1st yr male	18.4	18.0-18.9	99
1st yr female	18.9	18.4-19.5	76
(b) Winter			
Adult male	17.5	17.1-18.0	36
Adult female	17.8	16.9-18.7	15
1st yr male	18.0	17.7-18.3	97
1st yr female	18.1	17.6-18.6	41
(c) Spring			
Adult male	18.0	17.5-18.5	100
Adult female	18.5	18.0-19.0	83
1st yr male	18.9	18.5-19.4	94
1st yr female	18.8	18.3-19.3	79

All weights in grammes

TABLE 3.8. Amount of fat in the tracheal pit of nominate Blackcaps at Gibraltar in autumn, winter and spring.

	Number of observations		
Fat Score	Autumn	Winter	Spring
0	0	1	0
1	6	4	5
2	17	16	4
3	15	9	17
4	38	9	101

$X^2_4 = 53.30$ $p < 0.001$. Fat categories 0 and 1 have been lumped to give expected values of 5 or over. Fat scores follow Fry et al. 1970.

similar increase in March but this was not as conspicuous (Fig.3.7.). The wing lengths of birds trapped in November and December did not differ from those of birds trapped in September and October (Sep/Oct, $\bar{x}$ = 58 mm, s.d. = 1.64; Nov, $\bar{x}$ = 58 mm, s.d. = 1.52, Dec, $\bar{x}$ = 58 mm, s.d. = 0.98) and so this does not indicate that different populations may have been involved. There was nevertheless a tendency for the November and December birds to have more birds with average wing length and fewer with long or short wings (Table 3.9.).

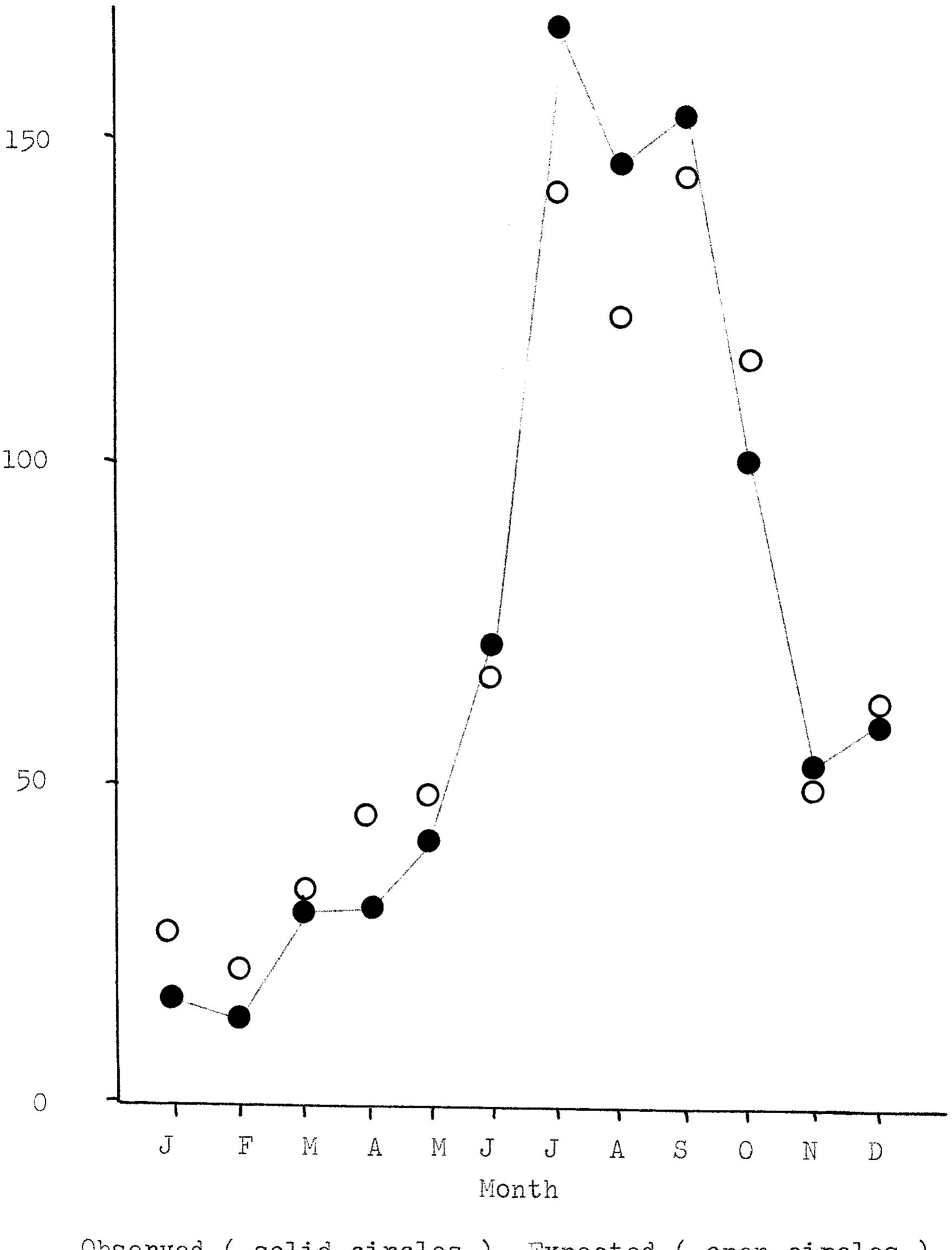
During the early part of the autumn, first year Sardinian Warblers outnumbered adults by about 10 to 1. There was a gradual increase in the proportion of adults, reaching about 2 first years to 1 adult by December (Table 3.10.). There was no evidence of an uneven age distribution in November. The sex ratio did not depart significantly from 1 : 1 between August and December (Table 3.10.).

At no stage in the autumn were Sardinian Warblers extremely light or heavy, and for the period August to November, the average morning weight varied between 12.1 g and 12.3 g (Table 3.11.). Birds trapped in October and November had greater quantities of fat in the tracheal pit than those caught in August or in September (Table 3.12.).

Recoveries

There are seven long-distance recoveries of Blackcaps ringed at Gibraltar and, in addition, there is a Gibraltar

FIGURE 3.7. Number of Unringed Sardinian Warblers trapped at Jews' Gate.



Observed (solid circles), Expected (open circles).

Expected values calculated from total number of birds trapped in each month

TABLE 3.9. Wing lengths of Sardinian Warblers trapped at Gibraltar between September and December.

Wing Length	Number of observations	
	Sep/Oct	Nov/Dec
-55	7	0
56	9	3
57	20	13
58	20	11
59	14	9
60	15	1
61+	3	2

All measurements in millimetres. Data lumped into -56, 57-59, 60+ categories to give X^2 expecteds above 5.
$X^2_2 = 6.78$ $p < 0.05$.

TABLE 3.10. (a) Proportion of first year Sardinian Warblers in samples of birds trapped between August and December, (b) Sex ratio in Sardinian Warblers between August and December.

(a)

Month	Number of lst yrs	adults	proportion of lst yrs
Aug	139	14	0.908
Sep	97	19	0.836
Oct	101	25	0.802
Nov	33	14	0.702
Dec	37	18	0.673

$X^2_4 = 21.023$ p 0.001

(b)

Month	Number of males	females	proportion of males:females
Aug	57	36	1.58:1
Sep	57	58	0.98:1
Oct	66	60	1.10:1
Nov	27	25	1.08:1
Dec	34	31	1.10:1

$X^2_4 = 3.352$ $p > 0.05$

TABLE 3.11. Weights of Sardinian Warblers at Gibraltar between August and November.

Month	Mean	s.d.	N
Aug	12.1	0.86	141
Sep	12.1	0.75	129
Oct	12.3	0.86	69
Nov	12.2	0.80	54

All weights in grammes. All years lumped

TABLE 3.12. Amount of fat in the tracheal pit of Sardinian Warblers trapped at Gibraltar in autumn and early winter.

Fat Score	Number of observations			
	Aug	Sep	Oct	Nov
0	27	17	13	1
1	16	18	18	10
2	9	15	24	5
3	7	13	16	1
4	4	3	20	1

$X^2_8 = 28.85$ $p < 0.001$. October and November data have been lumped to give expected values above 5. Fat scores follow Fry et al. 1970

recovery of a German-ringed bird (Table 3.13.). These recoveries suggest the origins of most of the nominate Blackcaps which are present on Gibraltar between September and May each year.

Of the three long-distance recoveries in Spain, two are from the province of Cordoba, to the north-east of Gibraltar. One is of a bird which was ringed in Gibraltar in February where it may have been on passage. It was recovered in November of the same year at Iznajar, Cordoba, where it may have been on southward passage. The second bird was ringed at Gibraltar in December and must have been wintering there. It was recovered the following winter in February, near Cordoba. This bird may have been northbound when recovered or it may have wintered further north. The other Spanish recovery is from the north-east coast, near Vinaroz. This bird was ringed at Gibraltar in February and may have been passing north. It was recovered after two winters, in January, and must have wintered further north.

Two French recoveries are also to the north-east of Gibraltar. One bird was ringed in December at Gibraltar and was found in spring, a year later, at Condrieu, Rhone where it may have been nesting. The other bird was ringed at Gibraltar in February and may have been on passage. The following winter it was recovered at Albi, Tarn, also in south-east France. Since it was recovered in January, it must have wintered further north that year.

TABLE 3.13. Long distance recoveries of Blackcaps ringed at Gibraltar or controlled there.

(a) Birds ringed at Gibraltar

Date ringed	Recovered	
	Location	Date
19.2.75	Iznajar (Cordoba),Spain. 37°15' N 4°19' W	15.11.75
3.2.75	Vinaroz (Castellon), Spain. 40°29' N 0° 28' W	28.1.78
27.12.76	near Cordoba,Spain. 37°53' N 4°46' W	5.2.78
21.12.76	Condrieu (Rhone),France. 45°27' N 4°46' W	24.4.77
21.2.77	Albi (Tarn),France. 43°56' N 2°08' W	7.1.78
6.5.75	Oudensken (Brabant), Belgium. 50°47' N 4°12' E	25.6.75
6.12.74	Douar Ouled-Azem (Taouante),Fes, Morocco. 34°25' N 4°39' W.	7.3.76

(b) Birds controlled at Gibraltar

Date controlled	Ringed	
	Location	Date
17.11.74	Bad Wurzach, Wangen/Allgau (Sudwurttenberg) W.Germany. 47°54' N 9°54' E	7.8.74

Gibraltar co-ordinates: 36°07' N 5°21' W.

The two north European recoveries are of interest. A German bird ringed in south-east Germany as a juvenile in August was retrapped in Gibraltar in November of the same year. The other bird was ringed at Gibraltar in May (a late migrant) and was retrapped in Oudenaken, Brabant, Belgium, just over a month later. Finally, there is a recovery from Morocco. This is of a bird which was ringed at Gibraltar in December and which was retrapped the following season in March near Fes. It must have wintered further south the second year.

These recoveries illustrate the extent of the geographical area from which the nominate Blackcaps which visit Gibraltar come. Several of these recoveries will be discussed later (3.5.5.).

Discussion

The main wintering grounds of the west European populations of the Blackcap are thought to be in south-western Spain and in Morocco (Bannerman 1954, vol.3), although some authorities consider that they lie mainly south of the Sahara Desert (Lack 1971, Moreau 1972).

The Blackcap density at Gibraltar in mid-winter was of about 5 birds/ha. This places the wintering nominate Blackcap population on Gibraltar at an average of 500 birds. In February the density reached 10 birds/ha, and in March it was 7 birds/ha.

If it assumed that half the Blackcaps stopping at the Jews' Gate site in spring were trapped during each mist-netting session, and that the Blackcap density was the same anywhere else in the Maquis, then theoretically,

in two months 101,400 Blackcaps could stop at Gibraltar in spring. Moreau (1972) has estimated that about 200 million Blackcaps enter Africa from Europe in the autumn. In spring the number returning to Europe will be lower. If we assume that Blackcaps enter Africa on a broad front (Casement 1966), then a strip of coastline the length of Gibraltar should receive about 200,000 Blackcaps in the autumn. Only a small fraction would probably land and most would overfly. In spring, the estimate may be cut by half due to winter mortality so that 100,000 Blackcaps would fly over Gibraltar even though only a few of these would actually land there. These crude estimates suggest that Gibraltar may be attracting more Blackcaps than expected. The Strait is known to concentrate migrants (2.3.4.) and the Wild Olive Maquis (rare in the area around Gibraltar, pers. obs.) is especially attractive to Blackcaps (3.5.6.).

Similar calculations for the autumn migration give an estimated 24,300 Blackcaps potentially trapped at Gibraltar in two months in the autumn. The figure is lower and suggests less of a concentration in the autumn, when more birds should be available. Since fewer Blackcaps are retrapped in autumn than in spring (Fig.3.5.), a more rapid migration may take place at that time, and fewer birds may land or remain grounded for long.

In Donana, in south-west Spain, the autumn migration of Blackcaps is more rapid than the spring passage, lasting only 50 days, instead of 80 days in spring

(Murillo & Sancho 1967). The duration of the migration at Gibraltar cannot be estimated as many birds remain to winter. In Donana, adults pass before first year birds in spring and males outnumber females by 2 : 1. Females are common only amongst the later migrants in spring. At Gibraltar, first year birds did not migrate later than adults. First year birds were commonest in autumn and gradually dropped in numbers towards the spring. Males commenced the migration before the females at Gibraltar too and outnumbered them by 2 : 1, as in Donana.

In the autumn, all sexes and ages arrived at Donana at the same time, as at Gibraltar. The first year : adult ratio was 4 : 1 in Donana at this time (Murillo & Sancho 1967) but in Gibraltar it was higher, 6.88 : 1. Males outnumbered females by 1.1 : 1 in Donana and Murillo & Sancho suggest that females take a different route. At Gibraltar, males were more numerous than females in autumn but the differences were not statistically different from a 1 : 1 ratio. Although they were not significantly heavier, Blackcaps trapped at Gibraltar in spring carried more fat than those trapped in the autumn. If the migration is more rapid in autumn, Blackcaps may have less time to deposit large amounts of fat. This also suggests that many Blackcaps which moved south from Gibraltar were not aiming to cross the Sahara Desert but that the wintering grounds were fairly near, probably in Morocco. In spring the migration started early and the birds then spent

more time fattening. The heaviest Blackcap trapped at Gibraltar in spring weighed 31.5 g . At Defilia, an oasis in south-east Morocco, the leanest Blackcaps trapped after having crossed the Sahara Desert in spring weighed only 11 g (Ash 1969). The area between the northern edge of the Sahara and the southern portion of Iberia must be a very important fattening ground for Blackcaps (and other migrants) which winter in the area and for those which come from south of the Sahara Desert (Langslow 1976, Smith 1979). Populations of Sardinian Warblers are known to move south in autumn and some reach tropical West Africa (Moreau 1972). In Malta, Gauci & Sultana (1979) trapped some extremely heavy Sardinian Warblers in March. At Gibraltar there appears to be a small movement in late autumn and in spring, but the evidence is inconclusive. The strongest evidence in favour of such a movement existing is that many individuals trapped in late autumn had large quantities of fat in the tracheal pit, in many cases comparable to that in trans-Saharan migrants.

Local Movements

The resident Blackcaps and Sardinian Warblers moved freely throughout the vegetated areas in Gibraltar outside the breeding season. Known movements of individual birds, based on ringing evidence, are shown in Fig.3.8. Since most of the trapping during the study period was carried out at the Jews' Gate site (Fig.1.2.), most retraps were of birds ringed

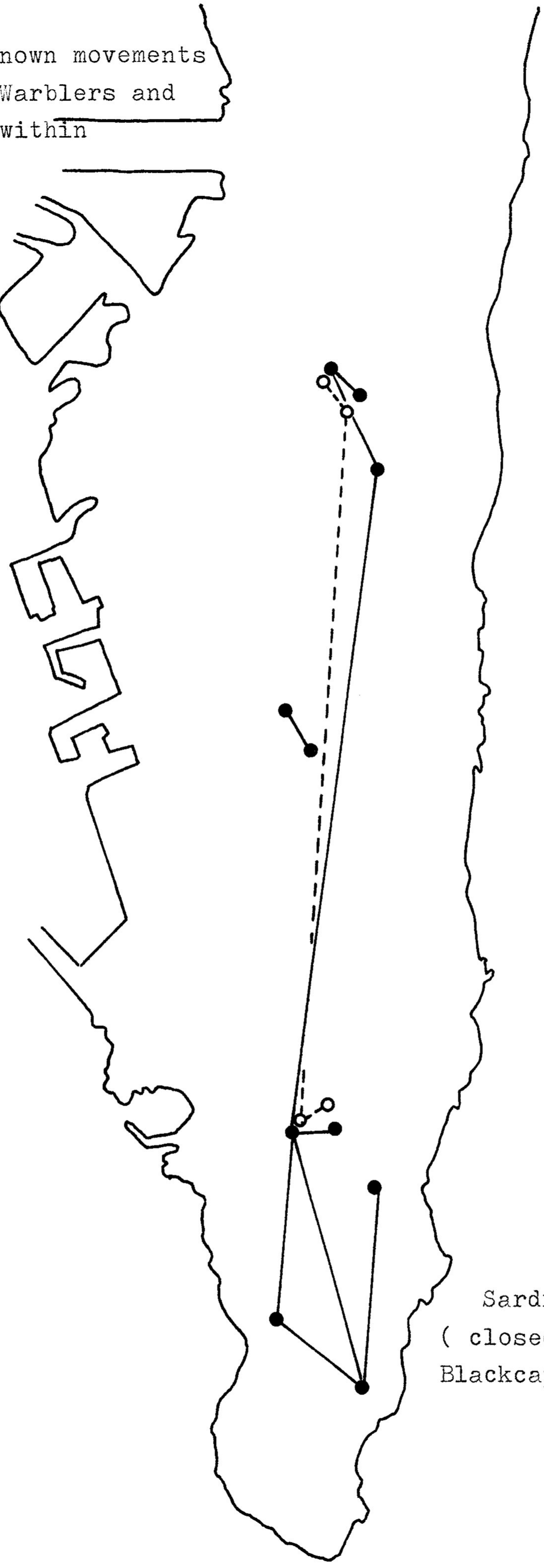


FIGURE 3.8. Known movements of Sardinian Warblers and of Blackcaps within Gibraltar.

Sardinian Warbler (closed circles), Blackcap (open circles).

there. Also, the number of retraps would probably have been greater had more intensive trapping been carried out at the other sites. The results however illustrate the extent of the movements within Gibraltar.

3.4. RESOURCE PARTITIONING

Blackcaps and Sardinian Warblers are resident at Gibraltar. They occupy areas with similar vegetation and often come into contact with each other. In what ways do they partition the resources available between them and is there seasonal variation in the resource partitioning ?

3.4.1. Habitat Occupation

In this, and in the following sub-sections, the year has been divided into four seasons. These are (i) spring, the breeding period for the two species and also the time when many migrants are passing northwards, mid-February - late May. (ii) summer, the time when the young of the Sylvia species become independent and also the time when adults moult fully and juveniles moult partly. There are few migrants and the drought reaches its worst point at the end of the period, June - end of September. (iii) autumn, the period when the first rains arrive and when many migrants pass through southwards, end of September - end of November. (iv) winter, the wet season. Several other insectivorous passerines share the vegetated areas

with the Blackcap and the Sardinian Warbler, including many nominate Blackcaps, December - mid-February.

The two resident Sylvia species at Gibraltar occupy three habitats between them, Garigue, low Maquis and High Maquis (Fig.1.3.). Blackcap and Sardinian Warbler densities in the three habitats, including those during the breeding season, were estimated by the line transect method (Emlen 1971, Nilsson 1974, Franzreb 1976). Since both warbler species behaved in a similar manner, it is unlikely that one would have been detected more frequently than the other. Both species were noisy throughout the year and birds could be heard calling from a distance of over 50 metres; migrating Blackcaps also called loudly contrasting with the silent behaviour of most other migrating passerines at Gibraltar. See 3.4.10 for a comparison with results obtained from territory mapping during the breeding season.

The Maquis habitats were the best for both species (Table 3.14.). Sardinian Warblers also occured frequently in Garigue and nested in that habitat. Blackcaps were rare in Garigue. Of all the Blackcaps trapped in Garigue, none had the characteristics of resident birds (3.2.2.), so that the habitat was only used temporarily by a few transient individuals.

The Sardinian Warbler had a broader habitat choice than the Blackcap (Table 3.14.). The habitat choice of the Sardinian Warbler varied little between seasons. The Blackcap had a more restricted distribution of

TABLE 3.14. Habitat Occupation by Blackcaps and Sardinian Warblers at Gibraltar.

Blackcap

Season	Garigue density	p_i	low Maquis density	p_i	High Maquis density	p_i
Autumn	0.14_{-3}	0.02_{-3}	3.39	0.39	5.21	0.60
Winter	3.33^{-3}	3.04^{-3}	7.52	0.69	3.45	0.31
Spring	0.04	0.01	3.64	0.61	2.27	0.38
Summer	0.00	0.00	2.23	0.63	1.33	0.37

Sardinian Warbler

Autumn	1.39	0.25	1.53	0.28	2.64	0.47
Winter	1.07	0.30	1.30	0.36	1.20	0.34
Spring	1.10	0.31	1.17	0.33	1.27	0.36
Summer	2.62	0.20	7.49	0.58	2.85	0.22

Season	Niche Breadth Sardinian	Blackcap	Niche Overlap
Autumn	2.76	1.95	0.92
Winter	2.98	1.75	0.81
Spring	2.99	1.94	0.82
Summer	2.35	1.87	0.94

Niche Breadth throughout this section is based on the Simpson Index (2.2.2.).
Overlap measures are based on the Index in 3.3.1., following Pianka (1973)

habitats and this varied little between seasons. Nevertheless its choice was narrowest in winter when most birds occupied low Maquis. This concentration coincided with the many fruiting bushes (Wild Olives, Lentisc, Rubia) in that habitat in winter.

Habitat overlap between the two species was high, particularly in summer and autumn. Therefore, even though both species occupied different habitats in differing proportions, they overlapped extensively all year. For the greater part of the year, low Maquis was the main habitat for the two resident Sylvia species.

3.4.2. Plant Species Preferences

This part of the study was carried out in low Maquis at Jews' Gate from July 1978 to July 1979 (Fig.1.2.). The vegetation at the site consisted of a mosaic of shrubs and small trees which did not exceed 4 metres in height in most places. Some scattered Wild Olives reached 6 metres. The main bushes were Spiny Asparagus 34.1%, Wild Olive 25.1%, Buckthorn 12.1%, Thorny Broom 12.1%, Broom (Teline)4.5%, Lentisc 4.0%, Osyris 3.6%. There were also many grasses and ground plants which were used for foraging in by warblers at particular times of year, for example the Giant Fennel Ferula tingitana and the Culinary Fennel Foeniculum vulgare.

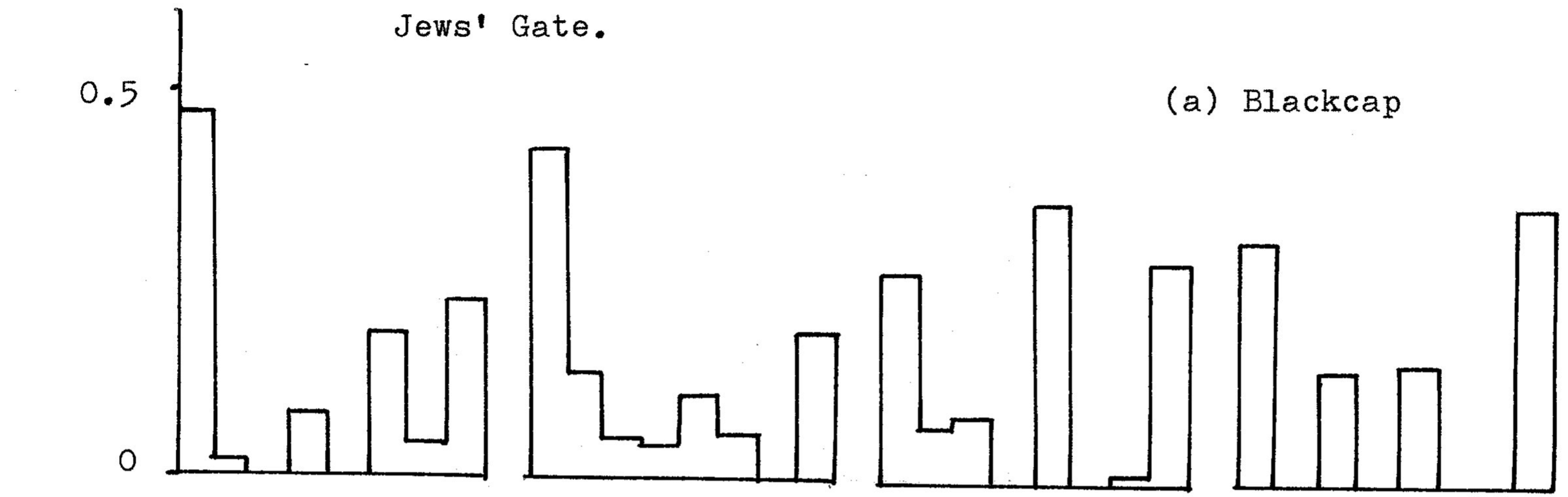
Did the two warbler species visit bushes in the proportion they encountered them while

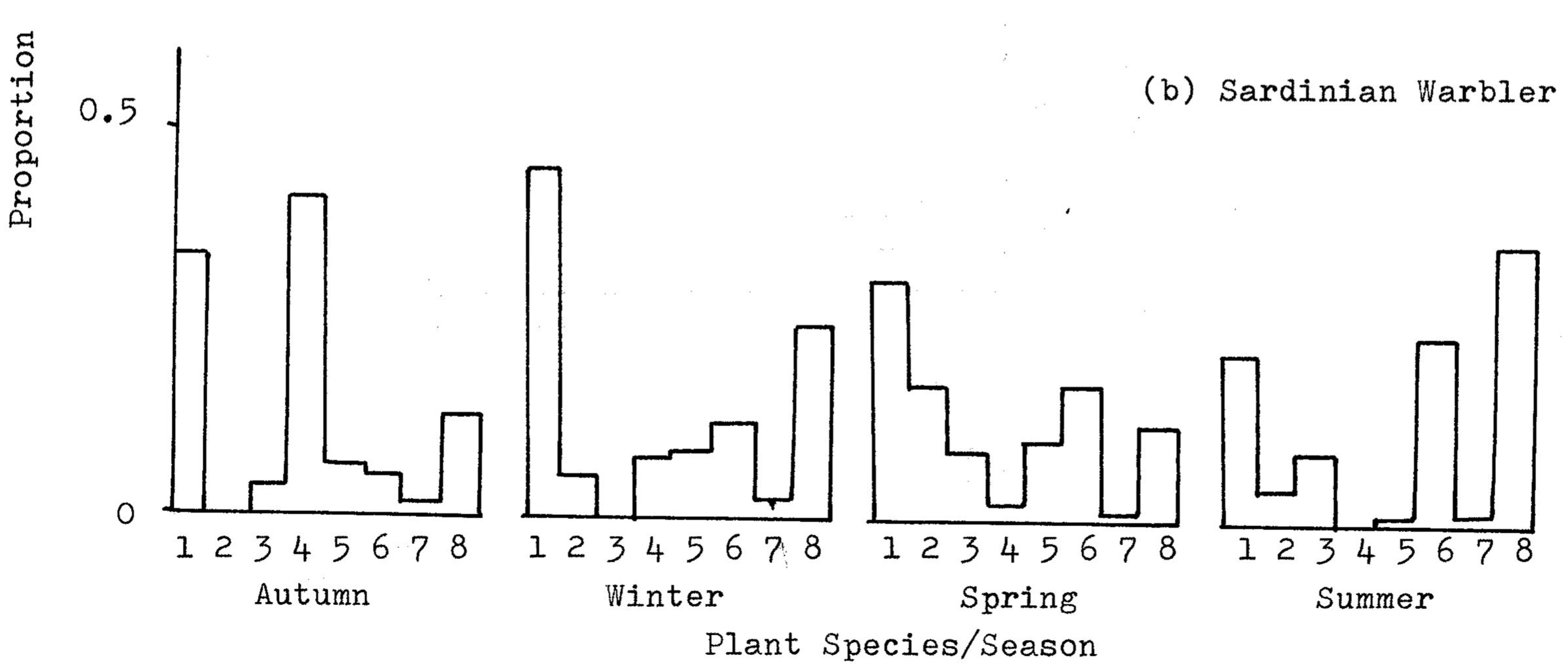
travelling through the site or did they occur with greater frequency than expected in some plants ? The Blackcap and the Sardinian Warbler foraged in some plant species more than in others and the main plant species visited were different in different seasons (Fig.3.9., Table 3.15.). Some observations of the plants visited by Phylloscopus warblers at the same site were taken and are included in Fig.3.9., and Table 3.15 for comparison with the Sylvia results. The main Phylloscopus species were Chiffchaff, Willow Warbler and Bonelli's Warbler.

Blackcaps and Sardinian Warblers visited Wild Olives all year. Their visits to olives were most pronounced in autumn and winter when over 40% of all the plants visited by the Sylvia species were of this type. Olives were visited less frequently in spring and summer (Table 3.15.). Blackcaps visited all other plants species available except Teline in autumn but this plant was incorporated in winter. Sardinian Warblers visited all plant species, except Calicotome in autumn and Teline in winter. Osyris and Lentisc were visited fairly frequently by Blackcaps in autumn and at this time of year Sardinian Warblers were most often seen on Lentisc. In winter, Blackcaps abandoned Osyris and visited olives less frequently than in autumn. Sardinian Warblers were less confined to one or two plants in the winter than in autumn but they ignored Lentisc.

Buckthorn was the main species visited by the

FIGURE 3.9. Occupation of plant species by foraging warblers in low Maquis at Jews' Gate.





1 Wild Olive, 2 Calicotome, 3 Teline, 4 Lentisc, 5 Buckthorn, 6 Osyris, 7 Asparagus, 8 Others

FIGURE 3.9. continued.

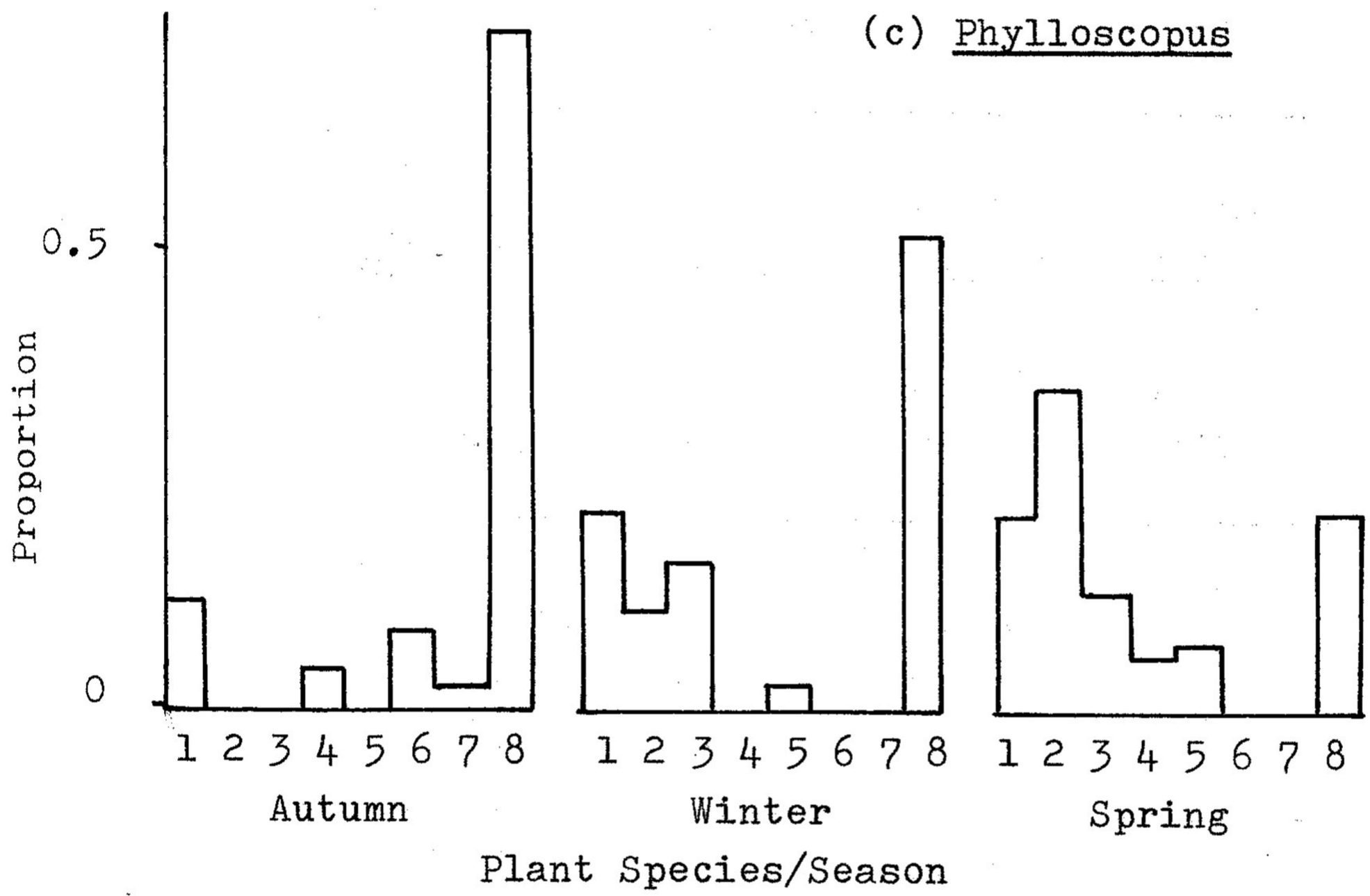


TABLE 3.15. Occupation of different plant species for foraging on by Blackcaps, Sardinian Warblers and Phylloscopus species at Gibraltar.

Species	Number of observations			
	Autumn	Winter	Spring	Summer
Blackcap				
Wild Olive	73(63)	60(60)	22(30)	22(24)
Other berry-producing spp.	13(17)	13(16)	15(8)	6(6)
Others	7(13)	15(12)	7(6)	7(5)
Sardinian Warbler				
Wild Olive	61(57)	72(62)	97(106)	49(54)
Brooms	1(9)	3(10)	31(16)	8(8)
Other berry-producing spp.	21(15)	13(16)	28(28)	12(15)
Others	4(7)	7(7)	7(13)	15(7)
Phylloscopus				
Wild Olive	21(23)	20(17)	51(52)	
Brooms	0(13)	8(10)	45(30)	
Others	31(15)	10(11)	20(34)	

Notes: 1. All observations at Jews' Gate
2. Expecteds calculated from contingency tables and given in parenthesis
3. Other berry-producing species are Lentisc, Buckthorn, Osyris and Spiny Asparagus.
4. Brooms are Calicotome and Teline. These flower in spring

Blackcap in spring but olives were also visited regularly (Fig.3.9.). Lentisc and Osyris were not visited at all. The Sardinian Warbler foraged on all plant species in spring (Fig.3.9.). Olive remained the main plant species for the Sardinian Warbler in spring but Calicotome and Osyris were visited often. Finally, in summer, Blackcaps were most frequently observed on the uncommon plant species ("others") and of the commoner species, they only visited Olive, Buckthorn and Teline (Fig.3.9.). In summer, Sardinian Warblers were also seen most often on the less-common plant species, but they occured on the commoner plants more often than Blackcaps. Only Lentisc was not visited by Sardinian Warblers, but Olive and Osyris were still visited frequently (Fig.3.9.).

Phylloscopus species generally occured on different plant species from those on which Sylvia species were most often observed. In winter, the only Phylloscopus species in the habitat was Chiffchaff; in autumn, the Willow Warbler was also present, and in spring the Bonelli's Warbler became the third species. All three species foraged in a similar manner and the data for all three have been lumped. In autumn and winter Phylloscopus foraged almost exclusively on fennels and grasses. Olives were sometimes visited in autumn and winter, as were Calicotome and Teline in winter (Fig.3.9.). In spring more plant species were visited and the only plant species Phylloscopus species were not

observed on was Osyris. Calicotome was the main plant species visited by Phylloscopus in spring. There were no Phylloscopus species in the habitat in summer (Fig.2.1.).

Seasonal changes in plant niche breadth and plant niche overlap are presented in Table 3.16. Blackcaps were broader-niched in this dimension than Sardinian Warblers, in winter and in summer. Blackcaps' range of plant species visited was narrowest in autumn. Sardinian Warblers were least specialized in spring (Table 3.16.). Phylloscopus species were narrow-niched except in spring, when they had wider preferences than Blackcaps.

Overlaps between Sylvia species were high all year, most markedly so in winter because they visited similar plants. The lowest overlaps, though still high, were recorded in spring and autumn (Table 3.16.). Overlaps between Sylvia species and Phylloscopus species were lower than between Sylvia species but in some seasons these inter-generic overlaps were high (Table 3.16.). The overlap between Phylloscopus species and Sardinian Warbler in spring was greater than that between Blackcap and Sardinian Warbler at the time.

These observations are based on frequency of visits by warblers to bushes, relative to the abundance of these bushes, in the study site; the observations show that some plant species are visited more frequently and others less so than encountered at

TABLE 3.16. Seasonal changes in plant species niche breadth and overlap in Sardinian Warblers, Blackcaps and Phylloscopus species at Jews' Gate, Gibraltar.

(a) Niche Breadth

Species	Breadth			
	Autumn	Winter	Spring	Summer
Blackcap	3.262	4.030	3.751	4.157
Sardinian Warbler	3.355	3.531	5.275	3.808
Phylloscopus	1.748	2.974	4.422	

(b) Niche Overlap

Species pair	Overlap			
	Autumn	Winter	Spring	Summer
Blackcap/Sardinian	0.738	0.964	0.731	0.817
Blackcap/Phylloscopus	0.561	0.713	0.647	
Sardinian/Phylloscopus	0.360	0.699	0.810	

random on the site. The absolute number of visits to bushes, irrespective to their relative abundance, will now be considered. A warbler may visit a plant species more frequently than it encounters it at random in the habitat but it may still forage more overall on the commonest plants in the habitat. At all times of year Blackcaps and Sardinian Warblers visited Wild Olives more than any other plant species. The presence of Wild Olives in the Maquis at Gibraltar appears to be extremely important for these two species. Wild Olive Maquis is scarce in the hinterland (Cortes 1979, pers.obs.). Phylloscopus species also occured most often on Wild Olives, except in autumn when they were observed most frequently on fennels. In autumn, Sardinian Warblers were often seen on Lentisc. In spring, the two Sylvia species occured frequently on Buckthorn, and Sardinian Warblers were also frequent on Callicotome. Phylloscopus species were abundant on Callicotome in spring.

Did the warblers occur on bushes with most food out of those available at the site ? The numbers of arthropods were sampled as described in 1.7. Within any season, the numbers of arthropods in different plant species varied greatly. Within a plant species, arthropod abundance also varied seasonally (Table 3.17.). In autumn, most plant species had similar arthropod densities, but Osyris had significantly lower densities than any other. Several species produced fruit in the autumn. About 30% (n = 25) of all the Wild Olives had berries and the mean number of berries

TABLE 3.17. Mean number of arthropods in different plant species at Jews' Gate.

Plant Species	Autumn		Winter		Spring		Summer	
	Mean	2 SE	Mean	2 SE	Mean	2 SE	Mean	2 SE
Wild Olive	0.7	0.2-1.1	1.2	0-2.6	1.6	0.7-2.6	0.3	0-0.6
Calicotome	0.9	0.3-1.5	4.2	0-14.0	3.4	2.4-4.4	0.4	0-0.92
Asparagus	0.8	0.2-1.4	0	0	0.4	0.2-0.6	0.4	0-0.83
Lentisc	0.5	0.1-0.9	0.6	0-1.4	0.9	0.4-1.4	0.8	0.31-1.29
Buckthorn	0.7	0.4-1.0	0.6	0-1.8	1.8	1.2-2.3	0.5	0-1.29
Osyris	0.1	0-0.3	0.8	0.1-1.5	0.8	0.4-1.2	0.5	0.2-0.8
Teline					2.2	1.3-3.1	0.6	0.1-1.1

per olive (number counted in a 1 minute interval, as with arthropods, see 1.7.) was 26.9 $\pm$ 36.7 (2 SE). 30% of the Lentiscs (n = 20) were fruiting in the autumn but their fruits were unripe. Associated almost exclusively with Lentisc was a creeper (Rubia peregrina) which had ripe berries in the autumn. The mean number of ripe Lentisc/Rubia berries per bush in the autumn was 41.4 $\pm$ 43.8 (2 SE). 70% of the Spiny Asparagus bushes had fruit (n = 40) but they were all unripe in the autumn. These berries gradually became ripe in winter so that by the middle of December, 80% of all the Spiny Asparagus berries were ripe. The mean number of berries per Spiny Asparagus bush was only 1.5 $\pm$ 1.0 (2 SE). 10% (n = 20) of the Osyris bushes were fruiting in the autumn. The mean number of fruits per bush was 2.1 $\pm$ 4.1 (2 SE).

Samples of berries were collected and weighed in a balance to the nearest 0.1 g . The weight of the stones was then subtracted to obtain a measure of the amount of edible material available. Spiny Asparagus berries were not examined. The mean amount of food per berry was 0.10 g for Wild Olive and Osyris. For Lentisc it was 0.07 g and for Rubia it was 0.04 g . The amount of fruit per unit volume of Wild Olive was then calculated at 2.69 $\pm$ 3.67, for Osyris at 0.21 $\pm$ 0.41, and for Lentisc/Rubia at 4.14 $\pm$ 4.38. Taking the absolute bush volumes (3.4.7.), Wild Olives would have on average 101.1 $\pm$ 90.8, Osyris 0.7 $\pm$ 0.6, and Lentisc/Rubia 21.7 $\pm$ 8.5. These calculations are explained

in more detail in 1.7.

In winter, the situation was very similar to the autumn, except that Spiny Asparagus were more ripe and Rubia berries were no longer available. The mean number of arthropods per bush at this time remained at a similar level to the autumn but there seemed to be more plants scoring 0 arthropods.

In spring there was a flush of insect life in most plant species (Table 3.17.). This was most pronounced in the brooms Calicotome and Teline which flowered profusely at the time. Small increases in arthropod content were noticeable in Wild Olive and in Buckthorn. The latter species had ripe berries in late spring and was the only plant species to regularly have fruit outside the autumn/winter period. Finally, in summer all bushes had very few arthropods as a result of the prolonged drought; plant growth ceased in summer (Mooney et al. 1974).

Within a season, the sizes of arthropods varied little between plants (Table 3.18.). There were also few differences between autumn and winter. In spring, the mean arthropod size rose for all plant species (Table 3.18.).

The product of the mean arthropod density and the mean bush volume for each plant species was obtained as for berries (1.7.) in order to obtain a measure of the mean total arthropod content for all the plant species. Wild Olives had the greatest quantity of arthropods at all times (Tables 3.19., 3.20.),

TABLE 3.18. Arthropod sizes in different plant species at Jews' Gate.

Plant Species	Autumn		Winter		Spring		Summer	
	Mean	2 SE	Mean	2 SE	Mean	2 SE	Mean	2 SE
Wild Olive	2.1	1.4-2.8	2.3	1.2-3.4	4.2	3.3-5.1	6.0	2.7-9.3
Calicotome	1.9	1.3-2.5	2.2	1.9-2.5	4.4	4.1-4.7	7.5	4.8-10.3
Asparagus	2.0	1.3-2.7			4.0	3.2-4.7	4.0	1.5-6.5
Lentisc	3.6	0.9-6.3	1.0		4.4	3.4-5.5	4.5	3.1-5.9
Buckthorn	1.0		2.3	0-4.9	4.2	3.5-5.5	2.0	1.4-2.6
Osyris			1.0		4.2	3.4-5.0	6.2	5.0-7.4
Teline					4.8	4.2-5.4	2.7	1.8-3.6

All measurements in millimetres.

TABLE 3.19. Volumes of bushes at Jews' Gate, Gibraltar.

Plant Species	Mean	s.d.	N
Wild Olive	37.58	39.91	10
Calicotome	4.13	2.54	10
Asparagus	0.08	0.13	10
Lentisc	5.25	3.13	10
Buckthorn	3.55	3.68	10
Osyris	3.49	2.36	10
Teline	2.35	1.94	10

All volumes in metres^3

mainly because they were the largest bushes. In autumn, Calicotome, Lentisc and Buckthorn had moderate quantities of arthropods, but Osyris and Asparagus had little. Winter was similar but Osyris had a few more arthropods than in autumn. In spring, Wild Olives had most arthropods of all the plant species per bush, but Calicotome also had large quantities. Lentisc and Buckthorn also increased (Table 3.20.). Summer was generally very poor but Wild Olives remained with most arthropods per bush.

We can now compare the warbler foraging observations described earlier with the food available in the various types of bushes available in the habitat. The two Sylvia species were always observed on Wild Olives, irrespective of time of year (Fig.3.9.). Because of their large size, Wild Olive bushes always had more arthropods per bush than any other plant species even though they did not always have most arthropods per unit volume. Warblers feeding on large bushes may have had an additional advantage in that the amount of time spent flying was reduced when compared to having to forage on the same volume of vegetation but broken up into small bushes. Wild Olives also had many ripe berries in autumn and winter when arthropods were scarce. Phylloscopus species did not take berries at all and only visited Wild Olives infrequently during the autumn and winter (Fig.3.9.).

Sardinian Warblers visited Lentisc frequently in autumn (Fig.3.9.) At this time of year they

TABLE 3.20. Mean number of arthropods per bush species in low Maquis at Jews' Gate.

Plant Species	Autumn	Winter	Spring	Summer
Wild Olive	26.31	45.10	60.13	11.27
Calicotome	3.72	(17.35)	14.04	1.65
Asparagus	0.06	0	0.06	4.80×10^{-3}
Lentisc	2.63	3.15	4.73	4.20
Buckthorn	2.49	2.13	6.39	1.78
Osyris	0.35	2.79	2.79	1.75
Teline			5.17	1.41

foraged on the Rubia berries attached to the Lentiscs rather than on the unripe Lentisc fruit. In winter, when Lentisc berries became ripe but Rubia stopped fruiting, warblers were rarely observed on these bushes. After Wild Olives, the Lentisc/Rubia complex produced most berry food by weight. The Sardinian Warbler is smaller than the Blackcap and is socially subordinate to it (3.4.10.). At the Wild Olives, Sardinian Warblers were chased off by Blackcaps so that they may have been forced to forage on the next best. The Rubia berries were not taken by Blackcaps. Rubia berries were smaller than Wild Olive berries and they have been more manageable to Sardinian Warblers, even though they were seen taking Wild Olives occasionally (see also 3.4.9.). The nutritive content of the berries could not be studied, but this may be another factor which may have modified the dietary preferences of the warbler species. Berthold (1976) points out that vegetal matter is generally inefficient as a food source to omnivorous birds such as Sylvia unless it is supplemented by animal material. Berries may only be of use to the warblers in that they provide large volumes of easily cropped food when arthropods are scarce but their nutritive advantage is probably minimal in all types of berries.

The other berry-producing plant species were only visited occasionally by the Sylvia warblers. In the 1977-78 winter, when hardly any Wild Olives fruited,

Blackcaps were frequently seen taking Spiny Asparagus berries but no data were collected at the time.

Blackcaps often visited Buckthorn in spring (Fig.3.9.). At this time of year Buckthorn had a fairly high arthropod content (Table 3.17.), ranking third after Wild Olive and Calicotome in total arthropod content (Table 3.20.). Buckthorn at this time also had numerous ripe berries which the Blackcaps took. Calicotome was not visited by Blackcaps despite their high arthropod content (Tables 3.17., 3.20.). Calicotome occured mostly among the patches of lowest vegetation within the site and they may therefore have been away from the Blackcap territories which were in taller vegetation (3.4.10.).

In spring, Sardinian Warblers were observed most times on Wild Olives (Fig.3.9.). They also visited Calicotome often as this had many arthropods. Some Osyris bushes were visited as they had berries remaining from the winter.

It was the Phylloscopus species which were most frequently observed on Calicotome in spring (Fig.3.9.) and they took many arthropods (which were in flowers on the periphery) by hovering and picking.

These observations show that different warbler species occured most frequently on plant species which appeared to have most food and which were most accessible to their methods of foraging. The main plant species visited varied between species, and within species

seasonally. In winter especially, Sylvia species foraged mainly on berries but at other times they took mainly arthropods. The Phylloscopus species appeared to be too small to handle berries and they usually occured in bushes with high arthropod content. They were abundant on fennels and on Calicotome on which Sylvia had perching difficulties.

3.4.3. Ground Foraging

The Sardinian Warbler and the Blackcap foraged on the ground. Phylloscopus species also did so from time to time. The Sardinian Warbler foraged on the ground much more than the other warblers. This was especially so in spring and autumn. Sardinian Warblers were rarely seen foraging on the ground in winter (Table 3.21.). Blackcaps rarely foraged on the ground, and were never seen to do so in spring. Phylloscopus species were more frequent on the ground than Blackcaps, especially in autumn.

Morphologically, the Sardinian Warbler is better adapted to ground foraging than either the Blackcap or the Phylloscopus species (3.4.9.). The latter are mostly adapted for foraging in the canopy. The seasonal variation in the amount of ground foraging by Sardinian Warblers does not appear to be related to the amount of food available in that stratum (Table 3.22.). The drop in ground foraging in winter could be due to the increase in berry consumption or to the fact that there are other ground foragers in the habitat at the time (chapter 2). The absence of

TABLE 3.21. Proportion of ground feeding by Blackcaps, Sardinian Warblers and Phylloscopus at Jews' Gate.

Species	Autumn	Winter	Spring	Summer
Blackcap	3.4	3.49	0	2.00
	94	86	47	50
Sardinian	21.18	3.33	12.97	5.84
	85	90	185	137
Phylloscopus	6.35	4.88	3.82	
	63	41	131	

For each species, the top figure indicates the proportion (%) of all the observations which were of individuals foraging on the ground. The lower figure is the total number of observations.
If the data for all seasons are lumped for each species, and the expected proportion of ground feeding is calculated for each species according to the relative number of observations of each, then following values are obtained : Blackcap O=7 E=19, Sardinian O=53 E=35, Phylloscopus O=11 E=17. $X^2_2 = 19.00$ $p < 0.001$

TABLE 3.22. Amount of food in ground stratum at Jews' Gate.

(a) Number of arthropods

Season	Mean	± 2 SE
Autumn	4.00	0 - 8.23
Winter	0.60	0 - 1.38
Spring	0.97	0.58 - 1.36
Summer	2.70	1.27 - 4.13

(b) Sizes

Season	Mean	± 2 SE
Autumn	2.0	1.5 - 2.5
Winter	3.3	1.0 - 5.7
Spring	3.6	2.9 - 4.1
Summer	3.7	1.8 - 5.6

All sizes in millimetres

frequent ground foraging in the summer cannot be explained since the ground stratum has some arthropod food left during the drought. The type of food may not be suitable for Sardinian Warblers.

3.4.4. Foraging Height

Blackcaps were observed foraging higher than Sardinian Warblers all year (Fig.3.10.). Overlaps in foraging height were nevertheless large all year (Table 3.23.) indicating that the two species had very similar vertical foraging stations. The relative height of a bird in a bush was recorded as

$$\text{Relative Height} = \frac{\text{Height of bird in bush}}{\text{Height of bush}} \times 100$$

Sardinian Warblers foraged lower, relative to the overall height of the bush they were foraging on, than Blackcaps which remained near the canopy (Fig.3.11.). Nevertheless, the two species were recorded most frequently on the upper half of bushes. This may be due to warblers being more visible near the tops of bushes or it may mean that Sylvia warblers found more food near the tops of bushes. Since both species foraged high, irrespective of the overall height of the bush, this suggests that they had a genuine preference for foraging high.

Blackcaps took to a greater range of foraging heights than Sardinian Warblers (Fig.3.10.). Niche breadth values in this dimension were always higher than for Sardinian Warbler (Table 3.23.). The difference

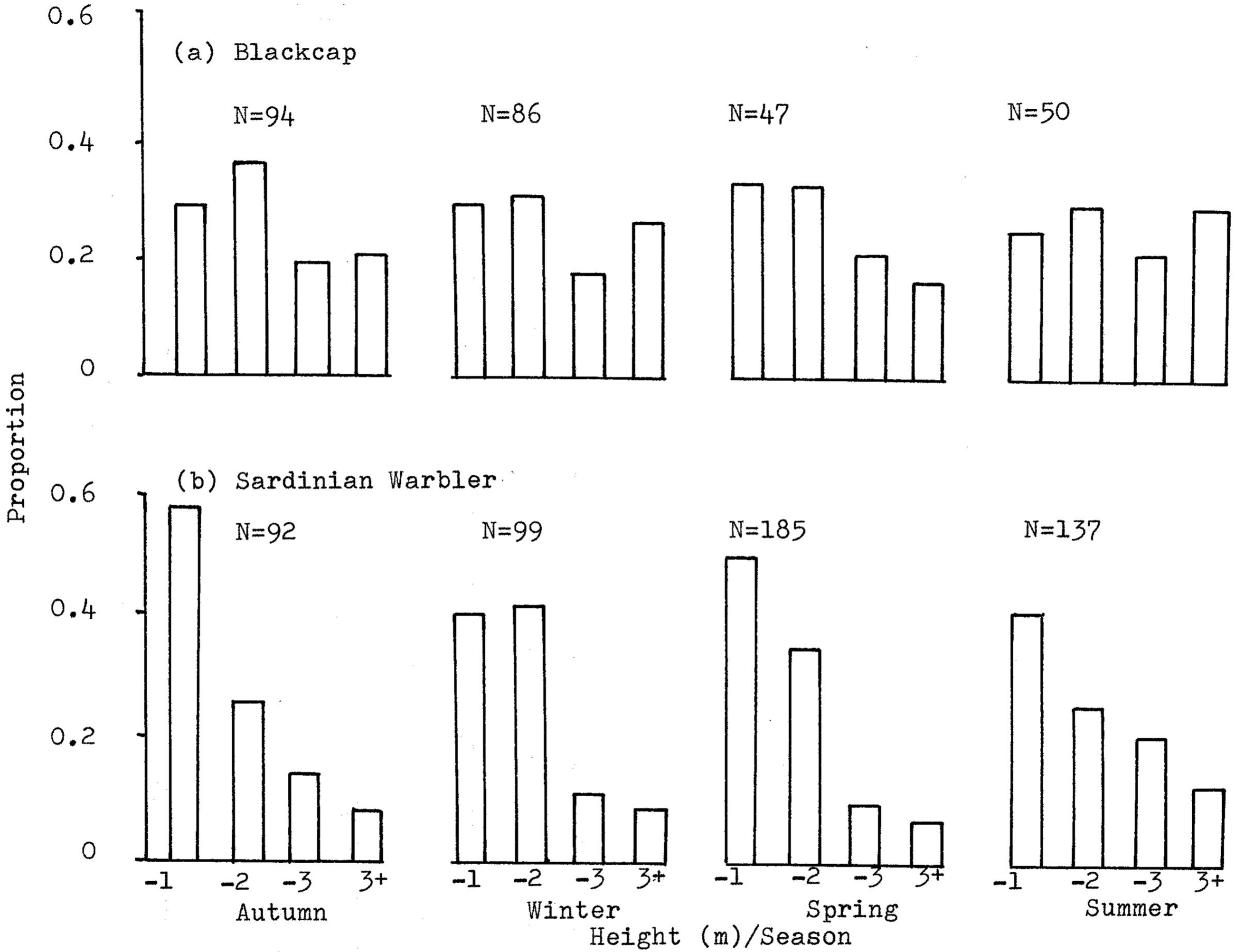


FIGURE 3.10. Foraging height distributions of Blackcaps and Sardinian Warblers in low Maquis at Jews' Gate.

TABLE 3.23. Foraging height breadth and overlap in Blackcaps and Sardinian Warblers at Jews' Gate.

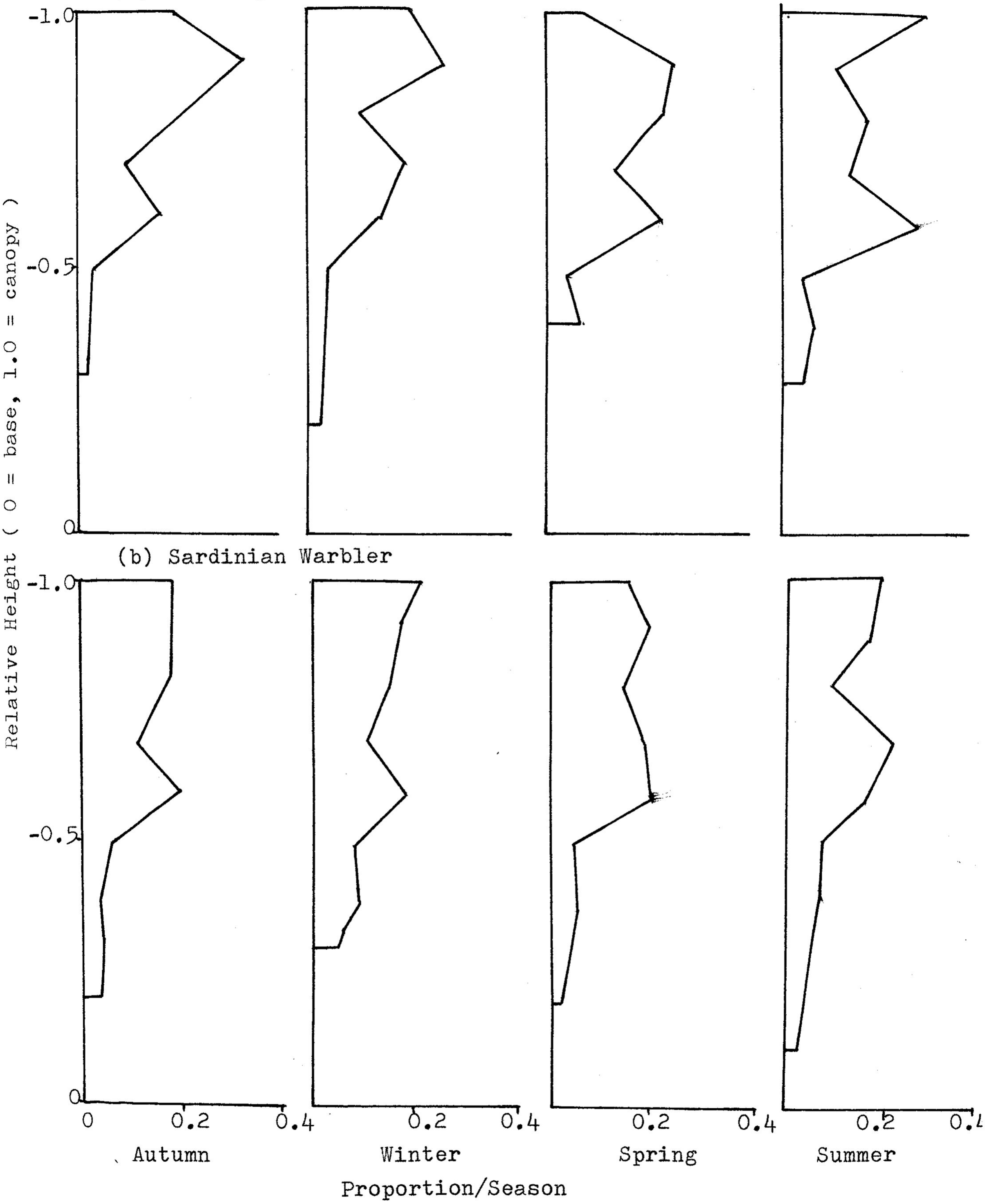
(a) Niche Breadth

Species	Season			
	Autumn	Winter	Spring	Summer
Blackcap	3.71	3.86	3.68	3.93
Sardinian	2.47	2.90	2.60	3.40

(b) Niche Overlap

Species pair	Season			
	Autumn	Winter	Spring	Summer
Blackcap/ Sardinian	0.85	0.90	0.93	0.90

FIGURE 3.11. Relative Foraging Heights of Blackcaps and Sardinian Warblers in low Maquis at Jews' Gate.



in the niche breadth values of the two Sylvia species was least pronounced in summer (Table 3.23.). Summer was the time of year when Sardinian Warblers foraged least often on the ground (3.4.3.).

3.4.5. Foraging Position

For ease, bushes were divided into two areas, the centre and the periphery or outside. The centre of the bush consisted of the trunk and the main branches and the outer portion had the small branches and twigs. The number of times Blackcaps and Sardinian Warblers were observed in either portion was recorded (Table 3.24.). Both species preferred the central portions of bushes and there was no significant difference between the two species except in winter when Blackcaps foraged more frequently in the central portions of bushes and Sardinian Warblers less so.

3.4.6. Foraging Height and Position

The data from 3.4.4., and 3.4.5 are combined in this sub-section. These indicate the feeding site preferences of the two Sylvia species as judged by their frequency of occurence in the different positions (Fig. 3.12.). For comparison, data from Phylloscopus warblers have been included (Fig. 3.13.).

The data may be summarised as follows. Blackcaps spent most of their time foraging in the upper half of bushes and rarely perched on the ground. They were observed most frequently in the centre of bushes rather than in the periphery (Fig. 3.12.). Sardinian

FIGURE 3.12. Foraging positions of foraging warblers in low Maquis at Jews' Gate.

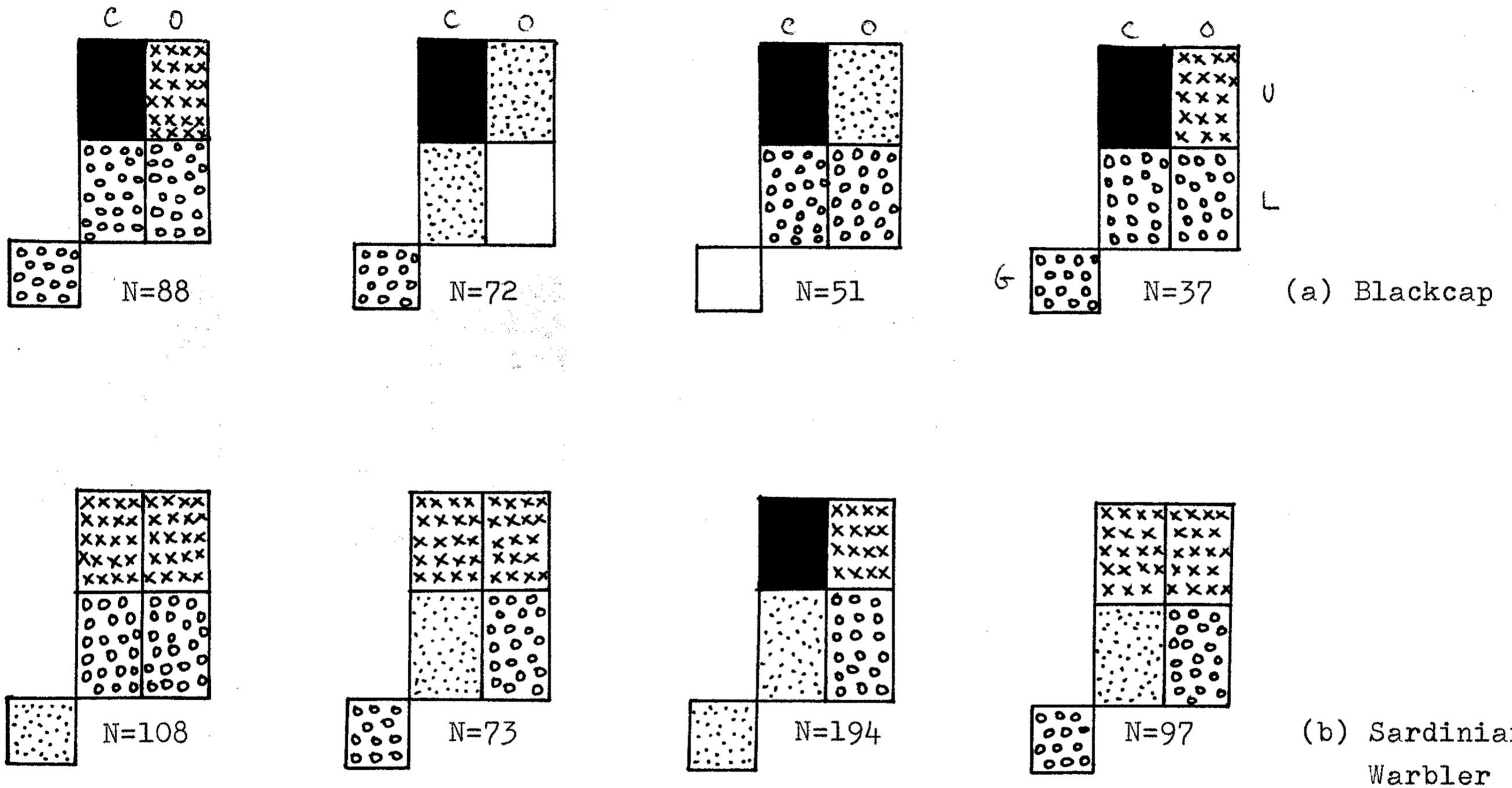
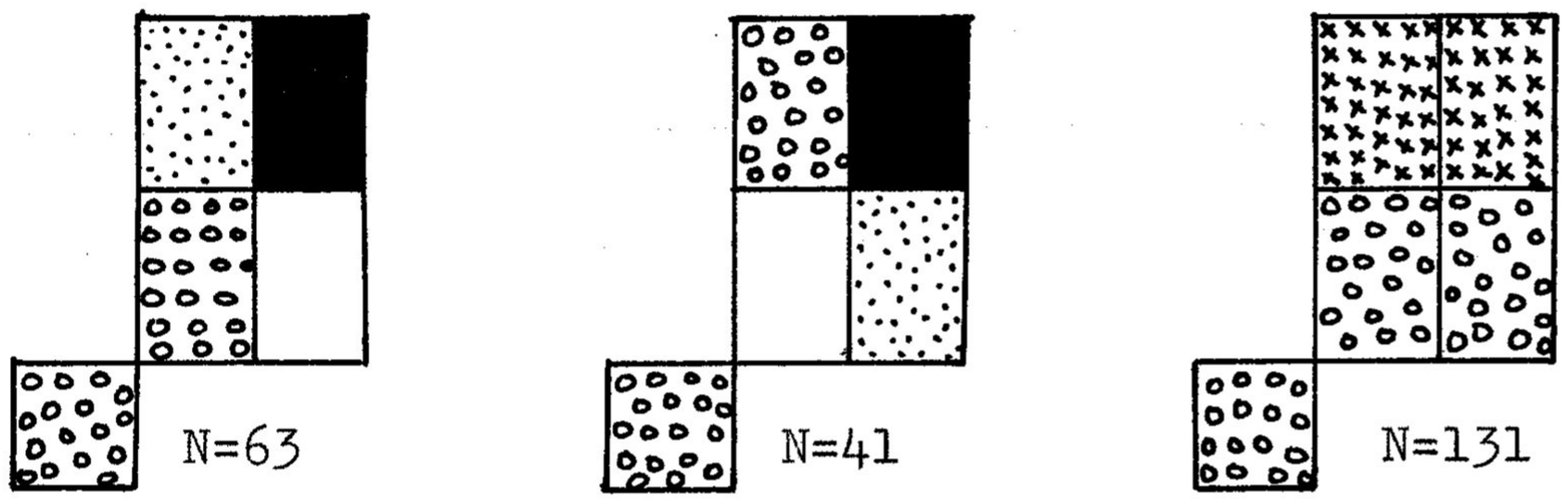


FIGURE 3.13. Foraging positions of foraging Phylloscopus warblers in low Maquis at Jews' Gate.



Legend as Figure 3.12.

TABLE 3.24. Foraging positions of Blackcaps and Sardinian Warblers in bushes at Jews' Gate.

Position	Number of observations							
	Autumn		Winter		Spring		Summer	
	BC	SW	BC	SW	BC	SW	BC	SW
Centre	55	48	59	49	35	124	22	56
Outer	25	40	10	27	14	45	14	31
% Centre	68.8	54.6	85.5	64.5	71.4	73.4	61.1	64.4

X_1^2 values, Autumn = 3.621, $p > 0.05$; Winter = 9.302, $p < 0.01$; Spring = 0.135, $p > 0.05$; Summer = 0.170, $p > 0.05$

Warblers behaved in a similar manner but were not so restricted to feeding in the centre and they tended to feed lower than Blackcaps. They foraged on the ground much more than Blackcaps.

Phylloscopus warblers also foraged mostly on the canopy but mainly in the periphery, especially on the outer twigs. In autumn and winter they spent most of their time taking small arthropods from the twigs (Fig. 3.13.). They foraged very little on the ground.

Sardinian Warblers had the broadest overall choice all year (Table 3.25.). Blackcaps were generally next except in spring when even Phylloscopus species had broader niches. Overlaps between the two Sylvia species were high all year but overlaps between Phylloscopus species and Sylvia species were low (Table 3.25.). Phylloscopus species overlapped most with Sylvia species in spring and least so in winter.

3.4.7. Bush Volumes

Did Blackcaps and Sardinian Warblers forage in bushes of different sizes ? There are insufficient data for an inter-season analysis but it is possible to compare lumped data. Large bushes were scarce at Jews' Gate and so the number of observations of birds foraging in bushes of volumes greater than 150 m^3 is low. Since the two warbler species are being compared directly and they were studied on the same site, a knowledge of the abundance of each bush category is not needed.

Blackcaps were observed foraging on large

TABLE 3.25. Foraging height niche breadth and overlap in Sylvia and Phylloscopus species at Jews' Gate.

(a) Niche breadth

Species	Season			
	Autumn	Winter	Spring	Summer
Blackcap	2.079	2.043	2.029	2.529
Sardinian	3.626	3.077	2.788	3.307
Phylloscopus	1.486	1.588	2.780	

(b) Niche overlap

Species pair	Season			
	Autumn	Winter	Spring	Summer
BC/SW	0.894	0.948	0.962	0.977
BC/Ph	0.48	0.26	0.83	
SW/Ph	0.72	0.51	0.86	

bushes more frequently than Sardinian Warblers (Table 3.26.). 9.17% of all the Blackcap observations were on bushes which were over 150 m^3 but only 3.3% of the Sardinian Warbler observations were in such bishes.

3.4.8. Foraging techniques

For each feeding observation, the method of food capture was recorded. The following methods were observed (Davies & Green 1976).

1. Stand Pick. The bird perched on a stem and, without changing position, picked an arthropod (or fruit) from the foliage.
2. Leap Pick. The bird leaped and picked an arthropod from the foliage, and then returned to the same or to another perch.
3. Leap Catch. The bird leaped and caught an arthropod in mid-air, then returned to the same or to another perch.
4. Hover Pick. The bird hovered and picked an arthropod from the foliage at the same time.
5. Hover Catch. The bird hovered and caught an arthropod in mid-air.
6. Fly Catch. The bird flew away from the vegetation and caught an arthropod in mid-air, then returned to the same or to a nearby perch.

Blackcaps and Sardinian Warblers foraged all year almost exclusively by stand picking (Table

TABLE 3.26. Occupation of bushes by volume, by Blackcaps and Sardinian Warblers.

Bush Volume (m^3)	Number of observations	
	Blackcap	Sardinian Warbler
0 - 50	85	188
51 - 100	24	17
101 - 150	5	4
151 - 200	6	3

$X_1^2 = 5.130$ $p<0.05$. The two lower categories and the two upper categories have been lumped to give expected values of over 5.

TABLE 3.27. Foraging techniques used by Blackcaps, Sardinian Warblers and Phylloscopus species at Jews' Gate.

Technique	Number of observations			
	Autumn	Winter	Spring	Summer
(a) Blackcap				
Stand Pick	92	67	43	32
Leap Pick	0	3	2	0
Hover Pick	0	1	0	0
Leap Catch	0	0	0	0
Hover Catch	0	0	0	0
Fly Catch	1	1	0	1
(b) Sardinian Warbler				
Stand Pick	96	92	181	64
Leap Pick	0	0	0	0
Hover Pick	1	0	1	1
Leap Catch	0	0	0	0
Hover Catch	0	0	0	0
Fly Catch	0	0	0	0
(c) Phylloscopus species				
Stand Pick	34	67	101	
Leap Pick	2	2	2	
Hover Pick	17	24	19	
Leap Catch	0	3	0	
Hover Catch	0	0	2	
Fly Catch	4	3	1	

3.27.). They only used other techniques rarely. Phylloscopus species also foraged mainly by stand picking but used hovering, and even flycatching, techniques more frequently than the Sylvia species (Table 3.27.). Phylloscopus species therefore overlapped less with the Sylvia species than did the Sylvia species between themselves (Table 3.28.). Overlaps were nevertheless high between any species pair.

3.4.9. Morphological Adaptations

There was no difference between the bill lengths of Sardinian Warblers and Blackcaps (nominate or local) trapped at Gibraltar (Tables 3.1. and 3.2.). This suggests that both species took similar prey sizes (Hespenheide 1975a). A small sample of faeces collected in spring 1978 supports this idea. Of five Sardinian Warbler faeces, all had remains of Coleoptera and Hymenoptera (ants), and three had remains of aphids, Hemiptera-Homoptera. Of eight Blackcap faeces, 6 had remains of Coleoptera, and 7 of Hymenoptera (again ants). One had remains of a spider and another two of Diptera. Although not extensive, the results suggest that the diets of the two species are similar. In autumn, remains of berries were easily found in faeces. Of ten Blackcap faeces, all had remains of Wild Olive, and three of Rubia. Of twelve Sardinian Warbler faeces, 11 had remains of Rubia, five of Wild Olive and two of Lentisc. Remains of Osyris were not found but Blackcaps were seen taking these berries at least three times in the 1978-79

TABLE 3.28. Foraging technique Niche Breadth and Overlap in Blackcaps, Sardinian Warblers and Phylloscopus species at Jews' Gate.

(a) Niche breadth

Species	Autumn	Winter	Spring	Summer
Blackcap	1.02	1.15	1.08	1.06
Sardinian	1.02	1.00	1.02	1.04
Phylloscopus	2.19	1.91	1.47	

(b) Niche Overlap

Species Pair	Autumn	Winter	Spring	Summer
BC/SW	1.00	1.00	1.00	1.00
BC/Ph	0.89	0.95	0.98	
SW/Ph	0.89	0.94	0.98	

winter. Bill length relative to size (weight) is also similar in the two Sylvia species, but Sardinian Warblers may have relatively longer bills (Fig.3.14.).

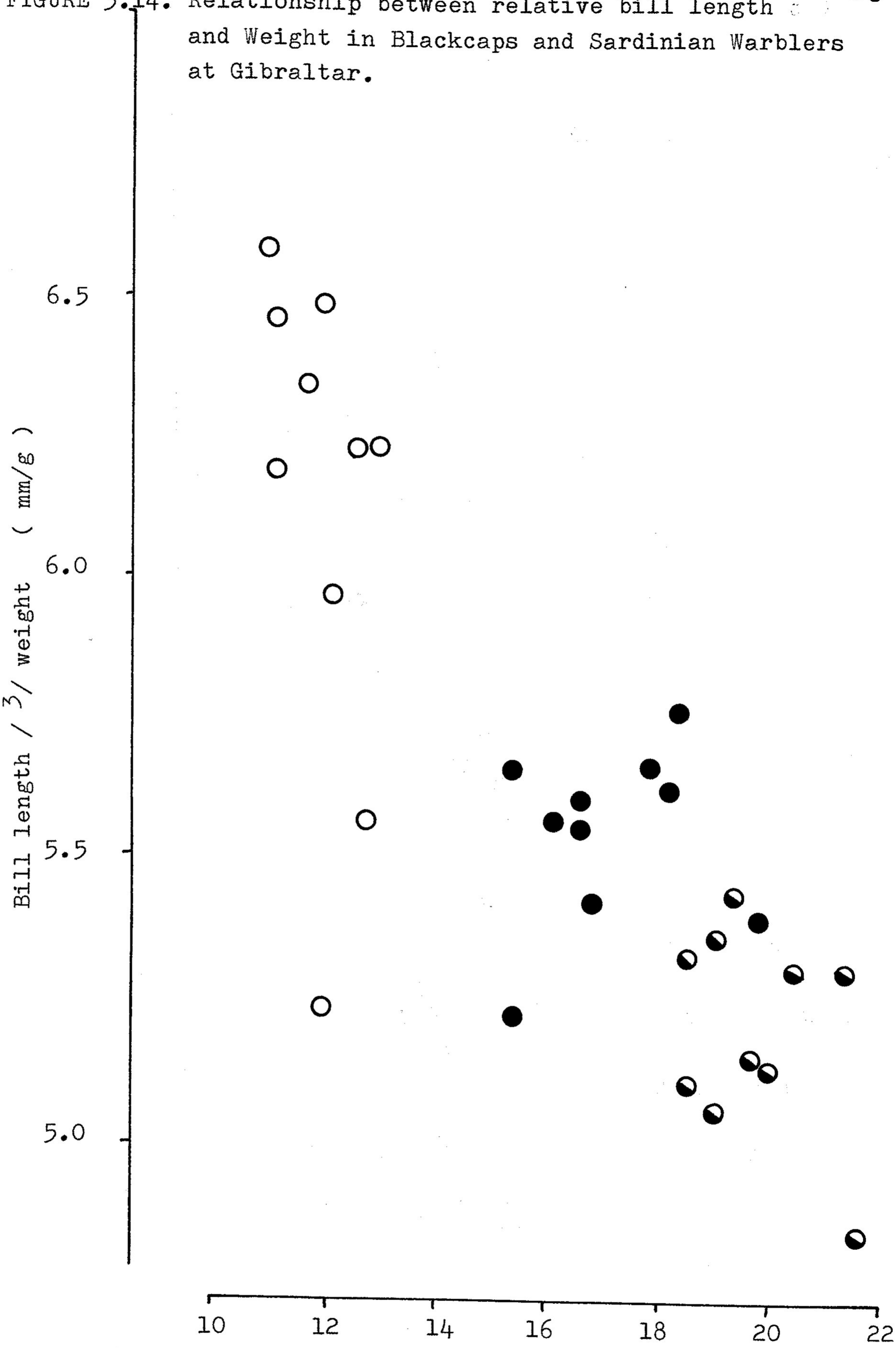
Other aspects of the morphology of the Sylvia species have been described in 3.2. The morphological adaptations of Sardinian Warblers and Blackcaps are summarised in Figs. 3.14. - 3.16. Local Blackcaps are in many respects intermediate between nominate Blackcaps and Sardinian Warblers probably due to their use of Maquis instead of mature woodland.

Sardinian Warblers are smaller than either form of the Blackcap. They are about 5 g lighter than local Blackcaps and 6 g lighter than nominate Blackcaps trapped under the same conditions (Table 3.1.).

The two forms of the Blackcap overlapped in all characters examined. Sardinian Warbler overlaps with the two forms were high except for weight (Table 3.29.). Wing length overlap was greater between the Sardinian Warbler and the local Blackcap than between the Sardinian Warbler and the nominate Blackcap. In bill length the Sardinian Warbler overlapped more with the nominate Blackcap than with the local Blackcap.

Morphological breadth was measured in the same way as the ecological measures dealt with so far. Of five measures, the Sardinian Warbler had the widest range of measurements for bill length and tail length (Table 3.29.). The local Blackcap had the widest range for wing length and for tarsus length, and the nominate Blackcap for weight (Table 3.29.).

FIGURE 3.14. Relationship between relative bill length and Weight in Blackcaps and Sardinian Warblers at Gibraltar.



Sardinian Warbler (open circles), Blackcap local (closed circles), Blackcap nominate (half closed circles).

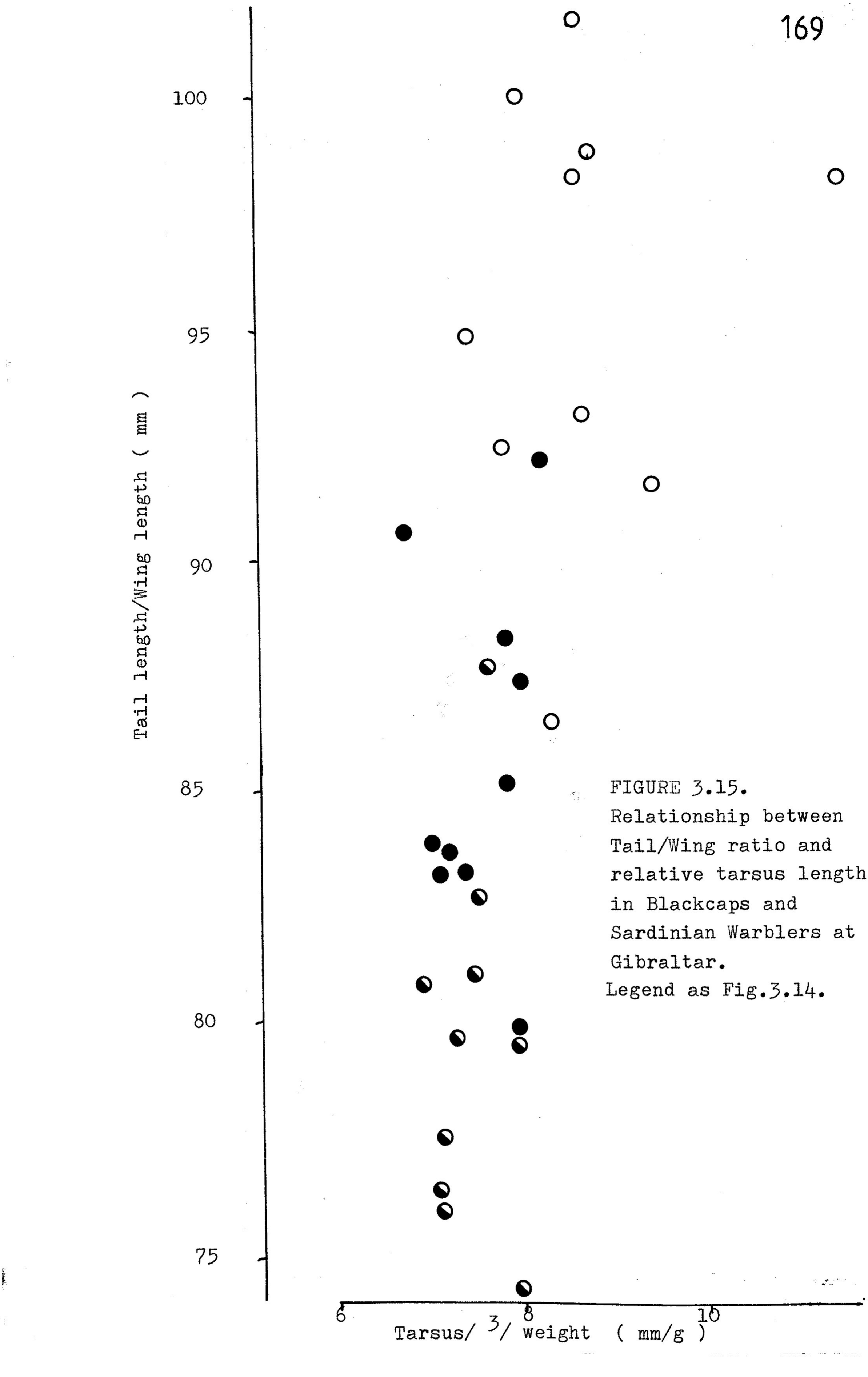


FIGURE 3.15.
Relationship between Tail/Wing ratio and relative tarsus length in Blackcaps and Sardinian Warblers at Gibraltar.
Legend as Fig.3.14.

FIGURE 3.16. Relationship between Index of wing roundness and relative wing length in Blackcaps and Sardinian Warblers at Gibraltar.
Legend as in Fig.3.14.

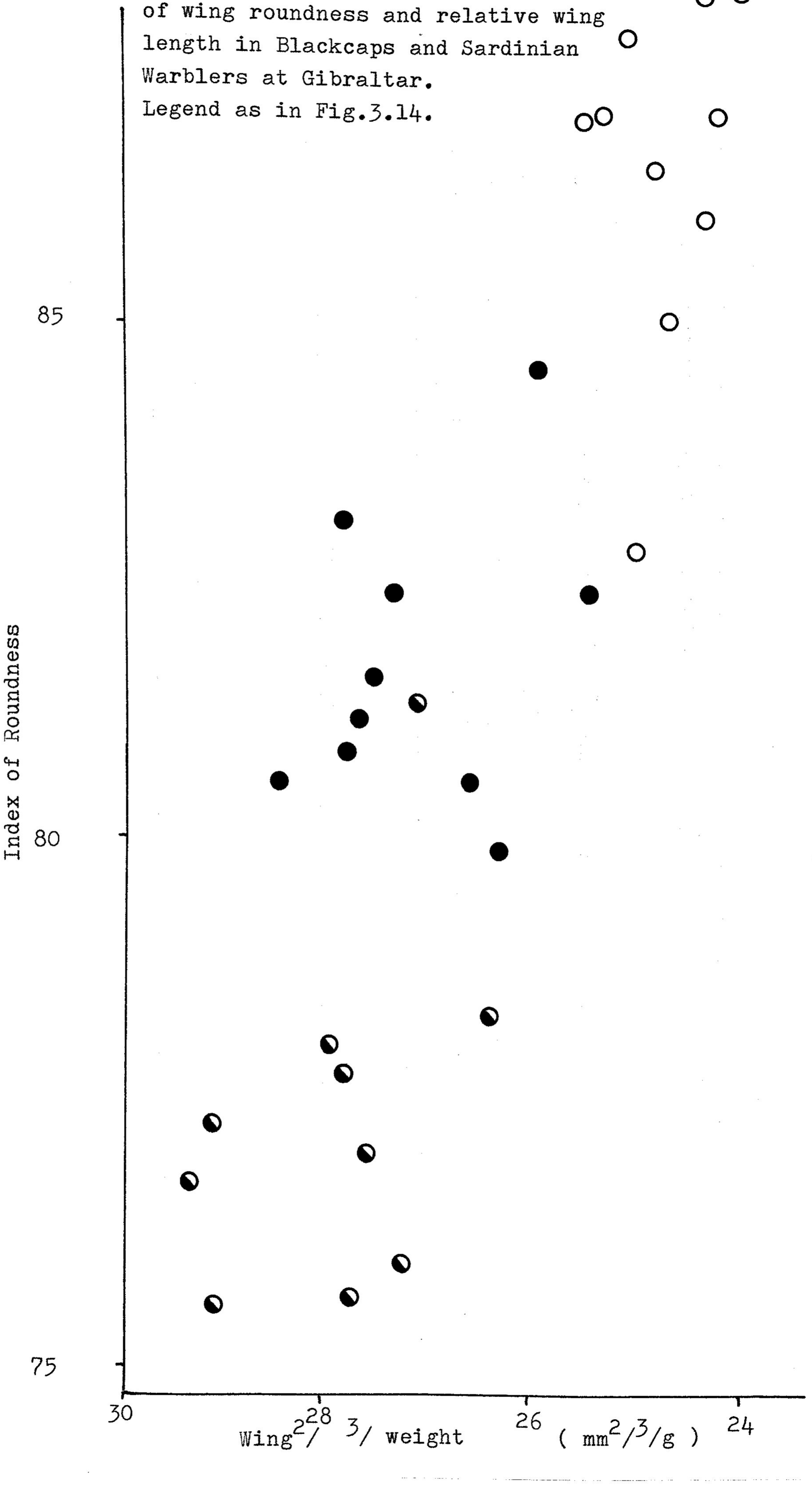


TABLE 3.29. Niche Breadth and Overlap in morphological characteristics of Blackcaps and Sardinian Warblers trapped at Gibraltar.

(a) Niche Breadth

Species	Bill length	Wing length	Tarsus length	Tail length	Weight
Blackcap(nominate)	2.51	3.25	2.71	6.63	6.28
Blackcap(local)	2.39	4.21	5.98	7.79	5.51
Sardinian	2.74	3.77	5.13	8.58	4.34

(b) Niche Overlap

Species Pair	Bill length	Wing length	Tarsus length	Tail length	Weight
BC(nom.)/BC(loc.)	0.94	0.82	0.59	0.85	0.93
BC(nom.)/SW	0.92	0.39	0.85	0.76	1.04^{-3}
BC(lôc.)/SW	0.78	0.69	0.84	0.88	0.01

3.4.10. Territoriality and Aggression

The most successful was to partition resources is to defend a territory, within which resources are available only to thw owner of the territory. This is the common way in which conspecifics partition resources in many species (Davies 1979), but interspecific territoriality, in which different species defend territories against each other, is also well documented (Simmons 1951, Orians & Willson 1963, Cody 1969, Cornwallis 1975). In this section, territoriality and aggression in the Blackcap and the Sardinian Warbler are examined with special reference to resource use and partitioning.

Breeding Season

During the breeding season (3.3.1.), Blackcaps were found holding territories in Maquis and Sardinian Warblers in Maquis and Garigue (Table 3.30., Figs. 3.17 - 3.21.). Three study sites were chosen, one in each of the habitats occupied by breeding Sylvia species. The High Maquis site was at Governor's Lookout and covered 4.5 ha, the low Maquis site was at Jews' Gate and covered 9.0 ha, and the Garigue site was at Windmill Hill and covered 13 ha (Fig. 1.2.). The lower the vegetation was in a site, the larger the area that was studied since territorial birds were more visible on the lower vegetation than in the dense Maquis which required more intensive effort. The site at Governor's Lookout was only studied in 1977, but the

TABLE 3.30. Blackcap and Sardinian Warbler territory sizes in three habitats at Gibraltar.

(a) Blackcap

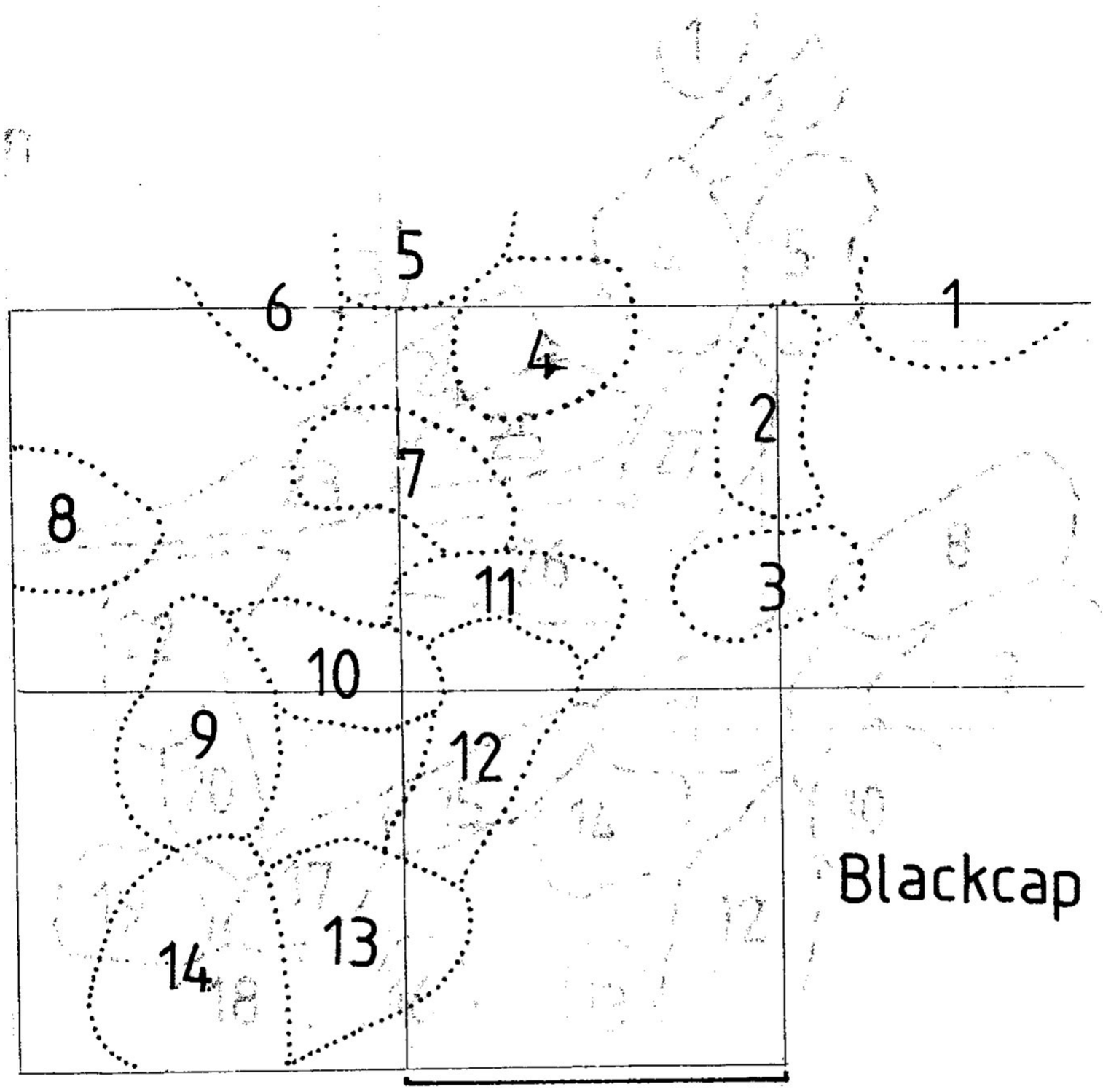
Site	Habitat	Territory Size[1] Mean	± 2 SE
Governor's Lookout	High Maquis	0.16	0.13 - 0.19
Jews' Gate 1977	low Maquis	0.17	0.13 - 0.21
Jews' Gate 1978	low Maquis	0.24	0.18 - 0.30

(b) Sardinian Warbler

Governor's Lookout	High Maquis	0.12	0.10 - 0.15
Jews' Gate 1977	low Maquis	0.13	0.12 - 0.15
Jews' Gate 1978	low Maquis	0.21	0.19 - 0.23
Windmill Hill 1977	Garigue	0.31	0.20 - 0.41
Windmill Hill 1978	Garigue	0.30	0.24 - 0.37

[1]All values in hectares (ha)

FIG. 3.17 Governor's Lookout. Sardinian Warbler & Blackcap breeding territories - Spring 1977.



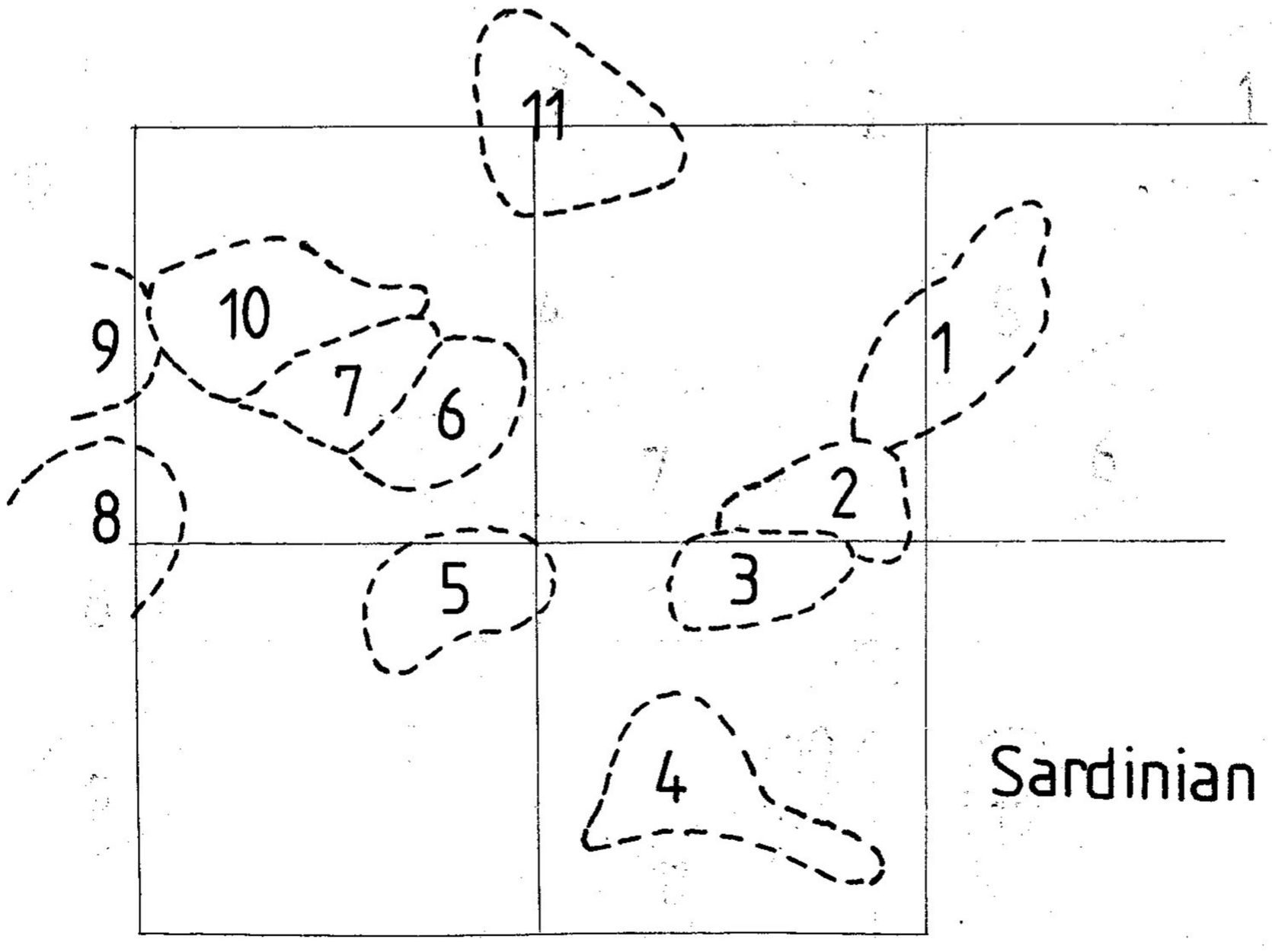


FIG.318 Jews' Gate. Sardinian Warbler & Blackcap breeding territories - Spring 1977.

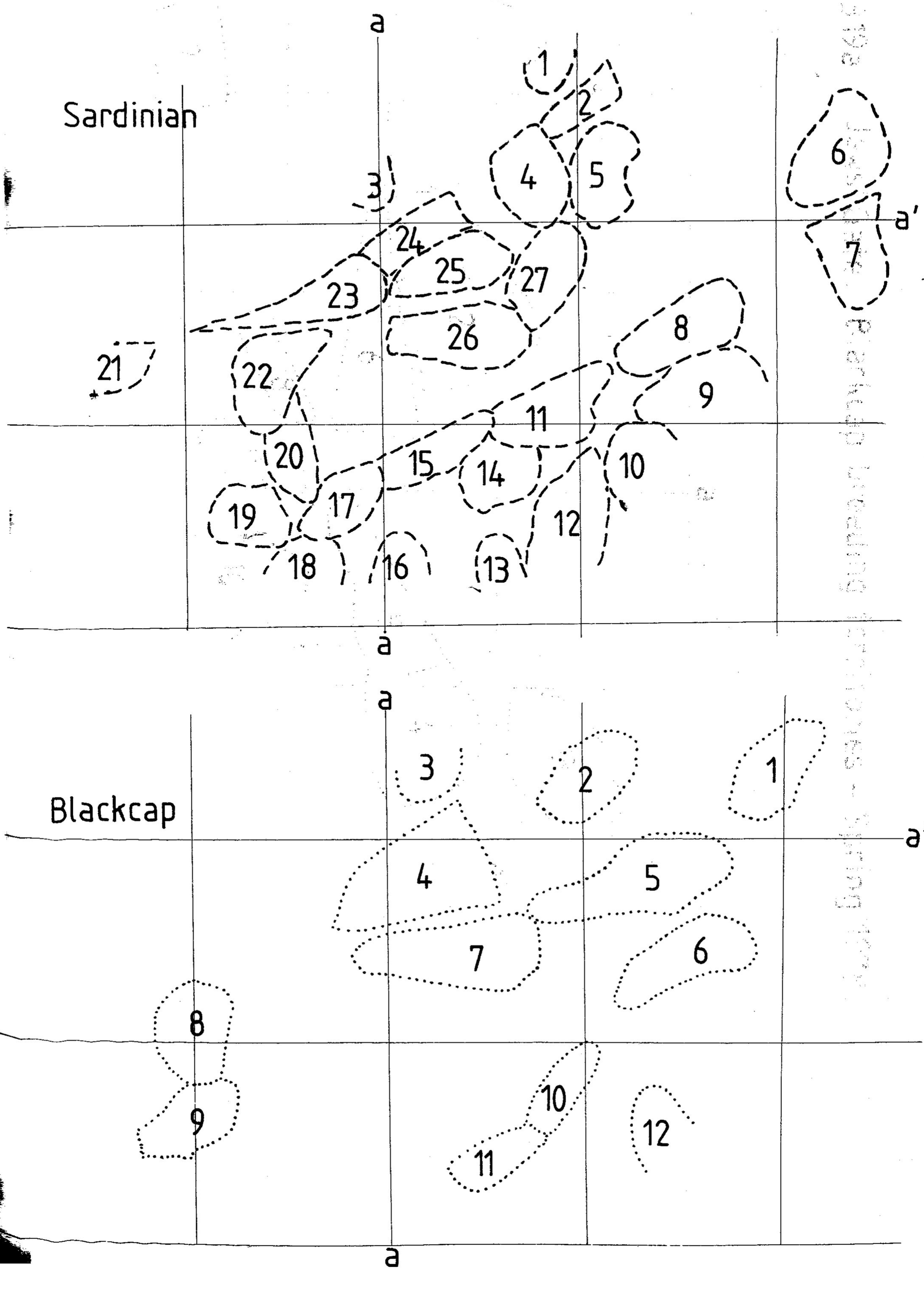


FIG.3.19a Jews' Gate. Blackcap breeding territories – Spring 1978.

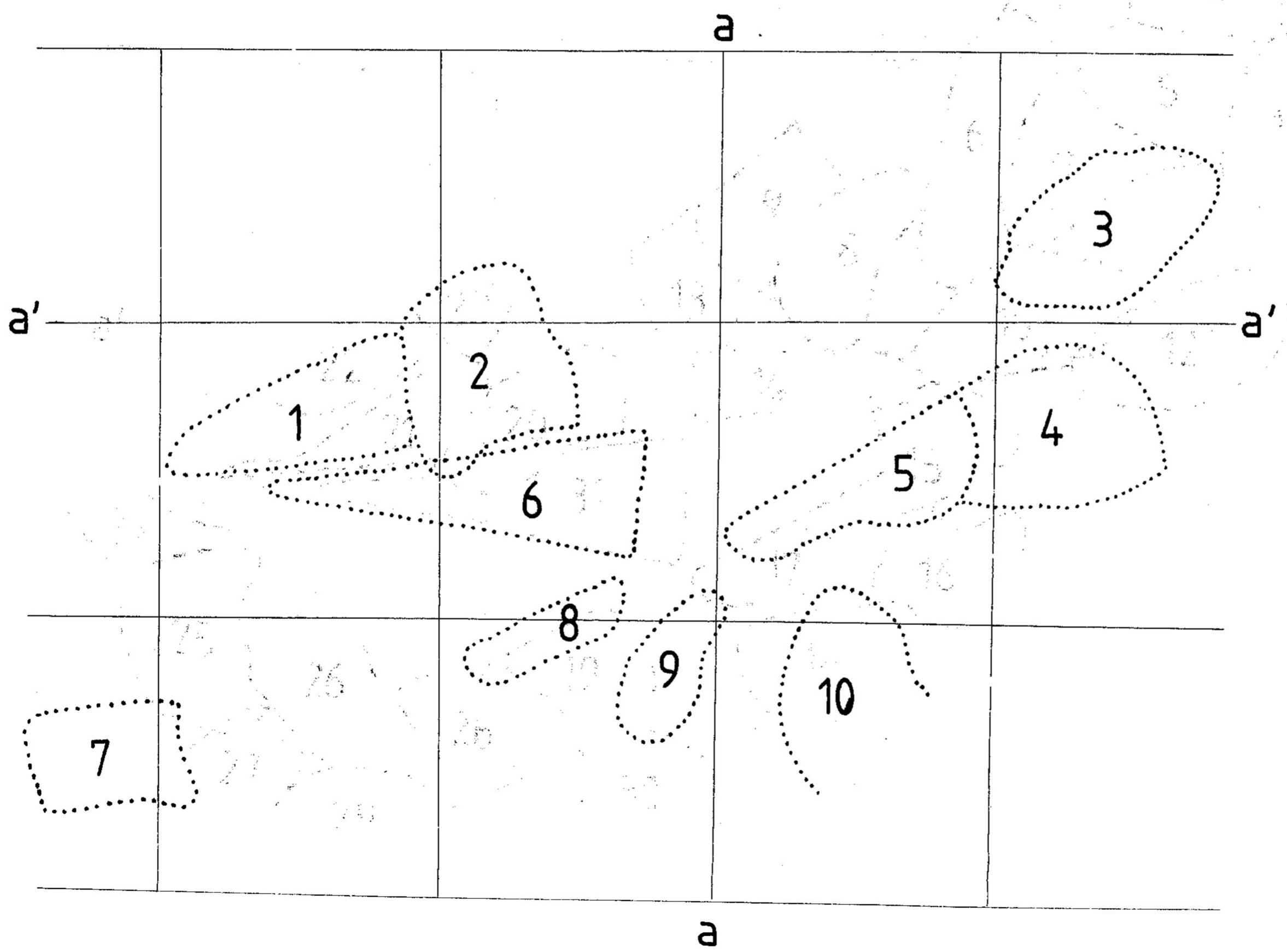


FIG. 3.19b Jews' Gate. Sardinian Warbler breeding territories - Spring 1978.

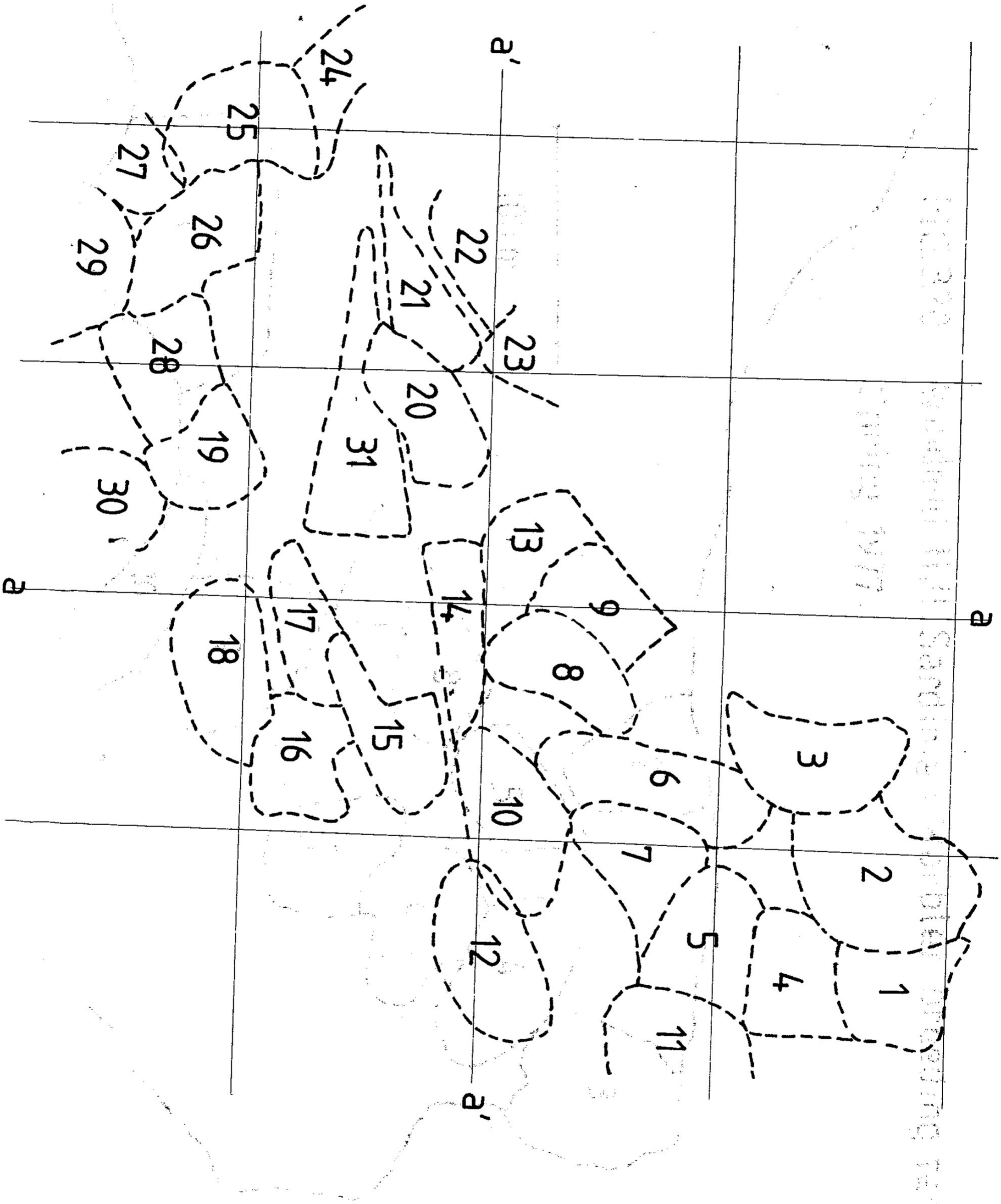


FIG. 3.20 Windmill Hill. Sardinian Warbler breeding territories – Spring 1977.

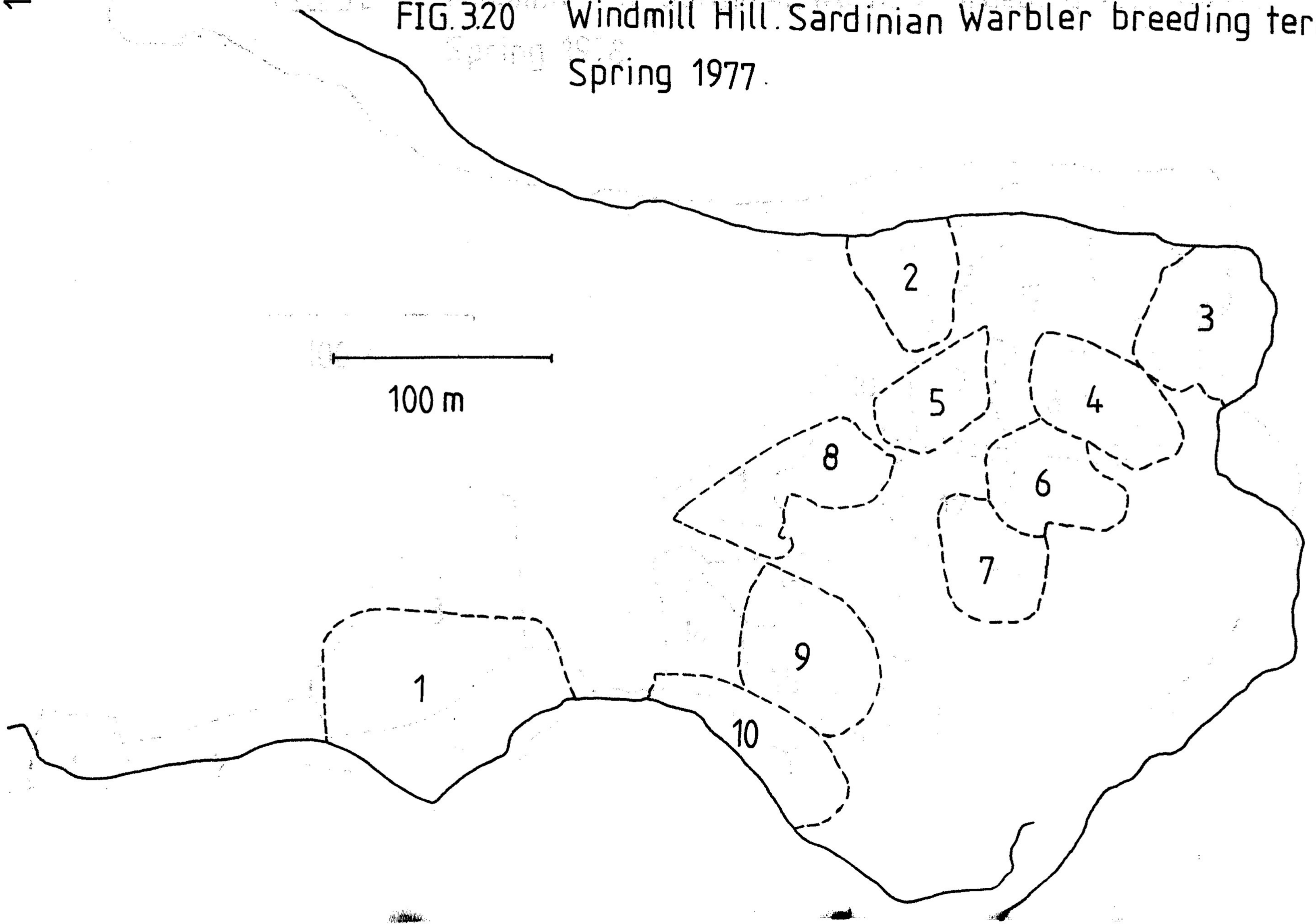
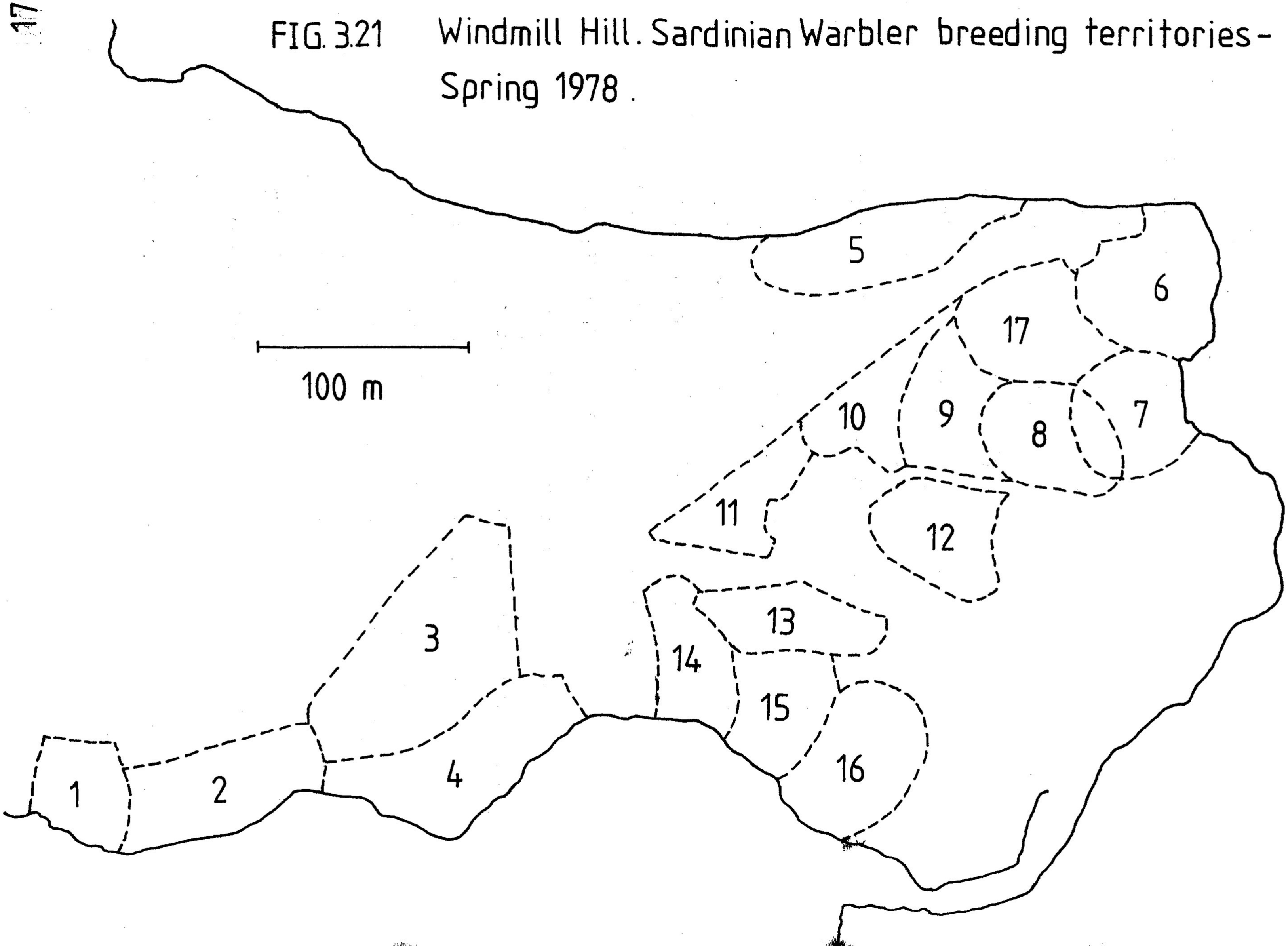


FIG. 3.21 Windmill Hill. Sardinian Warbler breeding territories - Spring 1978.



other two sites were also studied in 1978. In the latter year, the area of the Jews' Gate site was increased by 2 ha. Territories were plotted on grid maps of the study sites (scale 1 : 2500). The study sites were visited at least 15 times each and the position of singing males and their movements were marked on maps of the sites. In addition, data were gathered from playing back song recordings to territorial males and also by colour-ringing individual warblers.

At each site, vegetation height and the main plant species were recorded in 10 X 10 metre grid squares. Height was recorded to the nearest 0.25 m ; main plant species in a gris square were those which covered at least 10% of the surface of the square. A square could therefore have more than one main plant species.

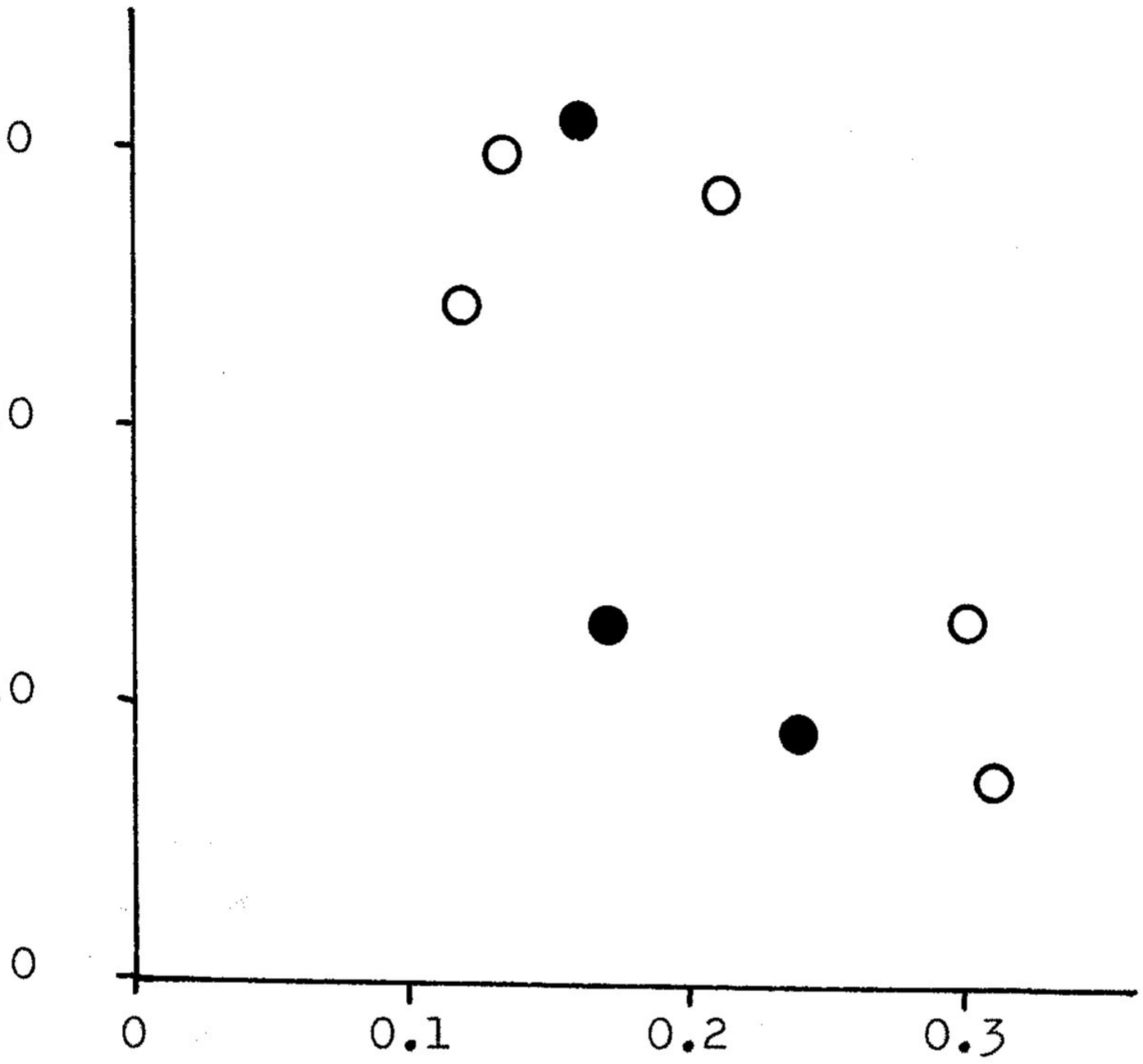
Blackcaps reached highest breeding density in High Maquis in 1977 (3.11 pairs/ha). The figure (and all that follow) is of breeding pairs; non-breeding males were occasionally observed in the study sites (e.g. unringed males appearing in territories with both holders colour-ringed) but the proportion of non-breeding males in the population could not be estimated because all birds in the site were not ringed. Barlain (1978) found that the proportion of non-breeding males in a population of Blackcaps is south-west Germany was 5% and 8.7% in successive years. In low Maquis, Blackcap breeding densities were 1.33 pairs/ha in 1977 and 0.91 pairs/ha in 1978. The

highest breeding densities of Sardinian Warblers were in low Maquis, 3 pairs/ha in 1977 and 2.82 pairs/ha in 1978. In High Maquis, Sardinian Warbler breeding density was 2.44 pairs/ha and in Garigue, 0.77 pairs/ha in 1977 and 1.31 pairs/ha in 1978.

Sylvia warbler breeding density was inversely related to mean territory size (Fig. 3.22.). For Sardinian Warbler, territory size was inversely proportional to vegetation height (Fig. 3.23 a) but there was no such relationship for Blackcap (Fig. 3.23 b). Nevertheless mean Blackcap territory size was slightly higher at the Jews' Gate site than at Governor's Lookout (Table 3.30.). As Blackcaps occupied a narrower range of vegetation heights than Sardinian Warblers, the territory size/vegetation height relation may have been obscured by lack of adequate data. The highest total Sylvia densities were therefore in the tallest vegetation and the lowest densities in the shortest vegetation. In High Maquis, the total Sylvia density in the breeding season was 5.55 pairs/ha; in low Maquis it was 4.33 pairs/ha and 3.73 pairs/ha, and in Garigue it was 0.77 pairs/ha and 1.31 pairs/ha. Only one species nested in Garigue.

In the tallest vegetation there must have been more food available per unit area of land so that warblers could breed in smaller territories (Cody & Walter 1976). In the lowest vegetation much larger territories had to be defended probably for a similar amount of food as in the smaller territories in the Maquis. In the lowest vegetation in Garigue

FIGURE 3.22. Relationship between territory size and density in Sardinian Warblers and Blackcaps in three habitats at Gibraltar.



Blackcap (closed circles), Sardinian Warbler (open circles).

$y = 3.981 - 9.852x \quad p < 0.001$

FIGURE 3.23. Relationship between vegetation height and territory size in Sardinian Warblers and Blackcaps in three scrub habitats at Gibraltar.

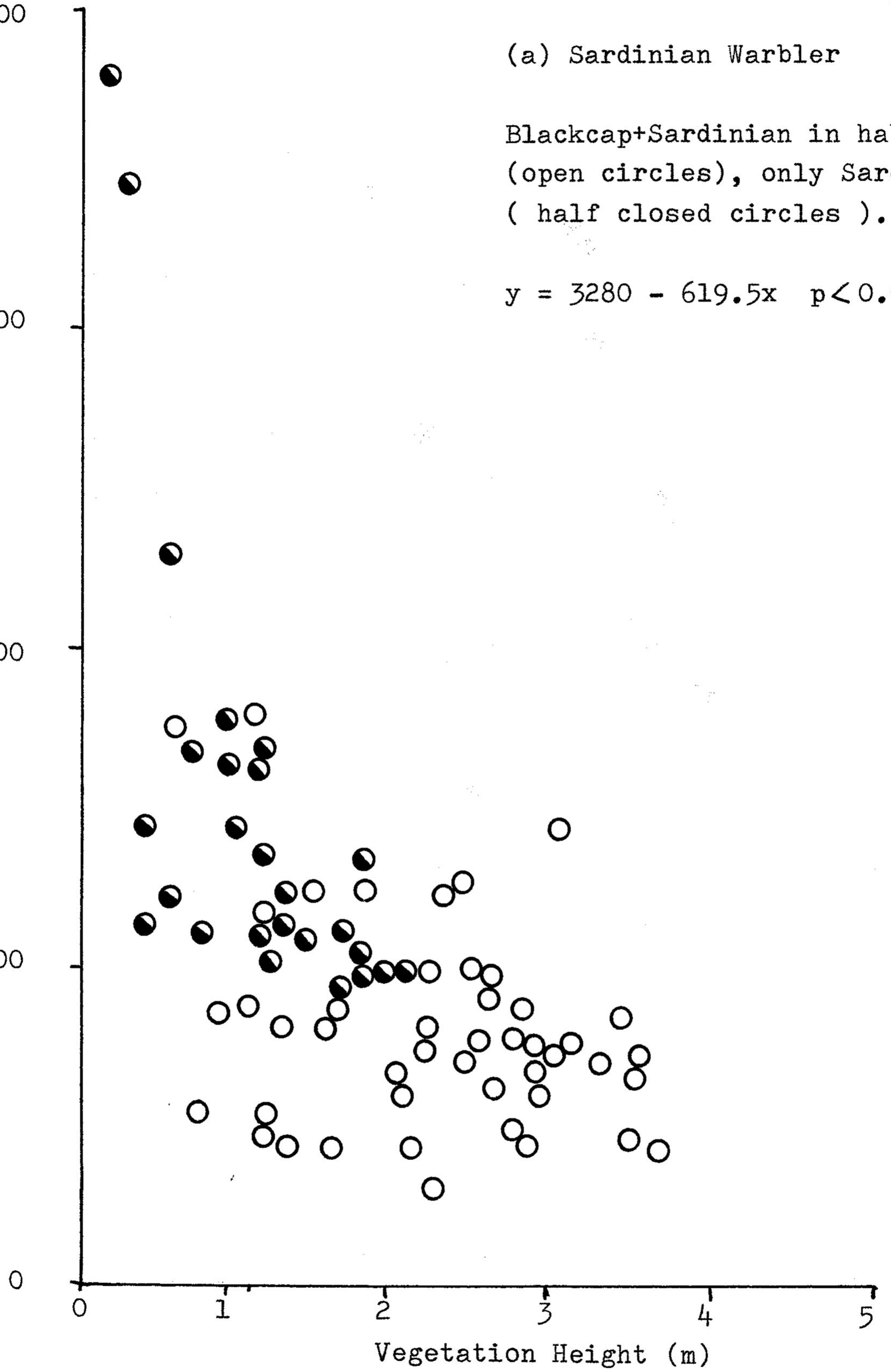
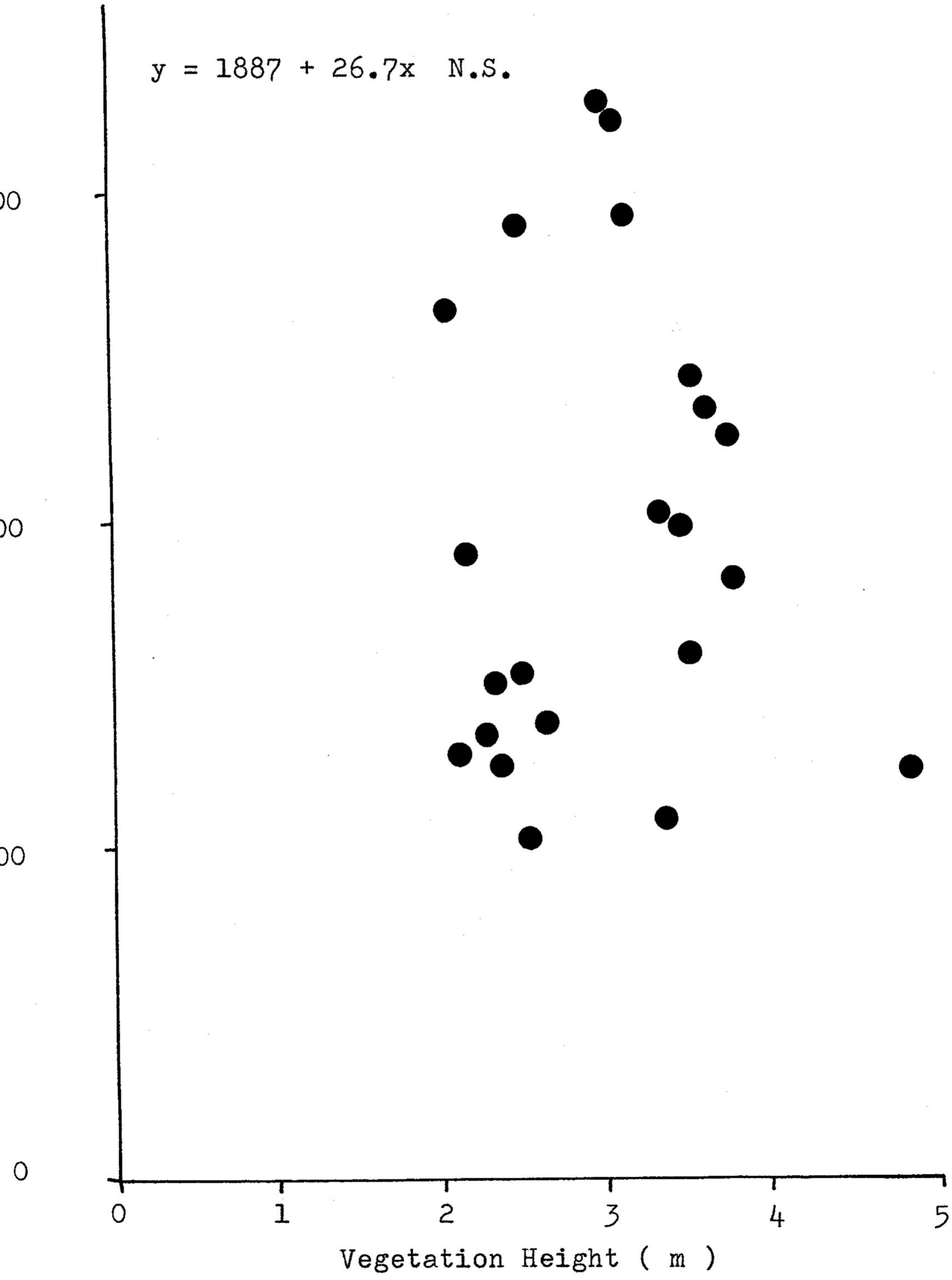


FIGURE 3.23. continued.



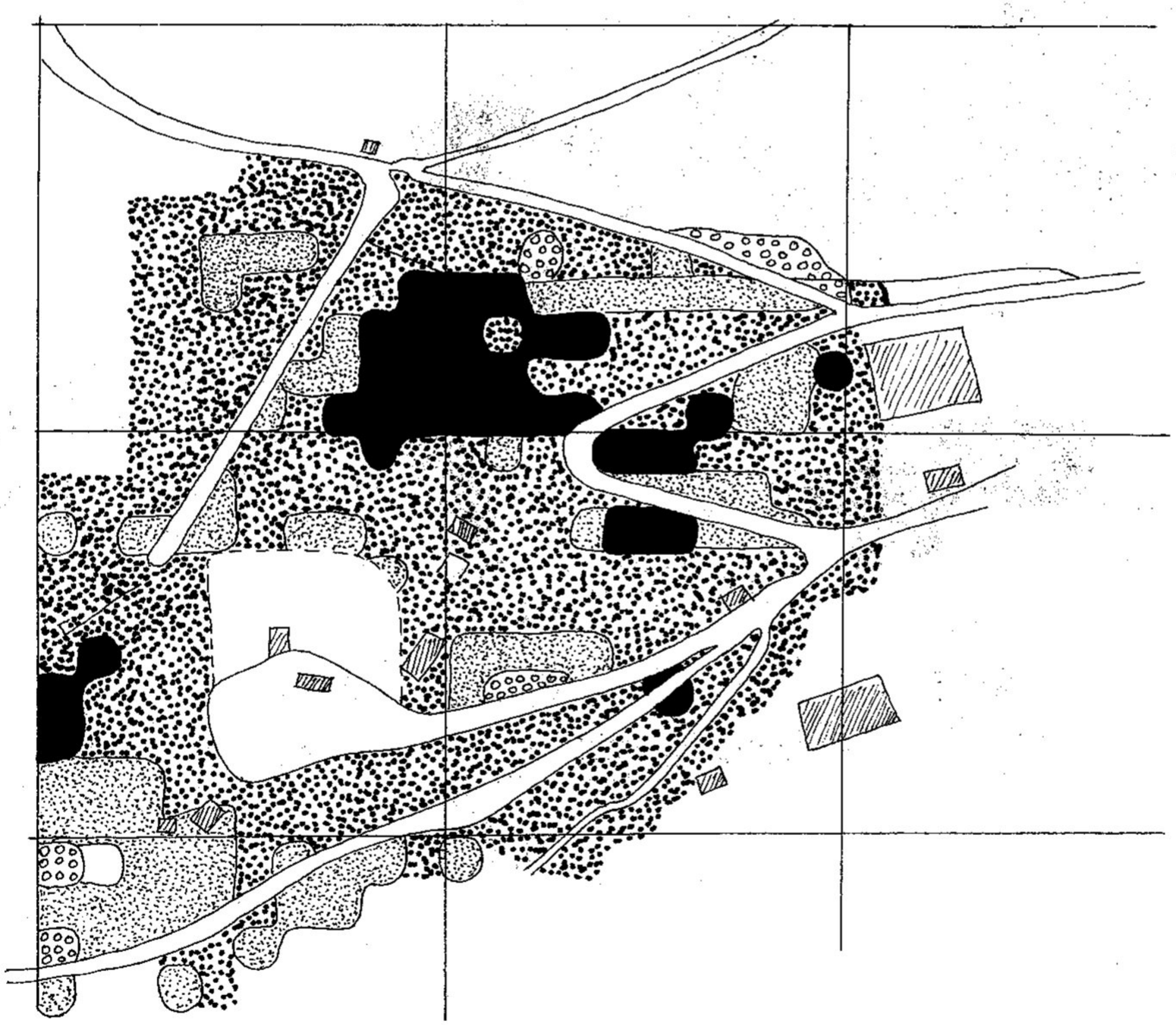
(low grasses below 0.5 m high), Sardinian Warblers did not breed (Figs. 3.20., 3.21., 3.26.). The only warbler species to attempt to nest there was the Fan-tailed Warbler Cisticola juncidis in 1978 and 1979 and they were in grasses all year (Finlayson in press).

At intermediate territory sizes (0.20 - 0.32 ha) Sardinian Warblers occupied taller vegetation in which to breed when Blackcaps were also present. The mean vegetation height in Sardinian Warbler territories when Blackcaps were present was 2.0 $\pm$ 0.4 m (2 SE) but it was reduced to 1.3 $\pm$ 0.3 m (2 SE) when alone (Fig. 3.23 a).

Are the Blackcap and the Sardinian Warbler interspecifically territorial ? Cody & Walter (1976) have devised a method of determining whether individuals of one species are avoiding the territories of a second apecies. The method is best illustrated with an example. We want to find out if Blackcaps and Sardinian Warblers are avoiding each other's territories at the Governor's Lookout site (Figs. 3.17., 3.24.). The site was divided into 10 X 10 metre squares, and the presence or absence of each species was noted in every square. The Sardinian Warbler occupied 165 squares, 34.8% of all the squares at the site. The Blackcap occupied 251 squares, 53% of the squares. Now, of the 165 squares occupied by Sardinian Warblers, 57 (i.e. 34.5%) were co-occupied by Blackcaps; but if Blackcaps were not avoiding Sardinian Warblers, they should occupy

FIG.324 Vegetation height at Governor's Lookout.

- bare ground
- 0 - 0.6 m
- - 1.8 "
- - 4.6 "
- - 9.1 "



zot

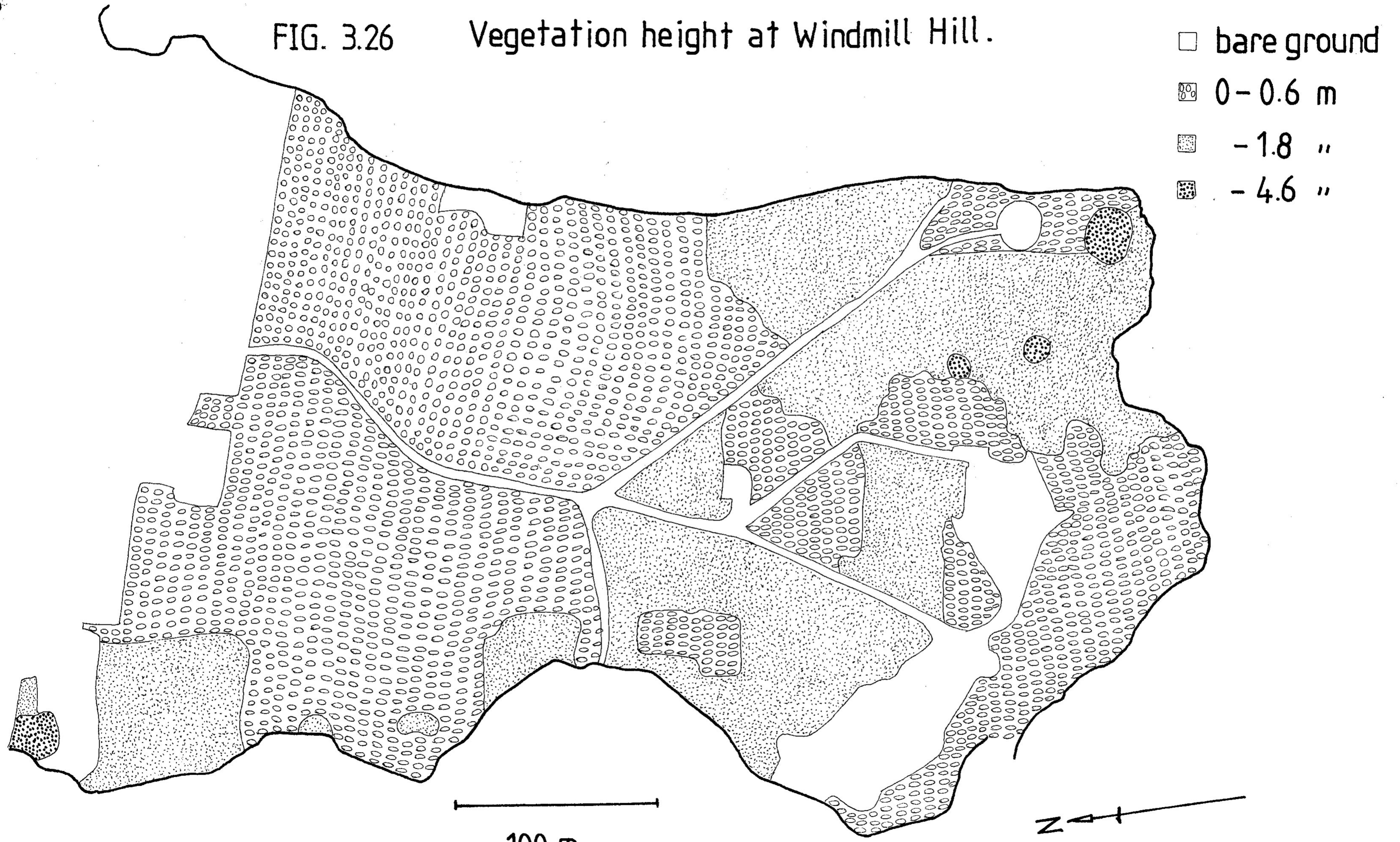
FIG. 325 Vegetation height at Jews' Gate.

□ bare ground ▩ -1.8 m

▩ 0 - 0.6 m ▩ -4.6 "

■ -9.1 "

FIG. 3.26 Vegetation height at Windmill Hill.



53% of the Sardinian Warbler squares, that is 88 squares. The difference between the observed and expected values is highly significant ($X^2_1 = 10.6$, $p < 0.01$). The reciprocal test is also done.

Cody & Walter (1976) used 2 X 2 metre squares for Sylvia species in Sardinia and Corsica and considered that such small squares overestimated sample sizes and so used X^2 analysis on the percentages. They considered that 5 X 5 metre squares would have given more realistic values. In Gibraltar 10 X 10 metre squares were always used so that, if anything, sample size was underestimated. Thus X^2 was performed on the actual number of squares rather than on the percentages. The results are listed in Table 3.31. These suggest that where the two species held territories in the same area, they tended to occur in different squares from each other. Since the exclusion is not complete, the system may be analogous to the partial interspecific territoriality described by Cody (1974).

A non-random disposition of territories could be due to the two species selecting different parts of the habitat which they may prefer, or it could be due to direct behavioural interaction and avoidance. The habitat preferences of the two species can be worked out since detailed descriptions of all warbler territories were taken. Then the observed spatial overlap can be subtracted from the habitat overlap so that the remainder may be due to behavioural interactions (Table 3.32.). It is

TABLE 3.31. Spatial Overlaps between Blackcaps and Sardinian Warblers in two habitats at Gibraltar.

Site/Year	Number of Squares co-occupied		X_1^2
	Observed	Expected	
Gov.Lookout 1977	57	88	10.6 $p<0.01$
Jews' Gate 1977	144	177	6.2 $p<0.05$
Jews' Gate 1978	155	195	8.1 $p<0.01$

TABLE 3.32. Habitat Overlap, Spatial Overlap, and Behavioural Interaction between Sardinian Warblers and Blackcaps territorial in two habitats at Gibraltar.

Site/Year	Habitat Overlap	Spatial Overlap	Behavioural Interaction
Gov.Lookout 1977	0.966	0.286	0.680
Jews' Gate 1977	0.981	0.454	0.527
Jews' Gate 1978	0.938	0.403	0.535

$$\text{Habitat Overlap} = \frac{\text{Vegetation Height O} + \text{Plant Species O}}{2}$$

possible that the criteria used by warblers to occupy a patch of habitat are not the same as those recorded, in which case the results may be partly invalidated. Other results, obtained from playback experiments and presented later in this sub-section, confirm that the two species do respond and interact with each other.

A knowledge of the vegetational characteristics of the territories occupied by the two species in the different habitats is required before continuing. In High Maquis, Blackcaps appeared to occupy squares of vegetation as these were encountered at random (Table 3.33., Figs. 3.27., 3.28.). Occupancy of squares of particular vegetation heights and plant composition paralleled that of the available squares. The Sardinian Warbler did not appear to occupy squares with particular plant species either in the High Maquis, but was present in many squares with vegetation over 2 metres high and occured infrequently in squares below that height (Table 3.33., Figs. 3.27., 3.28.). In High Maquis plant species niche breadth was greater for Sardinian Warbler than for Blackcap but vegetation height niche breadth was greater for Blackcap than for Sardinian Warbler (Table 3.34.). Plant species overlap (0.985) and vegetation height overlap (0.947) were high.

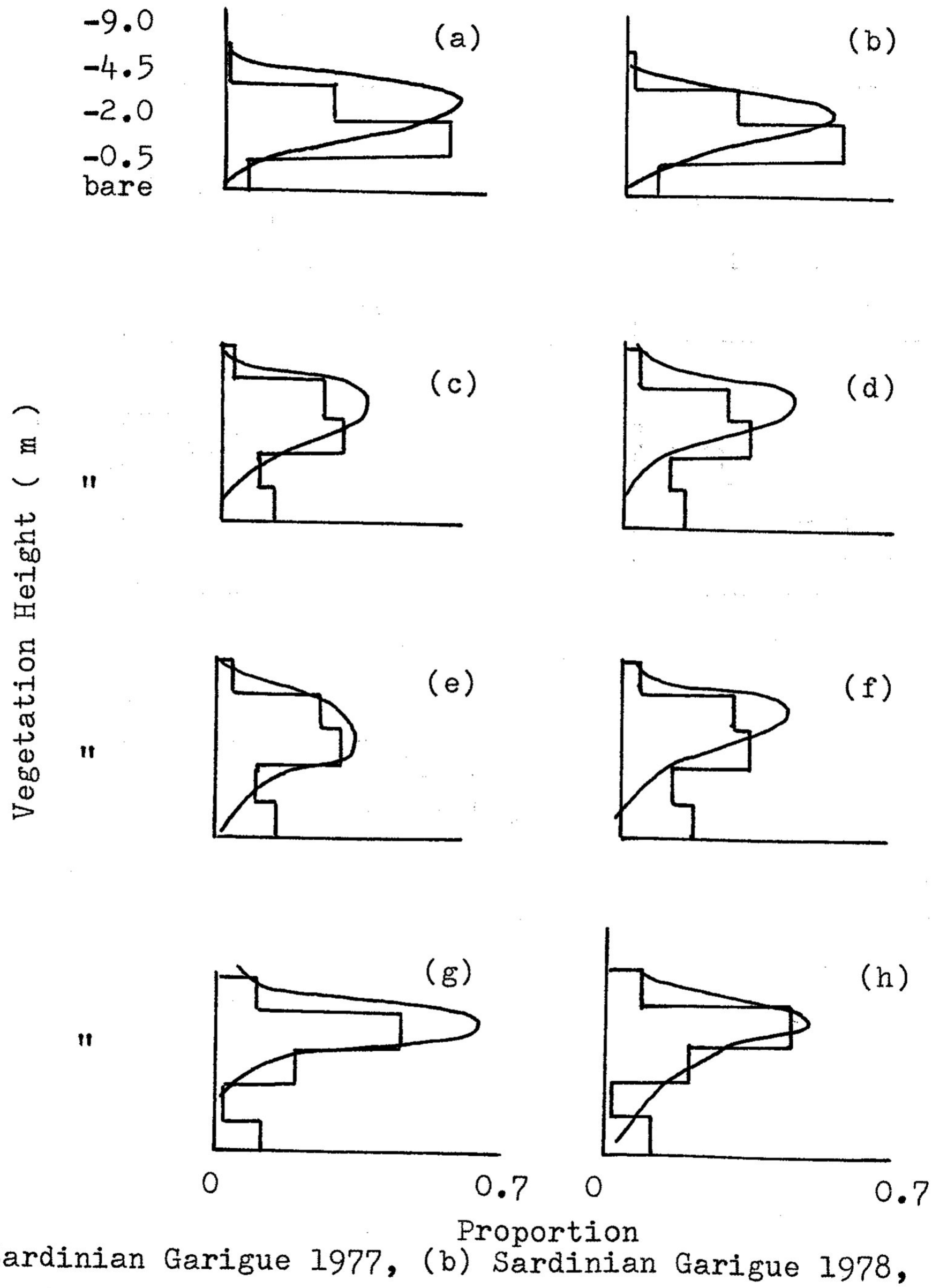
In low Maquis, Blackcaps occupied squares with vegetation height exceeding 2 metres and containing Buckthorn, Lentisc and Pine in proportions which were higher than if these plants had been incorporated into the territory as they were encountered. Sardinian

TABLE 3.33. Occupation of breeding territories by vegetation height and plant species composition by (a) Blackcaps and (b) Sardinian Warblers.

	(a) Blackcap		(b) Sardinian Warbler	
Vegetation Height (metres)	No Squares Observed	Expected	No Squares Observed	Expected
bare ground	11	13	4	11
0 - 0.5	2	3	0	2
0.6 - 2.0	30	30	10	24
2.1 - 4.5	64	67	74	53
4.6 - 9.0	19	13	12	10
Plant Species				
Osyris	77	68	48	57
Buckthorn	27	27	27	22
Wild Olive	96	99	83	82
Spiny Asparagus	6	7	7	6
Honeysuckle +	1	3	4	2
Lentisc +	15	15	9	13
Terebinth +	2	2	4	2
Teline	15	13	11	11
Calicotome	3	12	5	10
Pine	15	11	16	9
For vegetation height	(a) $X^2_3=4.033$ $p>0.05$		(b) 23.016 $p<0.001$	
For plant species	(a) $X^2_8=10.737$ $p>0.05$		(b) 9.52 (7df) $p>0.05$	

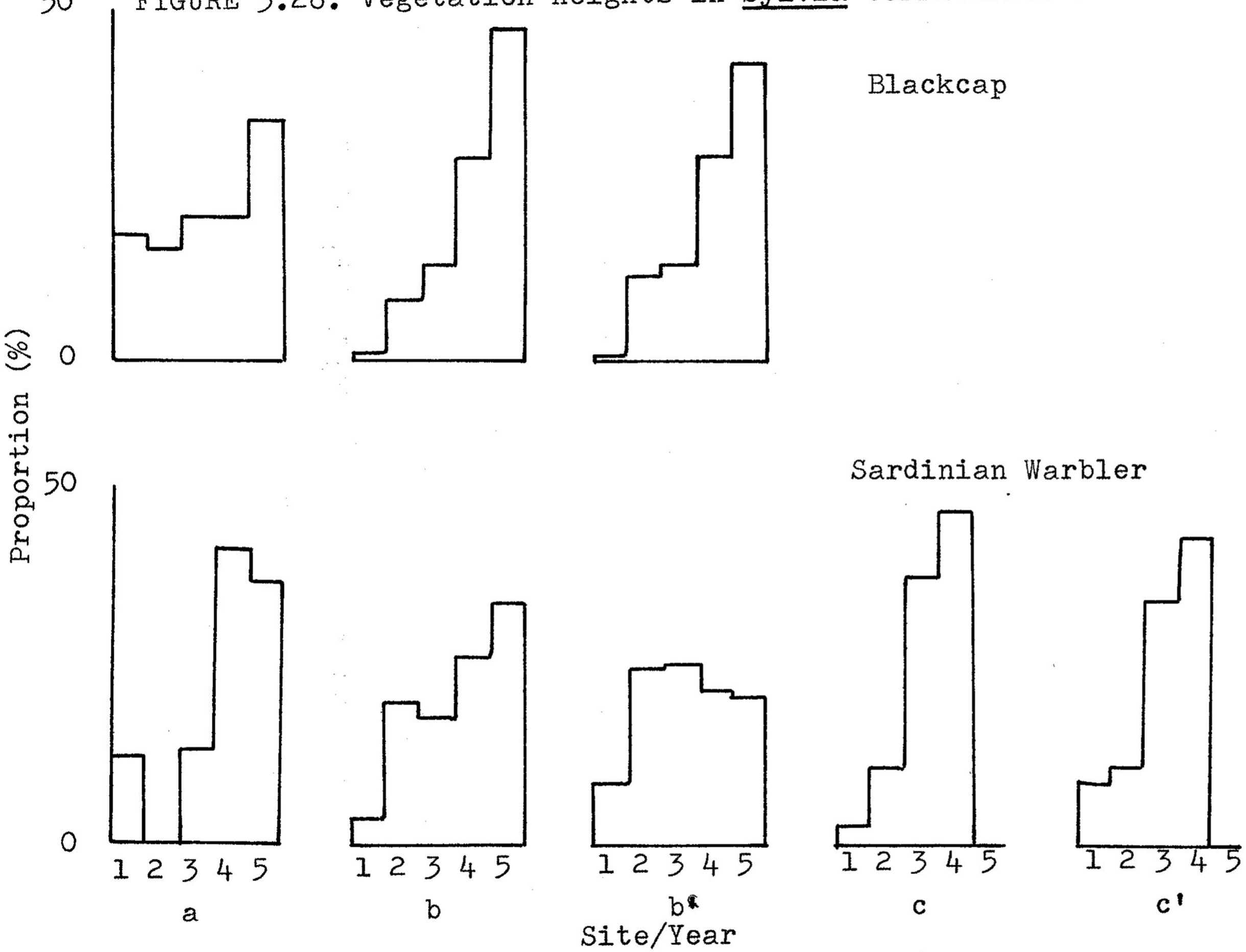
+ data lumped

FIGURE 3.27. Observed and Expected proportions of different vegetation heights in the territories of Sardinian Warblers and Blackcaps in three scrub sites at Gibraltar.



(a) Sardinian Garigue 1977, (b) Sardinian Garigue 1978,
(c) Sardinian Low Maquis 1977, (d) Blackcap low Maquis 1977,
(e) Sardinian low Maquis 1978, (f) Blackcap low Maquis 1978,
(g) Sardinian High Maquis 1977, (h) Blackcap High Maquis 1977
Bar = observed, line = expected

FIGURE 3.28. Vegetation heights in Sylvia territories in different habitats at Gibraltar.



Heights at 2 metre intervals, 1.=0-2, etc.

a. High Maquis 1977, b low Maquis 1977, b' low Maquis 1978, c. Garigue 1977, c'.Garigue 1978

TABLE 3.34. Plant Species and Vegetation Height Niche Breadth values for territorial Blackcaps and Sardinian Warblers at Governor's Lookout.

Species	Niche Breadth	
	Plant Species	Vegetation Height
Blackcap	3.979	2.896
Sardinian Warbler	4.367	1.743

Warblers also occupied vegetation over 2 metres more frequently than expected in low Maquis. In 1977 Sardinian Warblers appeared to occur more frequently than expected in Pine but this was not so in 1978 (Table 3.35., Figs. 3.27., 3.28.). Vegetation height niche breadth in low Maquis was the same as in High Maquis, but plant species niche breadth was much higher in low Maquis than in High Maquis (Table 3.36.). Plant species niche breadth was slightly higher in low Maquis than in High Maquis for Sardinian Warbler but the greater increase was with respect to vegetation height (Table 3.36.). In low Maquis, the Sardinian Warbler took a wider range of vegetation heights within territories than the Blackcap, a reversal from the situation in High Maquis. Both species took a similar range of plant species in low Maquis (Table 3.36.). Overlaps were high in low Maquis. Plant species overlaps were 0.983 and 0.979 in the two years studied, and height overlaps were 0.980 and 0.896 respectively.

Only the Sardinian Warbler nested in Garigue. Plant species composition was not looked at in detail in this habitat. There was no vegetation over 4.5 metres and Sardinian Warblers occupied the tallest vegetation available. Vegetation height niche breadth values were 1.950 and 2.086 for 1977 and 1978, the lowest in any of the habitats studied, no doubt partly due to the reduced range available.

Each of the two warbler species occupied particular microhabitats, judged by plant species

TABLE 3.35. Plant species and Vegetation height occupation by territorial Blackcaps and Sardinian Warblers at Jews' Gate.

(a) Blackcap 1977

Vegetation Height (metres)	Number of Squares Observed	Expected
bare ground	1	21
0 - 0.5	6	14
0.6 - 2.0	35	43
2.1 - 4.5	62	37
4.6 - 9.0	16	6

Plant Species	Observed	Expected
Osyris	39	40
Buckthorn	33	21
Wild Olive	107	104
Spiny Asparagus	9	11
Honeysuckle	5	2
Lentisc	17	17
Terebinth	10	4
Teline	24	33
Calicotome	14	22
Pine	11	7
Bear's Breach	6	9
Eucalyptus spp.	4	2
Others	0	7

For vegetation height $X^2_4 = 61.77$ $p < 0.001$

For plant species $X^2_{10} = 38.107$ $p < 0.001$

Honeysuckle, Terebinth, and Eucalypt have been lumped.

TABLE 3.35 (b).

(b) Blackcap 1978

Vegetation Height (metres)	Number of Squares Observed	Expected
bare ground	1	23
0 - 0.5	11	16
0.6 - 2.0	38	49
2.1 - 4.5	70	41
4.6 - 9.0	16	6

Plant Species	Observed	Expected
Osyris	31	39
Buckthorn	22	20
Wild Olive	95	102
Spiny Asparagus	13	10
Honeysuckle	4	2
Lentisc	22	17
Terebinth	9	3
Teline	20	33
Calicotome	22	22
Pine	14	7
Bear's Breach	6	9
Eucalyptus spp.	10	2
Others	6	8

For vegetation height $X^2_4=59.644$ $p<0.001$

For plant species $X^2_9=30.756$ $p<0.001$

Honeysuckle, Terebinth and Eucalypt have been lumped

TABLE 3.35 (c).

(c) Sardinian Warbler 1977

Vegetation Height (metres)	Number of Squares Observed	Expected
bare ground	5	38
0 - 0.5	27	26
0.6 - 2.0	73	79
2.1 - 4.5	96	67
4.6 - 9.0	19	10

Plant Species	Observed	Expected
Osyris	43	57
Buckthorn	29	30
Wild Olive	147	149
Spiny Asparagus	17	15
Honeysuckle	3	2
Lentisc	25	24
Terebinth	5	5
Teline	40	47
Calicotome	25	32
Pine	24	10
Bear's Breach	22	13
Others	18	14

For vegetation height $X^2_4=49.804$ $p< 0.001$

For plant species $X^2_{10}=33.774$ $p< 0.001$

Honeysuckle and others have been lumped

TABLE 3.35 (d).

(d) Sardinian Warbler 1978

Vegetation Height (metres)	Number of Squares Observed	Expected
bare ground	31	48
0 - 0.5	63	10
0.6 - 2.0	193	109
2.1 - 4.5	144	241
4.6 - 9.0	22	45

Plant Species	Observed	Expected
Osyris	135	108
Buckthorn	51	56
Wild Olive	267	282
Spiny Asparagus	25	29
Honeysuckle	6	5
Lentisc	53	46
Terebinth	11	9
Teline	87	90
Calicotome	61	61
Pine	21	24
Bear's Breach	15	24
Others	25	28

For vegetation height $X^2_4 = 386.487$ $p < 0.001$

For plant species $X^2_{11} = 14.44$ $p > 0.05$

TABLE 3.36 Plant Species and Vegetation Height Niche breadth values for territorial Blackcaps and Sardinian Warblers at Jews' Gate.

1977.

Species	Niche Breadth	
	Plant Species	Vegetation Height
Blackcap	5.014	2.682
Sardinian	5.494	3.092

1978.

Species	Plant Species	Vegetation Height
Blackcap	5.964	2.750
Sardinian	5.288	3.237

composition and vegetation height, within each habitat. The characteristics of the microhabitats occupied changed with habitat. The two species overlapped highly in the microhabitats occupied. This would seem to point further that the observed spatial separation of territories of the two species was in part at least due to behavioural interaction.

To test this further, I recorded the full song of the two Sylvia species in situ and played back the recordings in areas where both species were known to be present. Usually, territory boundaries were chosen, or areas where territories of the two species overlapped. The study was carried out in the low Maquis at Jews' Gate in 1979 spring and different territory owners were used in each playback. Presence or absence of response to a recording was scored according to whether a warbler appeared within 10 metres of the speaker during the time of the recording (the speaker was usually placed about 20 metres from the observer). Both the Blackcap and the Sardinian Warbler recordings lasted 3.5 minutes each. In most cases the warblers approached right up to the speaker and replied with song and display. Often, more than one individual was attracted and these would then chase each other.

Both species reacted to each other's song as well as to their own (Table 3.37.). Of 28 Blackcap playback recordings, 18 times Sardinian Warblers responded and 20 times Blackcaps did. Sardinian Warblers responded 19 out of 20 times to

TABLE 3.37. Response of Blackcaps and Sardinian Warblers to their own song and to that of the other species.

Response	Playback	
	Sardinian	Blackcap
Sardinian	19	18
Blackcap	7	20

$X_1^2 = 4.25 \quad p < 0.05$

their own song and Blackcaps 7 out of 20 times to the Sardinian Warbler song. There was a 95% response from Sardinian Warblers to their own song and a 64% response to the Blackcap song. There was a 71% response from Blackcaps to their own song and a 35% response to the Sardinian Warbler song. Therefore the two species reacted more frequently to their own song than to that of the other species (Table 3.37.). A mixture of noises, mainly songs of other birds like Blackbird or Blue Tit, was played back on 15 occasions from the recorder but produced no noteworthy responses from the warblers.

The Winter

In winter the two Sylvia species wandered through the vegetation and were usually solitary. At critical times, for example when arthropods were scarce, they changed foraging methods and diet, taking berries or nectar. Nectar foraging by warblers at Gibraltar is a recent phenomenon and there are no true nectarivores present. In winter, Blackcaps, Sardinian Warblers and Chiffchaffs regularly visited clumps of introduced Aloes Aloe arborescens which flowered at that time.

In contrast to the arthropods which were the main items in the warbler diet outside the winter, nectar and berries were clumped and easy to defend (Brown 1964). In the case of nectar-producing flowers especially, the resource (nectar) was renewable. Blackcaps and some Sardinian Warblers defended fixed

territories when these foods became available and they would do so for several weeks.

Warblers were observed taking nectar from aloes at Jews' Gate in the 1977-78 and 1978-79 winters. Almost every aloe clump observed at Gibraltar in winter contained warblers which were extracting nectar from the flowers. At Jews' Gate in 1977-78, three species took nectar in the legal way, that is by introducing the bill into the flower tube through its mouth without damaging the flower. These species were Blackcap, Sardinian Warbler and Chiffchaff.

In the 1977-78 winter, Blackcaps were territorial on aloes. Only one Sardinian Warbler was able to defend flowers and Chiffchaffs were never seen to do so. At the Jews' Gate site five Blackcaps were regularly defending aloe clumps. The relative abundance of the three species at the site (determined from the numbers of each species trapped that winter at the site) was Blackcap 3.45 : Sardinian Warbler 1 : Chiffchaff 1.64. In view of the small sample sizes definite conclusions cannot be drawn from these results, but Chiffchaffs were evidently non-territorial even though they were the second most abundant species. Also fewer Blackcap territories per Sardinian Warbler territory would have been expected had both species set up territories in proportion to their abundance.

All birds in the study area were colour-ringed and it was found that the same birds were

present in their respective territories each day; the same Chiffchaffs were recorded intruding each day despite continuous chasing away by territory owners. Blackcaps were dominant on the aloes (Table 3.38.). Occasionally Sardinian Warblers chased Blackcaps but more frequently they chased other Sardinian Warblers or Chiffchaffs. Only once was a Chiffchaff aggressive, towards a conspecific. Blackcaps were involved in a greater number of chases than expected and in a high proportion of these (70.15%) they were the chasers (Table 3.38.). Sardinian Warblers were less often involved in chases (Table 3.38 a) and they were the chasers only on 42.86% of the occasions. Chiffchaffs were frequently involved in chases but usually ended as victims; they chased on only 1.25% of the occasions. There is therefore a hierarchy which corresponds to the sizes of the three warbler species (Morse 1974). For weights of the three species at Gibraltar, see Tables 2.1., 3.2., 3.11.

Intruding warblers of the three species were never heard calling but territorial Blackcaps and Sardinian Warblers called loudly, probably to advertise possession of a patch of flowers. Of 232 Blackcap observations, 154 were of birds which were calling (66%); of 43 Sardinian Warbler observations, only 5 5 were of calling birds (12%); of 39 Chiffchaff observations, none were of calling birds. The amount of calling therefore reflected the level of territoriality of the three species. The Blackcap call was the " tac

TABLE 3.38. Hierarchical position of the three warbler species on aloes (a) differences in involvement in chases, (b) differences in aggressive behaviour.

(a) Species	Number of birds involved in chases	Number expected if proportional to relative abundance	
Blackcap	201	171	
Sardinian Warbler	21	50	
Chiffchaff	80	81	$X^2_2 = 22.096$ $p < 0.001$

(b) Species	Number of aggressive chases observed	Number of chases expected if proportional to number of territorial birds	
Blackcap	141	126	
Sardinian Warbler	9	25	
Chiffchaff +	1	0	$X^2_1 = 12.25$ $p < 0.001$

Victim	Aggressor Chiffchaff	Sardinian	Blackcap	
Chiffchaff	1	5	73	
Sardinian Warbler	0 ++	1 ++	11	
Blackcap	0	3	57	$X^2_7 = 83.337$ $p < 0.001$

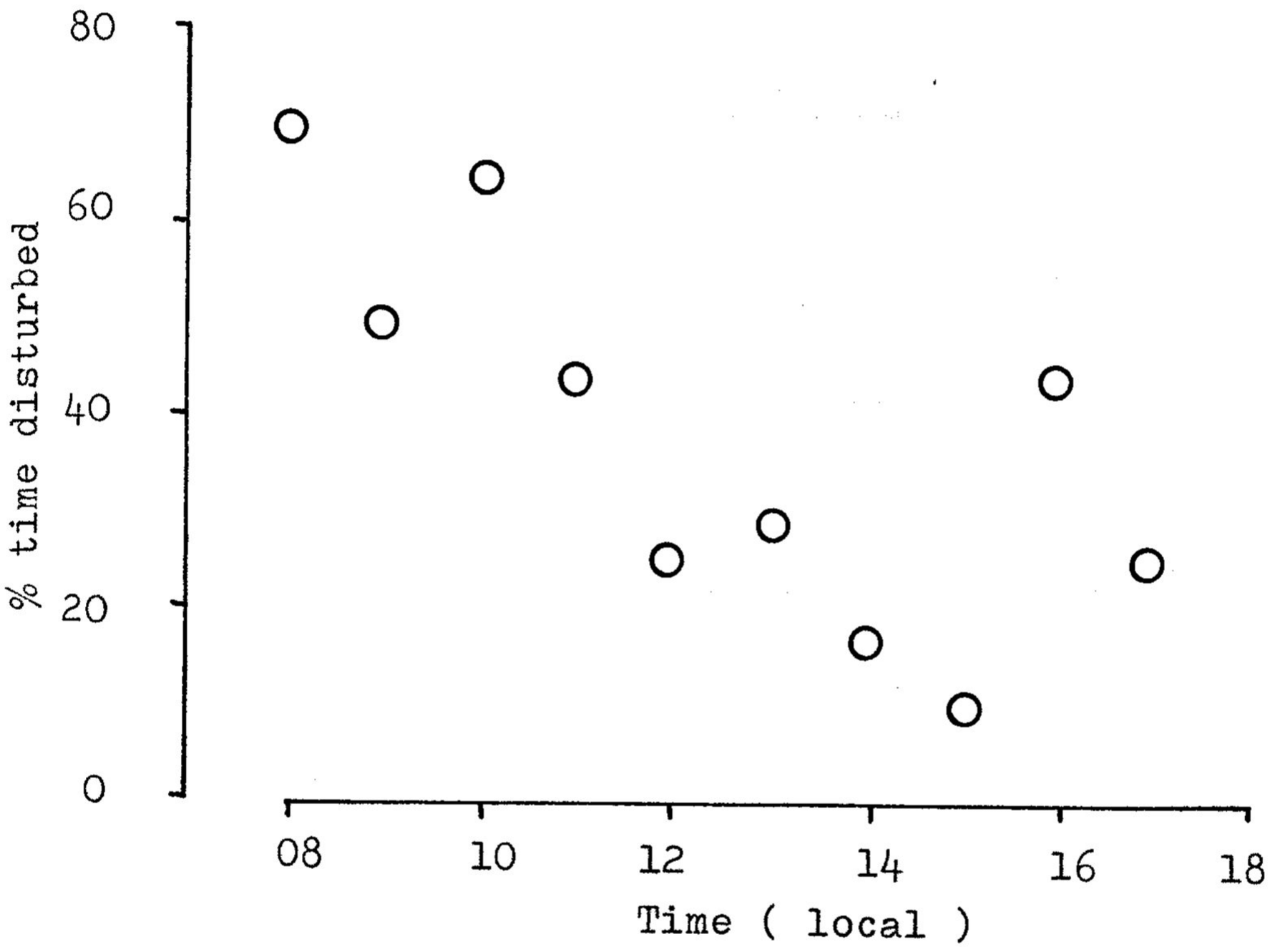
+ ignored from analysis ++ lumped to give expected over 5.

tac, tac " (Peterson et al. 1954) but song was not heard. The Sardinian Warbler call was the staccato " cha-cha-cha-cha " (Peterson et al. 1954).

If an intruding Blackcap failed to retreat after hearing a territory owner, the latter would approach and adopt a vertical posture, presumably threatening to attack. Usually the intruder would then perch horizontally (= ? submission) and retreat. On certain occasions the intruder would not submit and was usually chased off. Chiffchaffs responded little to Blackcap signals and so were chased more frequently. On the other hand they showed no tendency to retaliate.

Whenever observed, Blackcaps which held territories were noted to be calling frequently but the amount of calling varied during the day. Blackcaps spent a large part of their time calling during the morning (81.82% of 133 observations in the time period 0800 - 1100 hrs were of calling birds) but the amount dropped in the early afternoon (31.37% of 51 observations in the time period 1200-1400 hrs were of calling birds), rising again slightly in the evening (41.82% of 55 observations in the time period 1500 - 1700 hrs were of calling birds). The differences were statistically significant ($X_2^2 = 53.98$ $p < 0.001$). The amount of time territorial Blackcaps were disturbed by intruders (Fig. 3.29.) and the availability of nectar (Fig. 3.30.) showed similar diurnal variations. Although any relationship between the three factors can

FIGURE 3.29. Daily variation in disturbance to territorial Blackcaps defending clumps of Aloes.



For period 0800 - 1500 hrs, $y = 135.19 - 8.46x$

$p < 0.001$

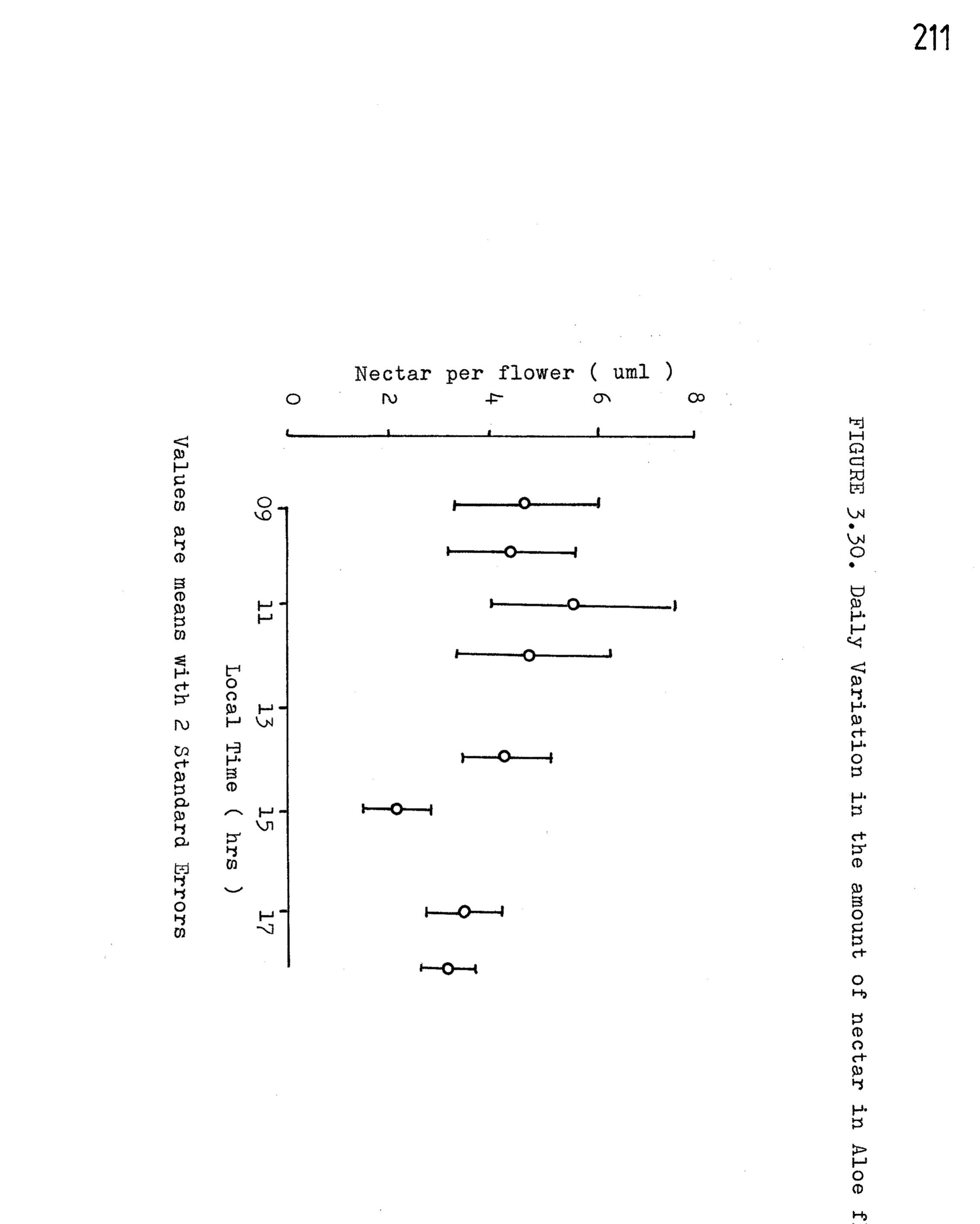


FIGURE 3.30. Daily Variation in the amount of nectar in Aloe flowers.

Values are means with 2 Standard Errors

only be considered tentatively on present evidence, it seems possible that intruder pressure (and hence the amount of disturbance) is highest when flowers have more nectar and that this pressure is reflected by greater periods of time spent calling by the owners of the territories.

For Blackcaps at least nectar was an alternative food source to berries when the latter were scarce. There were very few berries available during the 1977-78 winter and Blackcaps often took nectar at the Jews' Gate clump. No Wild Olives produced berries that winter. The following winter, 1978-79, berries were available (3.4.2.) and, even though aloes flowered as profusely as in the previous winter, no Blackcaps held territories at the Jews' Gate clump. The ratio of warblers at the site that year was Blackcap 1.42 : Sardinian Warbler 1 : Chiffchaff 0.42. Three Sardinian Warblers set up territories at this clump on this second year and Chiffchaffs continued to visit the flowers. Six Blackcaps were removed from the scrub at Jews' Gate ; there was no evidence that these had been taking nectar (no stained plumage, trapped away from aloes) but they had been foraging on berries (from faeces). They were released in an aloe clump 1 kilometre away but none remained there or attempted to establish a territory. There were 20 Chiffchaffs and 4 territorial Sardinian Warblers in this clump. Three of the six Blackcaps were retrapped at the original site at Jews' Gate 24 hours later where they were feeding on olives once more.

Non-breeding Season

At other times, Blackcaps and Sardinian Warblers wandered throughout the vegetation searching for arthropods (3.3.3.). They never flocked or formed any kind of association and were solitary all the time. In October 1978, I recorded the movements of individual Sardinian Warblers at the Windmill Hill site (Fig. 1.2.). Since the vegetation at this site was below 0.5 metres high, birds could be followed for relatively long periods. The site had the disadvantage that Blackcaps were rarely present and so most of the results obtained were of Sardinian Warblers only. Individual warblers were followed through binoculars and the presence of other birds in the vicinity was also recorded. The distance of any birds to the individual which was being followed was estimated to the nearest 10 metres, and also whether these neighbours called and if they became involved in chases.

Most of the time Sardinian Warblers were solitary and did not have any other warblers nearby (Table 3.39.). Of warblers that came within 30 metres of the individual under observation, very few called. Many of those which were over 40 metres away from the individual called (Table 3.40.). If warblers came within 10 metres of the individual under observation they would often be chased by it, but other individuals further away were not (Table 3.40.). It appears as if distant birds called in order to avoid encountering others and wasting time in chasing.

TABLE 3.39. Mean number of warblers observed at various distances from individual Sardinian Warblers at Windmill Hill, October 1978.

Distance (m)	Mean	s.d.
0 - 10	0.537	0.719
11 - 20	0.185	0.438
21 - 30	0.296	0.690
31 - 40	0.648	0.756
41 - 50	1.222	1.058

N = 54

TABLE 3.40. Behaviour of Sardinian Warblers at different distances from each other. Windmill Hill, October 1978.

(a)

Distance (m)	calling	silent
10	0	29
20	1	9
30	5	11
40	23	12
50	49	17

(b)

Distance(m)	chasing	not chasing
10	17	12
20	0	10
30	0	16
40	0	35
50	0	66

$X^2_4 = 57.625$ $p < 0.001$ (a)

$X^2_1 = 45.770$ $p < 0.001$ (b) (10+20 m lumped, 30-50m lumped)

At certain times of year many migrants passed through the site (2.3.1.). During October and November 1978, the behavioural interactions between Sardinian Warblers and insectivorous migrants were studied. Once more most of the work was carried out at Windmill Hill, which is why Blackcaps were not studied. It is assumed that in the denser scrub, the relationships between residents and migrants will be similar to those described below.

The numbers of birds trapped in a 1 hectare patch of Garigue at Windmill Hill varied greatly from one day to the next (Fig. 3.31.). The numbers of Sardinian Warblers trapped at the site were related to the numbers of insectivorous migrants trapped in the same patch on the same day (Fig. 3.32.). There is a very clear indication of an upper limit to the number of Sardinian Warblers in the patch depending on the number of migrants. The reverse is also true. Thus when there were few migrants in the area the number of Sardinian Warblers in the patch could be high or low but when there were many insectivorous migrants there were always few Sardinian Warblers present. Likewise, when there were many Sardinian Warblers in the patch, the numbers of migrants were low (Fig. 3.32.). This suggests that there may be some form of avoidance between Sardinian Warblers and other insectivorous migrants, even though some of these migrants may have very different ecological requirements from the Sardinian Warblers (e.g.

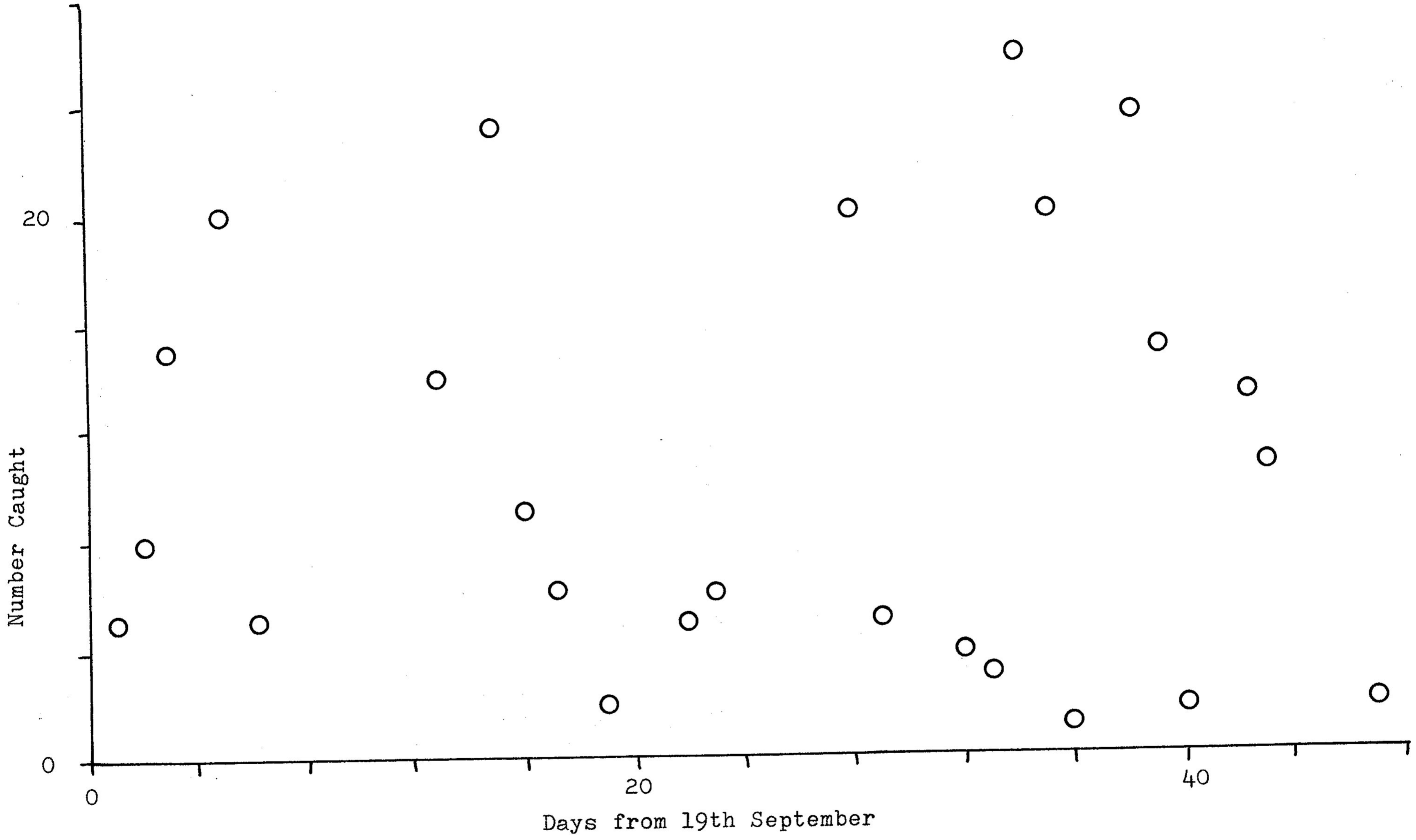
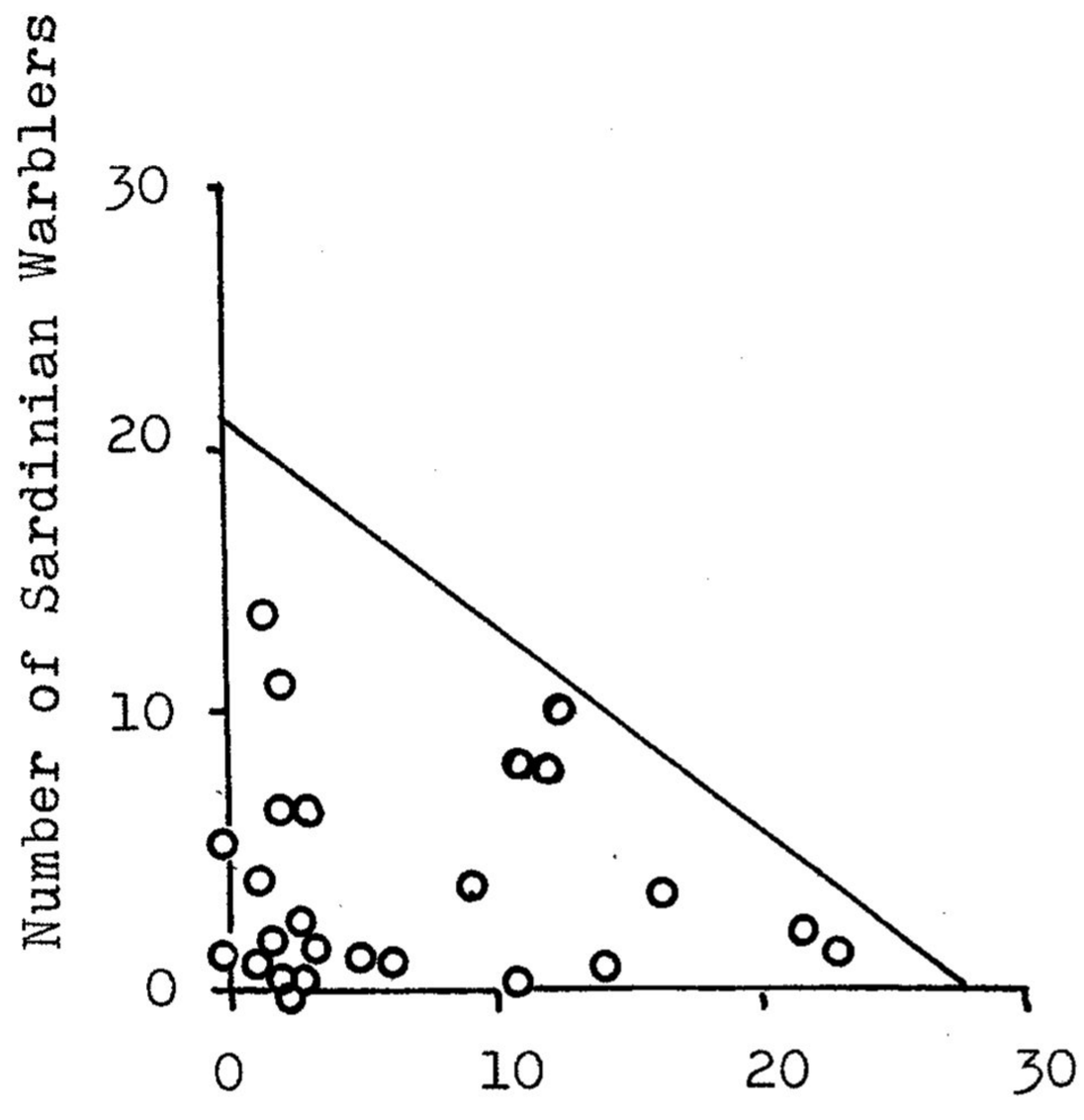


FIGURE 3.31. Number of passerines in a 1 hectare patch of Garigue during the autumn of 1978.

FIGURE 3.32. Numbers of resident and migrant insectivores trapped in a 1 hectare patch of Garigue during the autumn of 1978.



chats). Of the migrants trapped at this site, a large proportion were Sylvia warblers. Chats and warblers from other genera were also abundant (Table 3.41.). A similar relationship to that found for Sardinian Warblers and insectivorous migrants was found at the Jews' Gate site between Blackcaps of the local form and of the nominate sub-species (Fig. 3.33.).

At the Windmill Hill site chases and other aggressive forms of behaviour were often seen between individuals, often of different species. The number of interactions per minute per individual were recorded by watching individuals and noting the numbers of occasions on which they were involved in chases, fights, or supplanting actions (Recher & Recher 1969). The duration of each observation was recorded into a stopwatch. There was a positive relationship between the number of individuals in an area and the number of observed interactions (Fig. 3.34.). The relationship was clearest between chats which are well known for being interspecifically territorial (Hartley 1949, Simmons 1951, Cornwallis 1975), but a significant relationship was also obtained when warblers and chats were examined together. When all species in the area were analysed together, there was no relationship (Fig. 3.34). This means that even though very different species attacked each other, the aggression was mostly directed towards similar species. At this site, Sardinian Warblers were seen chasing other birds on 35 occasions. On 24 of these,

TABLE 3.41. Number of birds in different categories trapped on different days in a 1 hectare patch at Windmill Hill

Group	Mean[1]	s.d.
Sylvia	5.24	4.728
Other warblers	1.40	2.517
Chats	3.00	3.214
All passerines	10.56	7.864

[1] birds/day

FIGURE 3.33. Densities of local and nominate Blackcaps at Jews' Gate in the winter of 1978/1979.

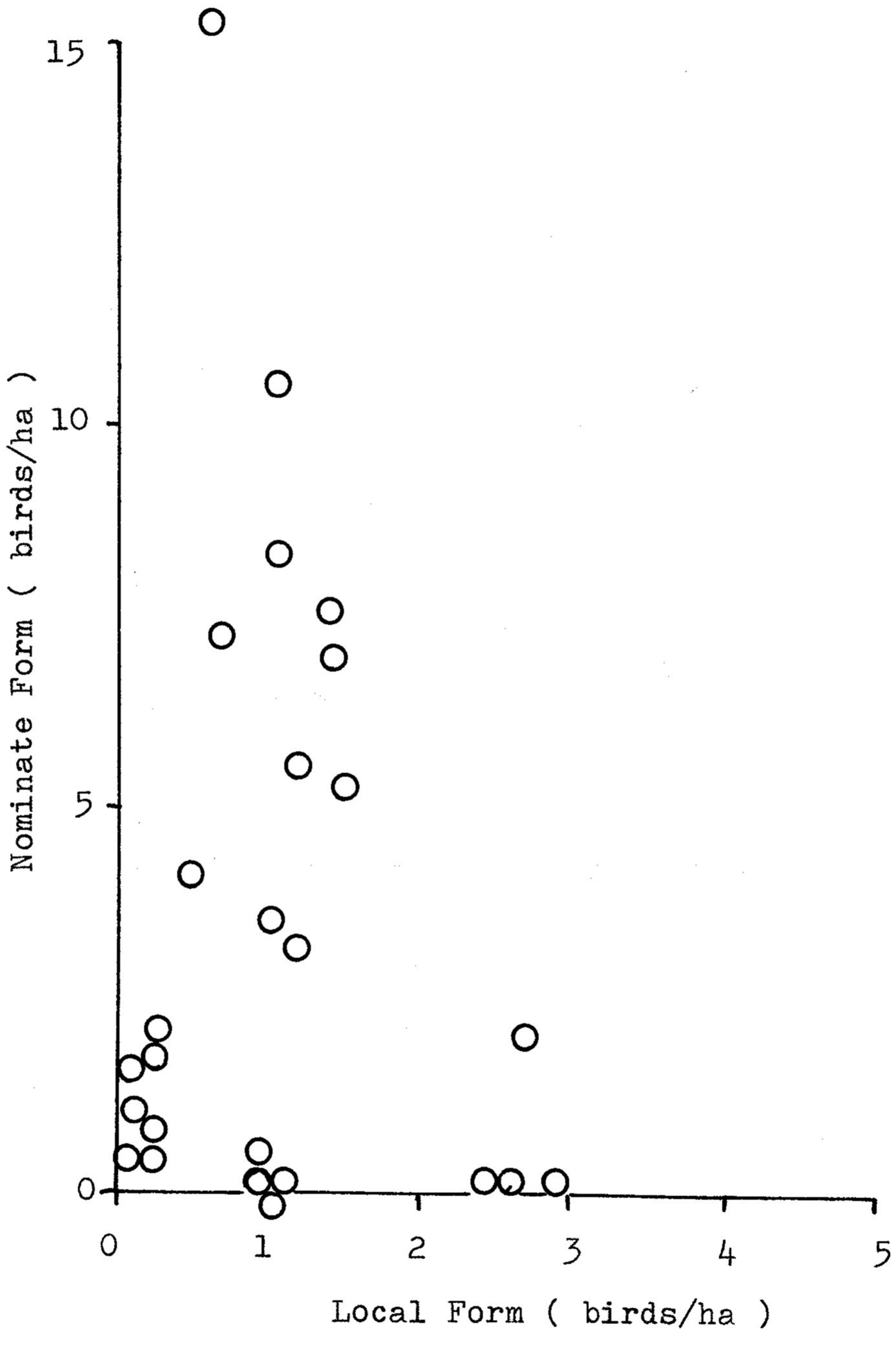
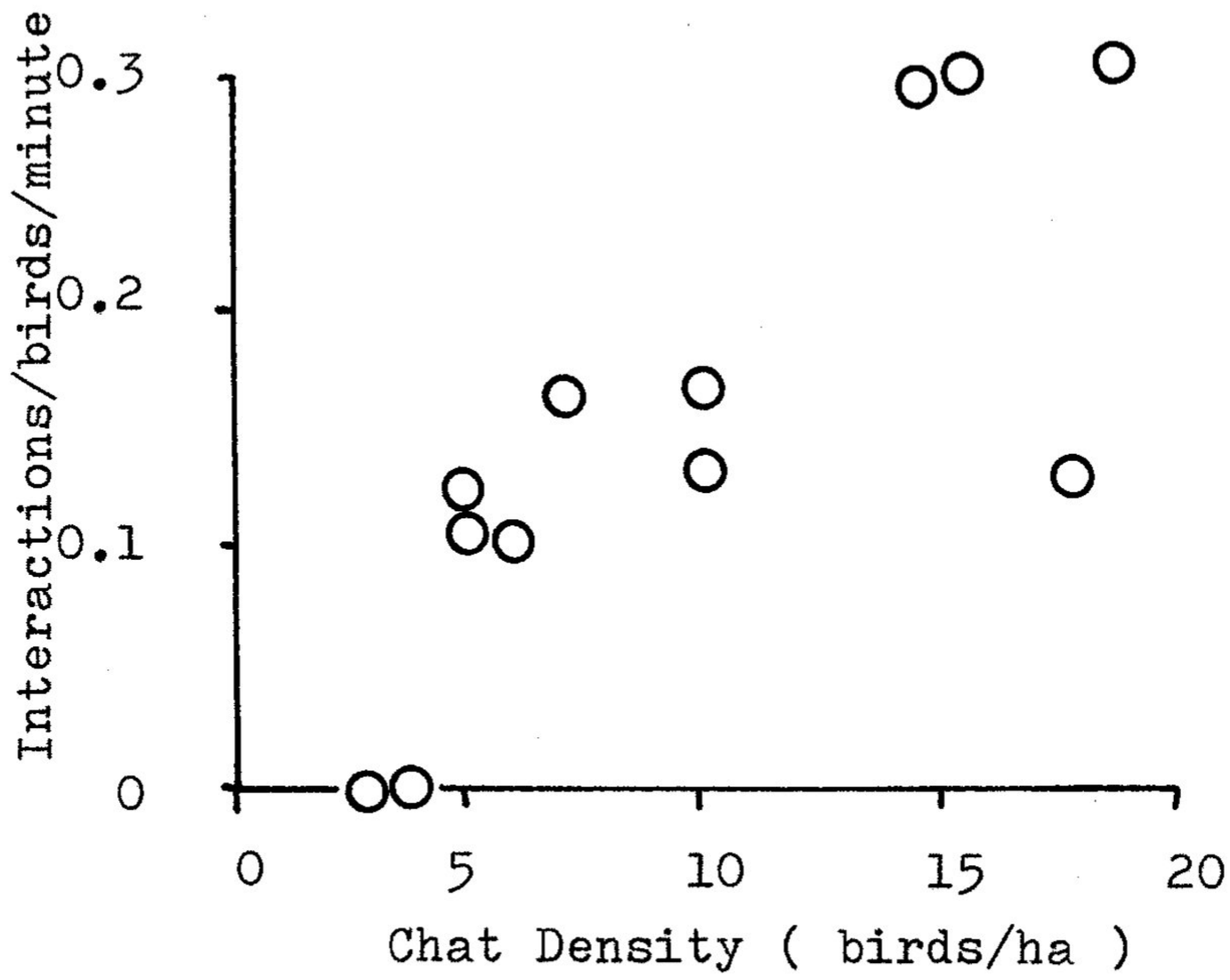


FIGURE 3.34. Relationship between density and frequency of Aggression in passerines at Windmill Hill Garigue in the autumn of 1978.



Slopes: Chats only, $b = 0.0148 \pm 0.0039$ $p < 0.01$

Chats + Warblers, $b = 0.0145 \pm 0.0054$ $p = 0.02$

all passerines, $b = -0.0010 \mp 0.0025$ $p > 0.05$

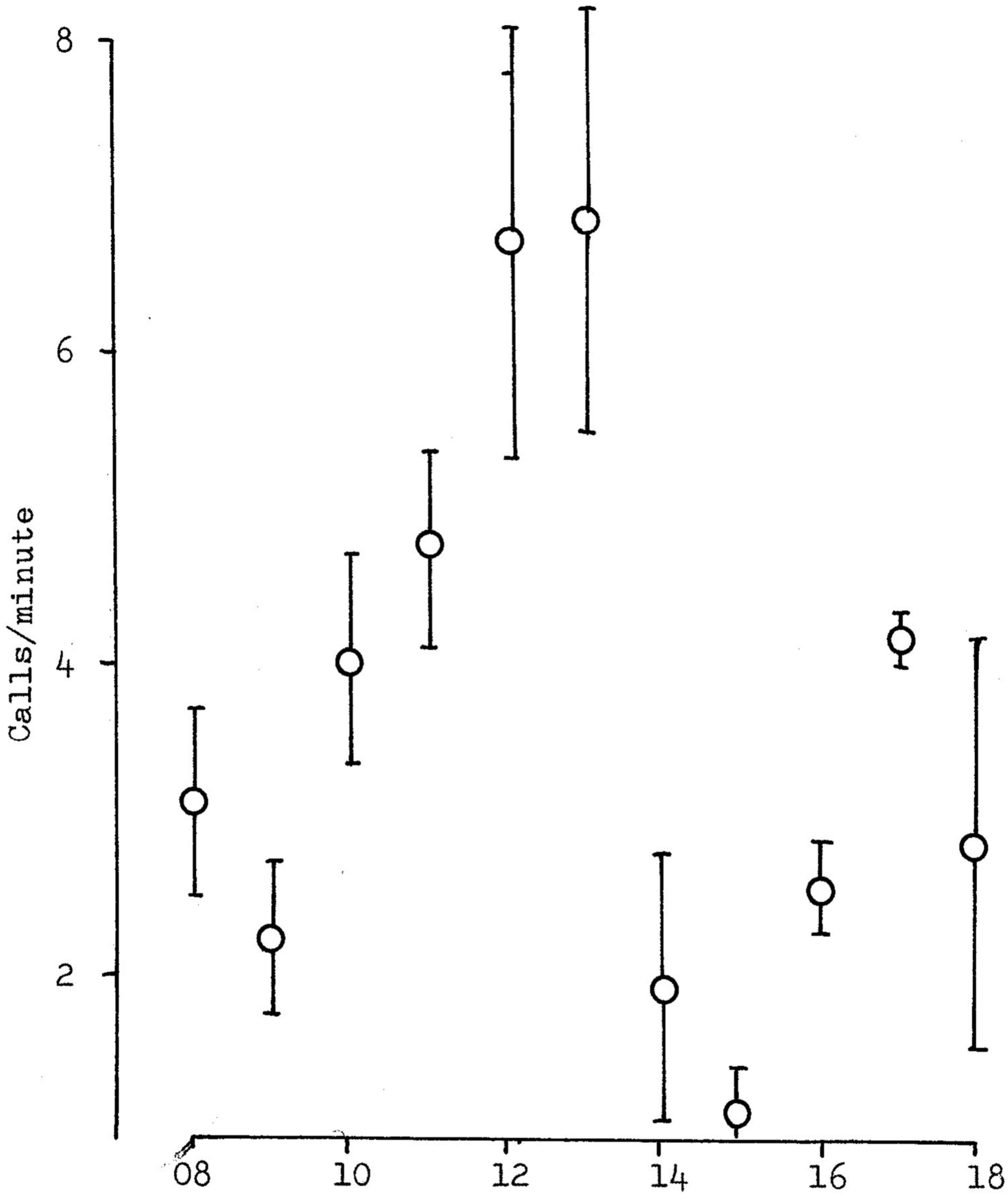
they chased other Sardinian Warblers. Other species which were chased by Sardinian Warblers were Stonechat, Redstart, Chiffchaff, Fan-tailed Warbler, Robin and Dartford Warbler. Sardinian Warblers were chased on 26 occasions, 24 of these by conspecifics, once by a Stonechat and another by a Redstart. There was therefore aggression between species with different ecological requirements. For example, the overlap in feeding technique between Sardinian Warbler and Stonechat was only 0.10, yet Sardinian Warblers did not hesitate to chase Stonechats when approached.

Calling

While foraging for arthropods outside the breeding season, Blackcaps and Sardinian Warblers called frequently. Warblers called just before changing feeding location and just after arriving at a new position. At Jews' Gate, the number of calls heard at minute intervals was recorded into a notebook; all calls from the two warbler species were noted, irrespective of distance. This was done every hour of the day by sitting on the same spot in the habitat. Records were taken during the last week of November and the first of December 1977 (Fig. 3.35.). In all, 721 minutes were recorded. The pattern of calling activity was different for the two species (Fig. 3.35.). Blackcaps called frequently at sunrise, and the rate dropped steadily towards late

FIGURE 3.35(a). Rate of Calling by warblers at Jews' Gate during November and December 1977.

(a) Sardinian Warbler

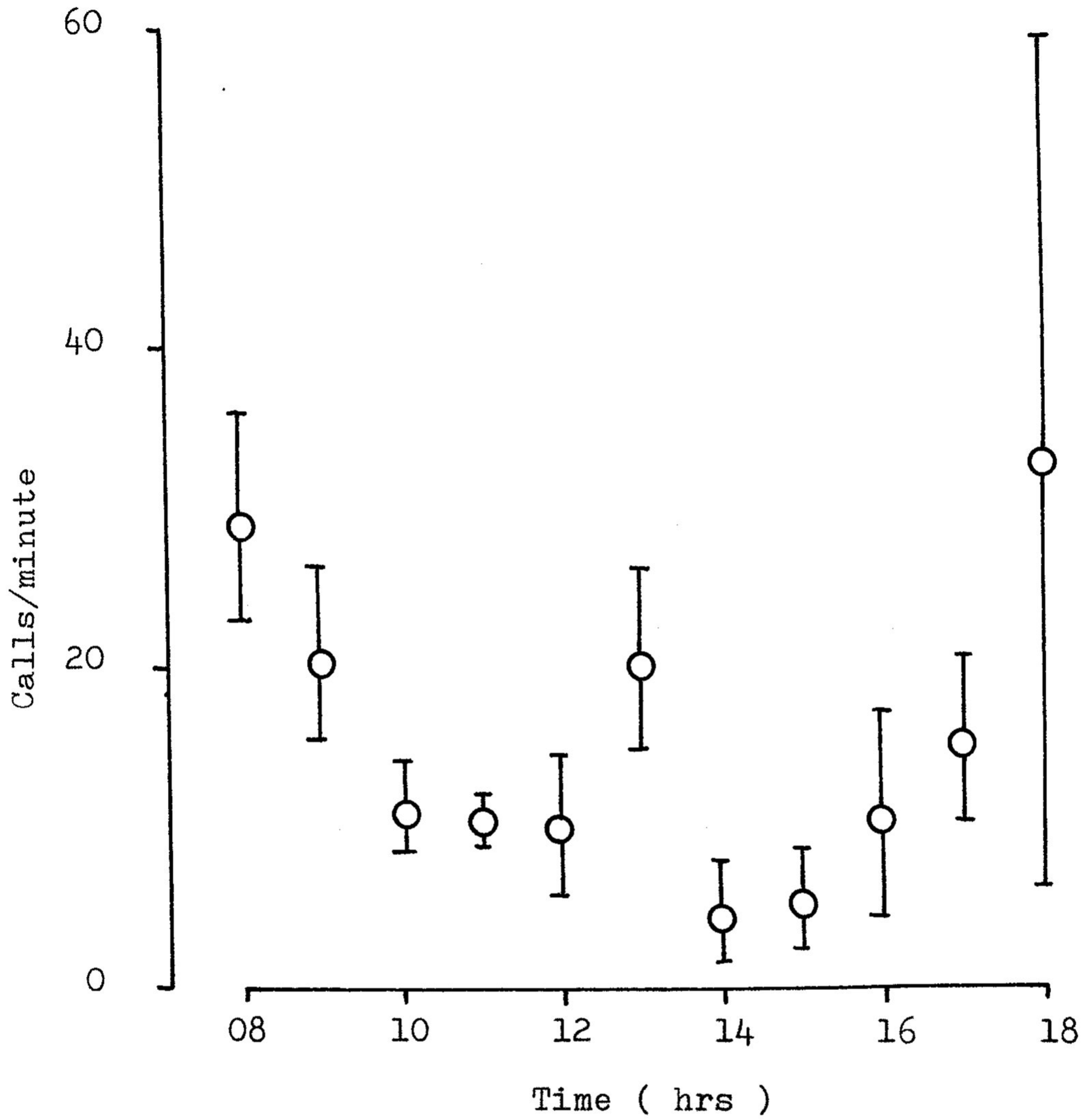


Niche Breadth = 8.613

"Niche" Overlap (with Blackcap, see (b)) = 0.794

see text for details

FIGURE 3.35 (b).



Niche Breadth = 8.293

morning; there was a small peak at 1300 hrs, followed by a sharp drop with a gradual recovery towards evening. The Sardinian Warbler slowly increased the rate of calling towards noon but this then dropped sharply in mid-afternoon. There was another peak in the evening but this was an hour before sunset instead of at sunset as was the case of the Blackcap (Fig. 3.35.). Nevertheless, the overlap in calling activity was high, at 0.794. As calling was related to foraging activity. it seems as if the two species, in winter at least, were segregated to a small degree by temporal means.

3.4.11. Resource Partitioning - a discussion

Within the same geographical area, bird species may differ in resource use in several ways (Cody 1974). These may be summarised as follows :

1. Habitat Choice - this has been termed local or between-habitat segregation (Cody 1974) and refers to the separation of two or more species by occupation of different habitats.

2. Within-habitat Choice - this term is reserved by Cody (1974) for cases where bird species segregate by occupying different horizontal positions within the habitat.

3. Vertical Segregation - Although this is also a form of within-habitat choice, Cody (1974) separates it.

4. Segregation by food or feeding.

5. Segregation in time.

There are other mechanisms which act to partition resources between species, in particular interspecific territoriality.

Even though mechansims of resource partitioning in birds have been known for some time (Lack 1971), examples of the different mechanisms have usually been observed in different species pairs or groups (Cody 1974), and it is rarer to find examples where all the possible alternatives have been examined in the same pair or group of interacting species (MacArthur 1958), especially if the different species have been followed through the annual cycle (Gibb 1954). In the case of the Blackcap/Sardinian Warbler pair at Gibraltar, all possible mechansims of partitioning resources within a geographical area have been examined over the course of the annual cycle.

Historical Background

The Maquis vegetation at Gibraltar has only developed in recent times. Last century, most of the vegetation at Gibraltar resembled Garigue and Steppe which now covers only small areas of the Rock. The vegetation was kept from developing by goats, sheep and cattle which were grazed on the Upper Rock (Cortes 1979). The breeding bird species at Gibraltar last century included Sardinian Warbler and probably Dartford Warbler (Irby 1895). The Blackcap was only an

occasional nesting species in gardens in the town (Irby 1895). With the removal of grazing animals, the vegetation developed rapidly everywhere on the western slopes and formed the dense Maquis which is typical of the present day. In the intervening period the Dartford Warbler has disappeared as a breeding species and the Blackcap has become an abundant breeding species alongside the Sardinian Warbler.

Mechanisms of resource partitioning

Differences between the two species were found in habitat occupation, within-habitat occupation, vertical stations, feeding behaviour, and in the timing of activities. Food was not analysed in great detail, but as differences were found in bill length and weight, both factors which influence choice of food (Hespenheide 1975a), there must have been some differences in diet, if only small ones. It is more interesting to ask how much difference there is in each dimension studied.

1. Habitat Occupation - the three habitats studied were used by Blackcaps and Sardinian Warblers, though the Blackcaps were absent from Garigue in summer (Table 3.14.). At all times the Blackcaps were scarce in the Garigue. Although the two species differed in habitat occupation, they overlapped greatly at all times. Overlap values ranged from 0.81 in winter to 0.94 in summer.

2. Within-habitat occupation - Within low Maquis at the Jews' Gate site, the two species showed

specific differences for occupying patches of the habitat (Fig. 3.9., Table 3.15.) and these differences appeared to be related to the varying amounts of food in the different patches occupied. The occupation of patches by Sardinian Warblers may have been influenced by that of Blackcaps. Despite differences in patch occupation, overlaps between the two species were high, ranging from 0.73 in spring to 0.96 in winter.

3. Vertical Segregation - The two warbler species differed in the height they most frequently foraged at (Fig. 3.10.). Overlaps were high, ranging from 0.85 in autumn to 0.93 in spring (Table 3.23.). When ground foraging and foraging position are added, the overlaps remain high (Table 3.25.).

4. Segregation by food and feeding behaviour - Bill length overlaps were high (Table 3.29.), but were higher between Sardinian Warblers and nominate Blackcaps than between Sardinian Warblers and local Blackcaps. It is possible that, as the latter pair are in contact all year, a better segregation by food has developed than between the former pair. Weight overlaps between the two species were low (Table 3.29.). The foraging techniques used by the two species were essentially the same and they varied little with season (Table 3.27.) and there was complete overlap in feeding techniques (Table 3.28.).

5. Segregation in time - This occured at the annual

level and at the diurnal level. The breeding seasons of the two species were not the same , as the Blackcap started later in the spring (Fig. 3.3.). The overlap was nevertheless high, 0.86. There were insufficient data to calculate overlap in the period of moult but it must have been high (3.3.2.). At the diurnal level, the two species appeared to forage most actively at different times of day (in winter at least) but they overlapped to a large degree (Fig. 3.35.).

Overlaps were high in all dimensions examined (Table 3.42.). The highest overlap for all dimensions combined was in summer and the lowest overlap in spring, but the differences are not significant statistically. Addition of diurnal overlap to the winter data does very little to reduce the total overlap; similarly addition of breeding season overlap to the spring and summer data changes little.

Niche Breadth

There was little tendency for the overall (= mean) niche breadth of either warbler species to change seasonally (Table 3.43.). The differences in mean niche breadth between the two species for each season are not statistically significant even though the Sardinian Warbler appeared to be broader-niched (Table 3.43.) than the Blackcap. The two species were very specialised in feeding technique, using stand pick most of the time. They were specialised in plant species occupation, usually foraging on one or two species at any time, but they were plastic in behaviour as they could change

TABLE 3.42. Mean overlaps between Sardinian Warblers and Blackcaps in different seasons at Gibraltar.

Method of segregation	Overlap/Season Autumn	Winter	Spring	Summer
Habitat	0.92	0.81	0.82	0.94
Plant Species	0.74	0.96	0.73	0.82
Height & Position	0.89	0.95	0.96	0.98
Technique	1.00	1.00	1.00	1.00
Mean	0.89	0.93	0.88	0.94
s.d.	0.11	0.08	0.13	0.08

If diurnal overlap added to winter, $\bar{x}$=0.90 s.d.0.10
If breeding season overlap added to spring and summer, $\bar{x}$=0.87 s.d.0.11 and $\bar{x}$=0.92 s.d.0.08.

TABLE 3.43. Blackcap and Sardinian Warbler mean Niche Breadths.

(a) Blackcap

	Season			
	Autumn	Winter	Spring	Summer
Mean	2.08	2.24	2.20	2.41
s.d.	0.92	1.25	1.12	1.32

	Dimension			
	Habitat	Plant species	Height	Technique
Mean	1.88	3.80	2.17	1.08
s.d.	0.09	0.40	0.24	0.05

(b) Sardinian Warbler

	Season			
	Autumn	Winter	Spring	Summer
Mean	2.69	2.65	2.52	2.63
s.d.	1.17	1.12	1.02	1.22

	Dimension			
	Habitat	Plant species	Height	Technique
Mean	2.77	3.49	3.20	1.02
s.d.	0.30	0.24	0.36	0.02

from being specialists on one plant species to being specialists on another plant species fairly rapidly (Morse 1971). Overall, the two species may be considered plastic specialists.

Interspecific Territoriality

Orians & Willson (1964) suggested situations where interspecific territoriality might be expected to occur, and these situations have been extended by Cody (1969) to cover a wider range of possibilities. Interspecific territoriality is expected to occur when the habitats are simple, when the species in question are specialists, and when there are many other species present. In the case of the two Sylvia species, all three conditions seem to be fulfilled. The habitat sequence at Gibraltar and the habitats themselves are simple (e.g. they have a narrow vertical spread), the two warbler species behaved as specialists, and at certain times of year there were many other species present.

In early spring the two species occupied territories in which to breed (Figs. 3.17 - 3.21.). The territories of the two species were non-randomly distributed in the habitat, partly because of occupation of different parts within the habitat and partly because of overt behavioural interactions. In some cases parts of territories overlapped between individuals of the two species but the territory owners were rarely seen together in the area of

overlap. There may be a form of temporal separation operating in such cases to reduce the chances of meeting. As individuals of the two species moved around calling frequently, it is possible that birds were aware of each other's positions in space at any point in time and that in this way they were able to avoid each other.

Outside the breeding season, the warblers ' carried ' small mobile territories with them while they searched for arthropods in the vegetation. They were usually well spaced out in the habitat. When two individuals came close to each other there was a chase. Since the two species foraged in different plant species, the chance of an encounter will have been low. Chasing was not confined to pairs of very similar species (e.g. congeners), and migrants of various species were chased off (Willis 1966). Migrants dominated the communities numerically at times (2.3.4.). They usually foraged actively while grounded and did so in similar ways to the Blackcap and the Sardinian Warbler (e.g. seven species of Sylvia warblers occured regularly as migrants). Most migrants probably did not know the area at all, and as they were generally silent, they often came into contact with the residents. Indeed, chases were frequent even between species with dissimilar ecological requirements suggesting that there was a large amount of interference between species. Alternatively, the habitats were so simple that many species may have been forced to take the same foods in a similar fashion.

The chances of contact became greater as the total bird density increased. The Strait of Gibraltar is known to concentrate migrants in the autumn and spring (2.3.4.) and sudden influxes of migrants were frequent at Gibraltar (Fig. 3.31.). Such density increases were accompanied by rises in the frequency of aggressive encounters (Recher & Recher 1969).

The behaviour of the resident warblers at Gibraltar changed little throughout the non-breeding season. The main deviation from this pattern occured when the warblers changed diet and foraged on fruit or nectar. These foods could be defended easily and individuals then established small territories around clumps and bushes. A more mobile system was used when foraging on arthropods.

The Blackcap and the Sardinian Warbler were in direct contact all year. Their ecological requirements were very similar and it appears that the main way they avoided competing with each other was by holding areas of space which were exclusive to themselves. These areas had various degrees of permanence, lasting for months in spring and for seconds or minutes in winter. It is not surprising that mechanisms of resource partitioning were weak between the two species. The resources at Gibraltar were simple and this must have precluded segregation. Even if this had been possible, the amount of interference in simple habitats like Garigue or Maquis would still be high since individuals would often be in close contact. The Sardinian Warbler

/Blackcap system at Gibraltar may be recent. Mechanisms of spatial separation between species by direct behavioural interaction are frequent in species which have recently come into contact (Cody 1974).

At present all the vegetation is fully occupied by the two Sylvia species, except for short grassland which is used by Fan-tailed Warblers (Finlayson in press). Despite the many other warbler species that passed through Gibraltar in spring, none managed to establish breeding populations on the Rock. Several warbler species nest near Gibraltar in similar vegetation and have nested or attempted to nest on the Rock several times. They include Melodious Warbler, Spectacled Warbler and Bonelli's Warbler. Other potential candidates are Orphean Warbler, Whitethroat and Subalpine Warbler.

By the time these migrants arrived at Gibraltar in spring, the resident warblers had established territories and chased off any intruders (Morse 1971). Lack (1971) has suggested that the Subalpine Warbler occupies breeding areas which the Sardinian Warbler is excluded from by the harshness of the winters. The Subalpine Warbler is a migrant and can capitalise on the temporary habitats (Morse 1971). The two resident Sylvia species found enough food to maintain them (and an additional Blackcap population) all winter. The many bushes which produce berries in winter at Gibraltar must be a major reason for the sedentary nature of the populations.

Morphological adaptations

The Sardinian Warbler is in many ways the typical Mediterranean Sylvia warbler. Morphologically, it is adapted for the Mediterranean Maquis and Garigue, especially for foraging in dense, low vegetation or on the ground (Gaston 1974). The local Blackcap departs morphologically from the nominate (3.2.2.) and these differences can be related to the habitats occupied at Gibraltar. In a sense the Blackcaps at Gibraltar have abandoned the woodland way of life and are evolving into scrub birds. Morphologically they are beginning to resemble Sardinian Warblers.

3.5. SOME OUTCOMES

So far, the annual cycles of the Blackcap and the Sardinian Warbler have been discussed, with reference to a seasonal environment and to resource partitioning. This section considers what may be termed outcomes of these processes. Ultimately, natural selection will favour individuals with adaptations which will maximise reproductive output. Outcomes, other than production of offspring, will also be considered. Short-term outcomes affecting individuals directly, such as weight and fat level, are treated first. Individuals best able to adapt to the environment should benefit most in terms of food intake and this will be reflected in their weights and in the amounts of extra fat they can accumulate. Long-term outcomes which will be discussed

are production of offspring, mortality, recurrence in winter quarters, and habitat impact.

3.5.1. Weight

In this, and in the following sub-sections, only average situations will be considered, with particular reference to contrasting the two warbler species which are being examined. Ideally, individuals should be examined but this was impossible during this study. Weights were recorded as described in 2.2.3. Seasonal variation in weights was negligible (Table 3.44.). Weight is probably not a good indicator of the condition birds are in when averaged, as many factors are likely to influence it. Little can therefore be said about the weights of local Blackcaps and Sardinian Warblers except that they varied little with season. Even in the nominate Blackcaps weight variations between seasons were not large, even when they were preparing for migration (Table 3.7.).

3.5.2. Deposition of fat

The level of fat in the tracheal pit was recorded following Fry et al. (1970), see also 3.3.3., and Table 3.8. The level of fat in the tracheal pit appeared to be more sensitive than weight to variations in the condition of birds. Variations in migrants were mostly due to fat deposition prior to migrating (Table 3.8., Fig. 3.36.). Differences in residents must be due to the accumulation of fat when conditions are favourable. The levels of fat in individuals trapped in different seasons ought to give an indication

TABLE 3.44. Seasonal variation in weights of Blackcaps and Sardinian Warblers at Gibraltar.

(a) Blackcap (local form)[1]

	Season			
	Autumn	Winter	Spring	Summer
Mean	17.6	17.8	17.3	17.9
s.d.	1.24	1.43	1.70	1.66

(b) Sardinian Warbler

	Season			
	Autumn	Winter	Spring	Summer
Mean	12.2	12.0	12.4	12.3
s.d.	0.78	0.82	0.95	0.97

[1]for comparable data on nominate Blackcap, see Table 3.7. All weights in grammes. Sample size = 40 in all cases.

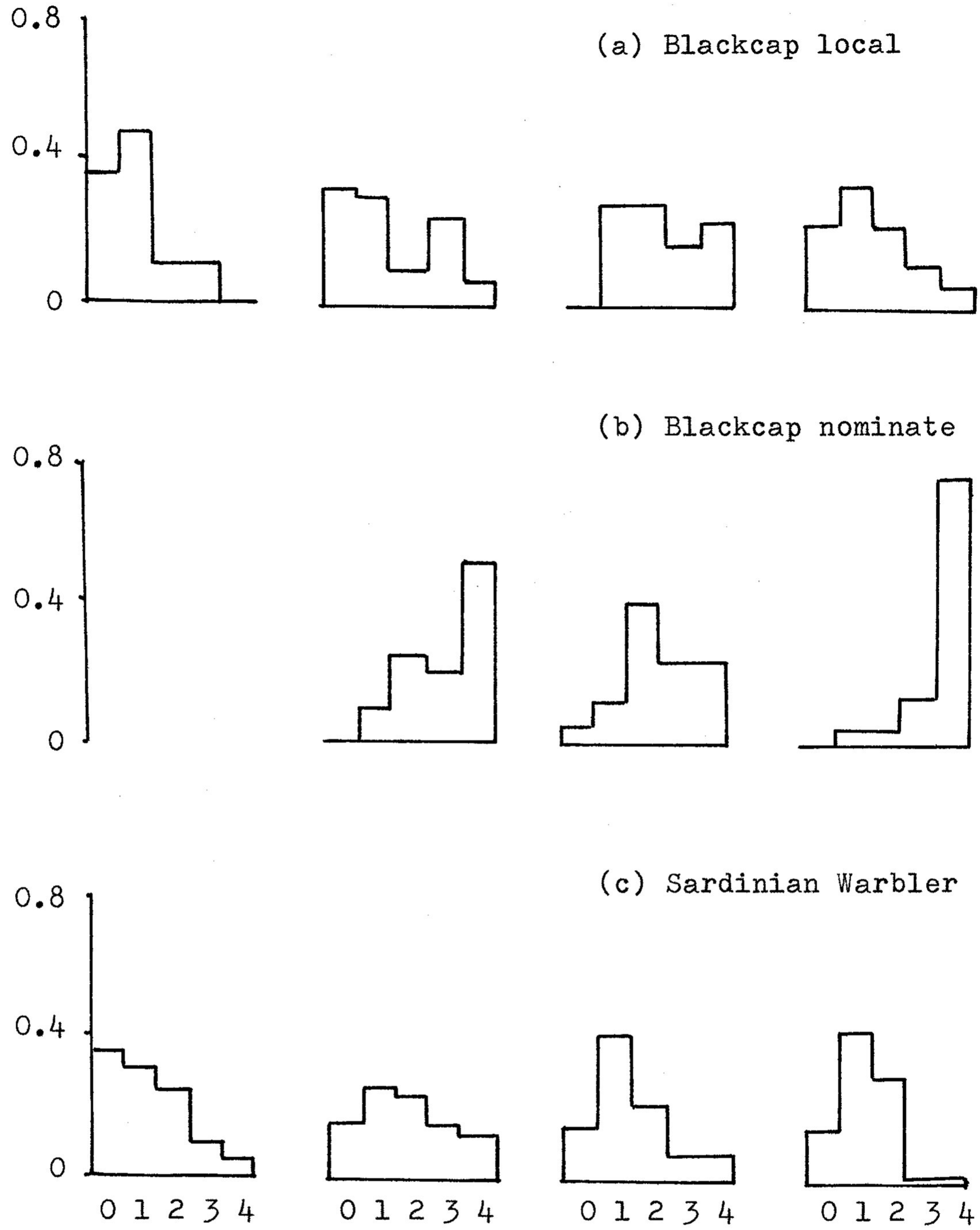


FIGURE 3.36. Fat levels of Blackcaps and Sardinian Warblers at Gibraltar.

of the best and the most critical periods in the cycle of the resident (Fig. 3.36.).

Neither of the two local warblers accumulated as much fat as the nominate Blackcaps which had to migrate (Fig. 3.36.). They nevertheless exhibited significant seasonal differences in fat levels (Table 3.45.). Summer, as expected, was a very critical period for the two resident warbler species; it coincided with the drought and when most individuals were about at the end of breeding (Figs. 2.4., 2.11.). It was also the time when they were moulting (3.3.2.). Mortality at this time was high, especially for juveniles (Fig. 3.38.). Spring was the other critical period, especially for the Sardinian Warbler (Fig. 3.36., Table 3.45). Even though the food supply was high in spring, there were many migrants about and the local birds were breeding. Since Blackcaps started to breed later than Sardinian Warblers, the spring may be a less critical time for them (3.3.1.).

There was a significant high in the fat level of the Sardinian Warblers in the autumn after the first rains (Fig. 3.36., Table 3.45.). This may partly have been due to Sardinian Warblers passing south at this time (3.3.3.). This was also the time when Sardinian Warblers foraged more on berries than at any other time of year (Fig. 3.9.). Berthold (1976) has pointed out that vegetal matter is nutritionally poor for warblers unless supplemented by some animal matter. In the autumn berries are so pletiful that it seems likely

TABLE 3.45. Seasonal variation in fat levels in Blackcaps and Sardinian Warblers at Gibraltar.

(a) Blackcap (local)

Fat Score	Season			
	Autumn	Winter	Spring	Summer
0	.327	0	.235	.348
1	.291	.294	.353	.478
2	.091	.294	.235	.087
3	.236	.176	.118	.087
4	.055	.235	.059	0

(b) Blackcap (nominate)

0	0	.026	0
1	,079	.103	.039
2	.224	.410	.031
3	.197	.231	.134
4	.500	.231	.795

(c) Sardinian Warbler

0	.177	.156	.171	.344
1	.263	.438	.463	.292
2	.251	.219	.317	.229
3	.171	.094	.024	.094
4	.137	.094	.024	.042

(a) $X^2_3 = 10.635$ $p < 0.05$

(b) $X^2_1 = 4.380$ $p < 0.05$ (autumn/winter lumped)

(c) $X^2_3 = 12.129$ $p < 0.01$

In all cases, 0-1 and 2-4 are lumped to give expected values over 5.

that warblers will use them for fattening provided they can ingest some arthropods. Similarly, in winter local Blackcaps had high fat levels (Fig. 3.36., Table 3.47.). The most demanding times of year for the resident Sylvia species at Gibraltar are spring and summer even though arthropod availability was highest in spring. Autumn and winter were relatively easy times of year. Even wintering Blackcaps of the nominate sub-species could maintain high levels of fat in winter (Fig. 3.36.). They were able to lay down large amounts of fat in spring prior to migrating north and this contrasts them with the local Blackcaps which were reaching a low at this time of year (Fig. 3.36.). At this time the nominate Blackcaps devoted all their time to depositing fat for migration but the local birds were preparing for breeding and so could not accumulate as much fat.

3.5.3. Production of offspring

The end result of the breeding activities of the local warblers was the production of a new generation of warblers (Figs. 3.1., 3.2.). A rough indication of the production of juveniles was obtained by comparing the numbers of juveniles and adults trapped at Jews' Gate during the period June to September (Table 3.46.). On average, about 71% of all the Blackcaps present at this time were juveniles and 79% of all the Sardinian Warblers were juveniles. The difference is highly significant

TABLE 3.46. Proportion of juveniles out of total captured in period June - September in the years 1973 - 1975 and 1977 - 1978.

(a) Blackcap (local)

Year	% Juveniles	N
1973	87.88	33
1974	84.13	63
1975	70.21	47
1977	41.76	91
1978	71.43	35

(b) Sardinian Warbler

Year	% Juveniles	N
1973	76.27	59
1974	81.11	180
1975	70.97	93
1977	90.05	191
1978	77.12	118

(a) $X^2_4 = 39.891$ $p < 0.001$

(b) $X^2_4 = 17.875$ $p < 0.01$

TABLE 3.47. Mortality in Blackcaps and Sardinian Warblers at Jews' Gate.

(a) Blackcap (local)

Retrap Interval (years)	Number Ringed	Retrapped	% Retrapped a_x	log a_x
1	468	75	16.03	1.205
2	324	31	9.57	0.981
3	309	11	3.56	0.551
4	198	5	2.53	0.403
5	58	0	0	

(b) Sardinian Warbler

1	697	91	13.06	1.116
2	474	30	6.33	0.801
3	403	9	2.23	0.348
4	306	4	1.31	0.117
5	99	1	1.01	0.004

(X_1^2 = 23.106 $p<0.001$). There were notable differences in the numbers of juveniles in different years. There were very few juvenile Blackcaps in 1977 and this coincided with a wet summer, especially in June and July (Table 1.2.). It was on the other hand, the best year for Sardinian Warblers (Table 3.46.). Since Sardinian Warblers breed earlier than Blackcaps, the summer rains came when many juvenile Sardinian Warblers had already fledged and the rains probably even helped them by alleviating the drought. The rains coincided with the peak of the Blackcap breeding season when many young were still in the nests.

3.5.4. Mortality

From ringing and retrap data recorded during the period 1973 to 1978, estimates of mortality have been calculated for the two resident warbler species using the method of Leslie & Chitty (1951). Mortality of adult birds (i.e. those over 1 year old) was calculated at an average of 58% per annum for Blackcap and at 45% per annum for Sardinian Warblers (Table 3.47., Fig. 3.37.). From the proportion of juveniles surviving in the different months after the breeding season, the mortality of juveniles in their first year of life was calculated at only 26% for Blackcaps and at 46% for Sardinian Warblers (Fig. 3.38.). Only data up to December were used as juveniles became progressively more difficult to separate from adults towards the next breeding season.

FIGURE 3.37. Mortality of Blackcaps and Sardinian Warblers resident on Gibraltar.

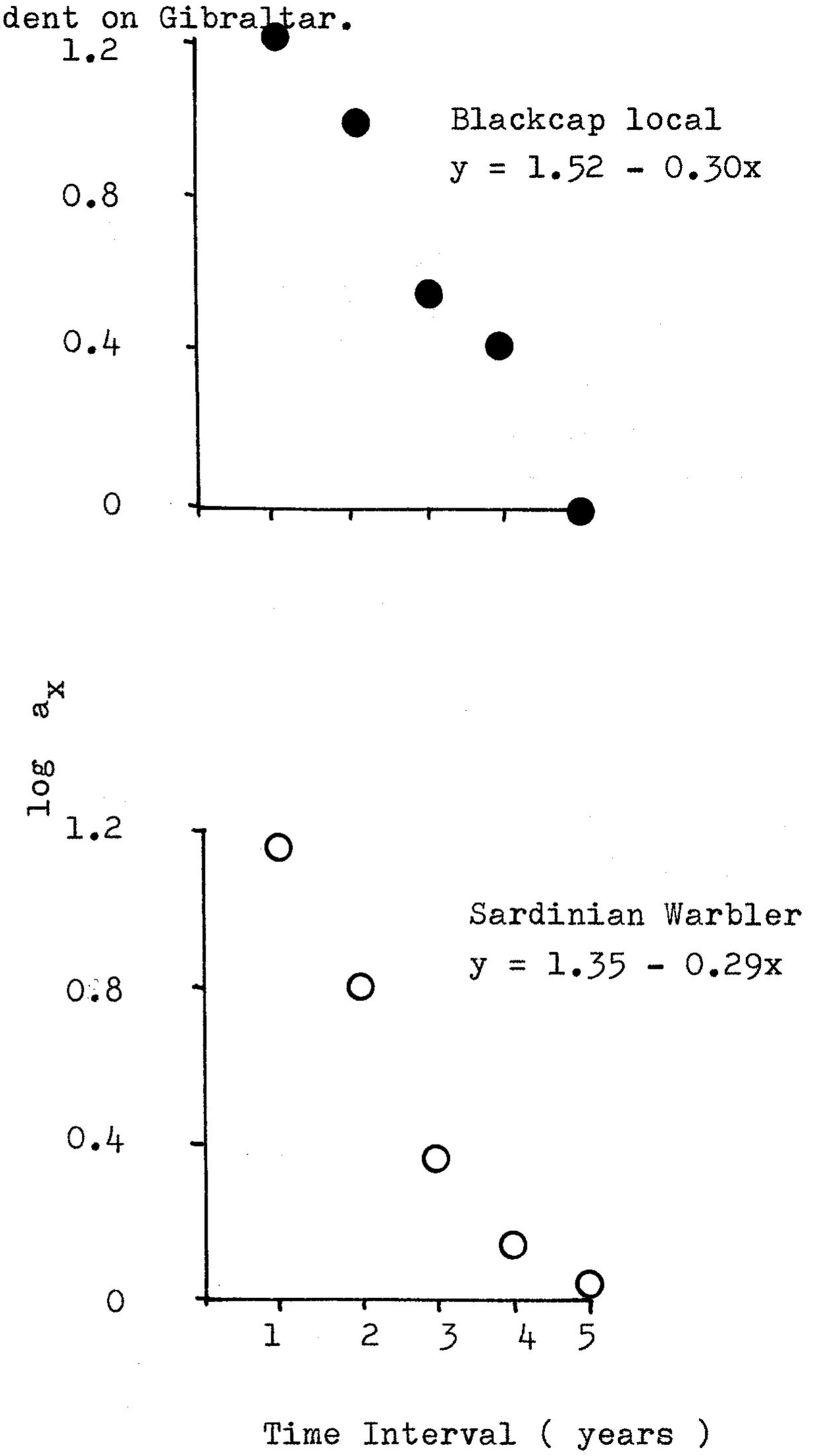
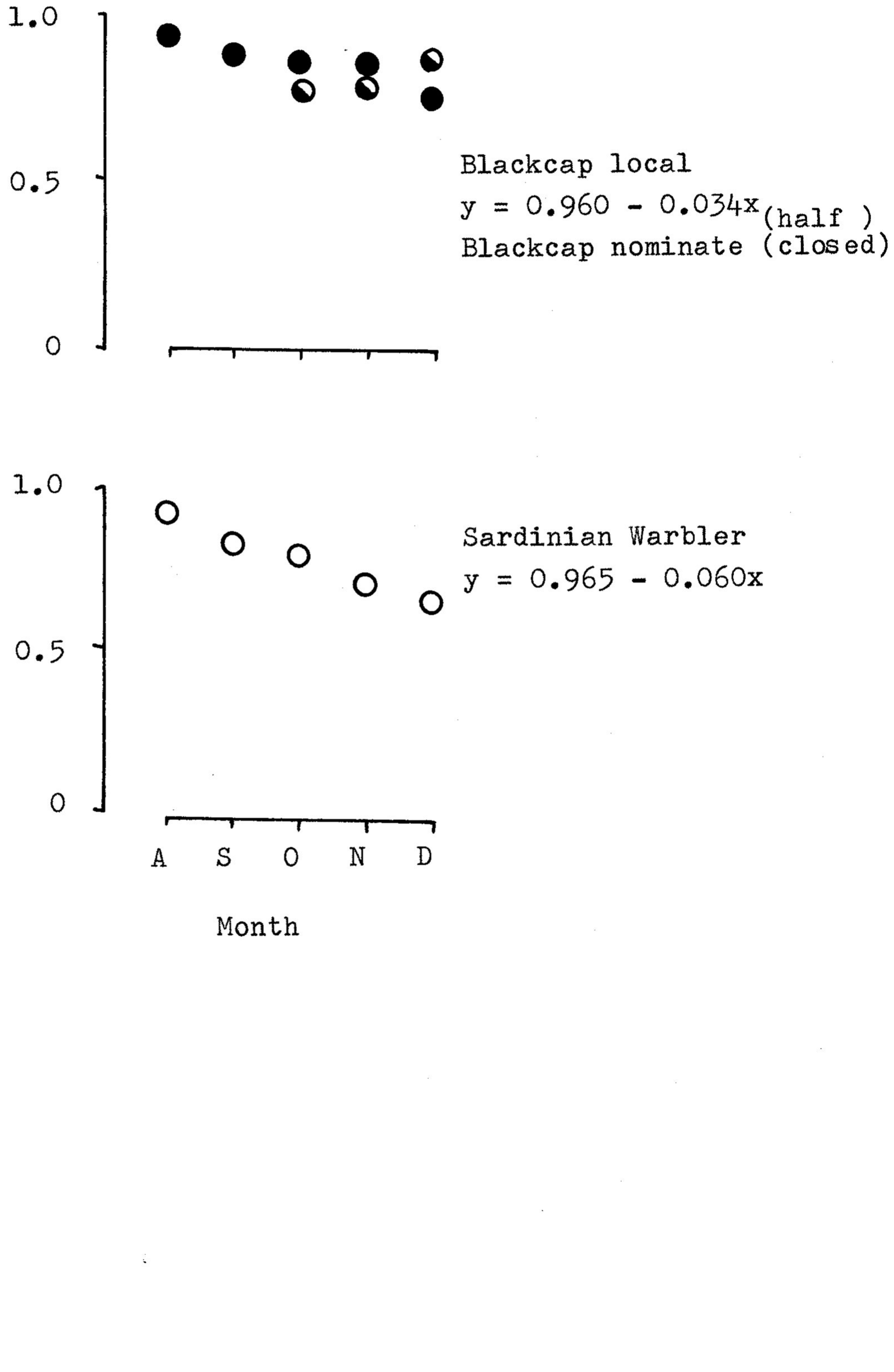


FIGURE 3.38. Decline in proportion of juveniles after the breeding season.



3.5.5. Recurrence in winter quarters

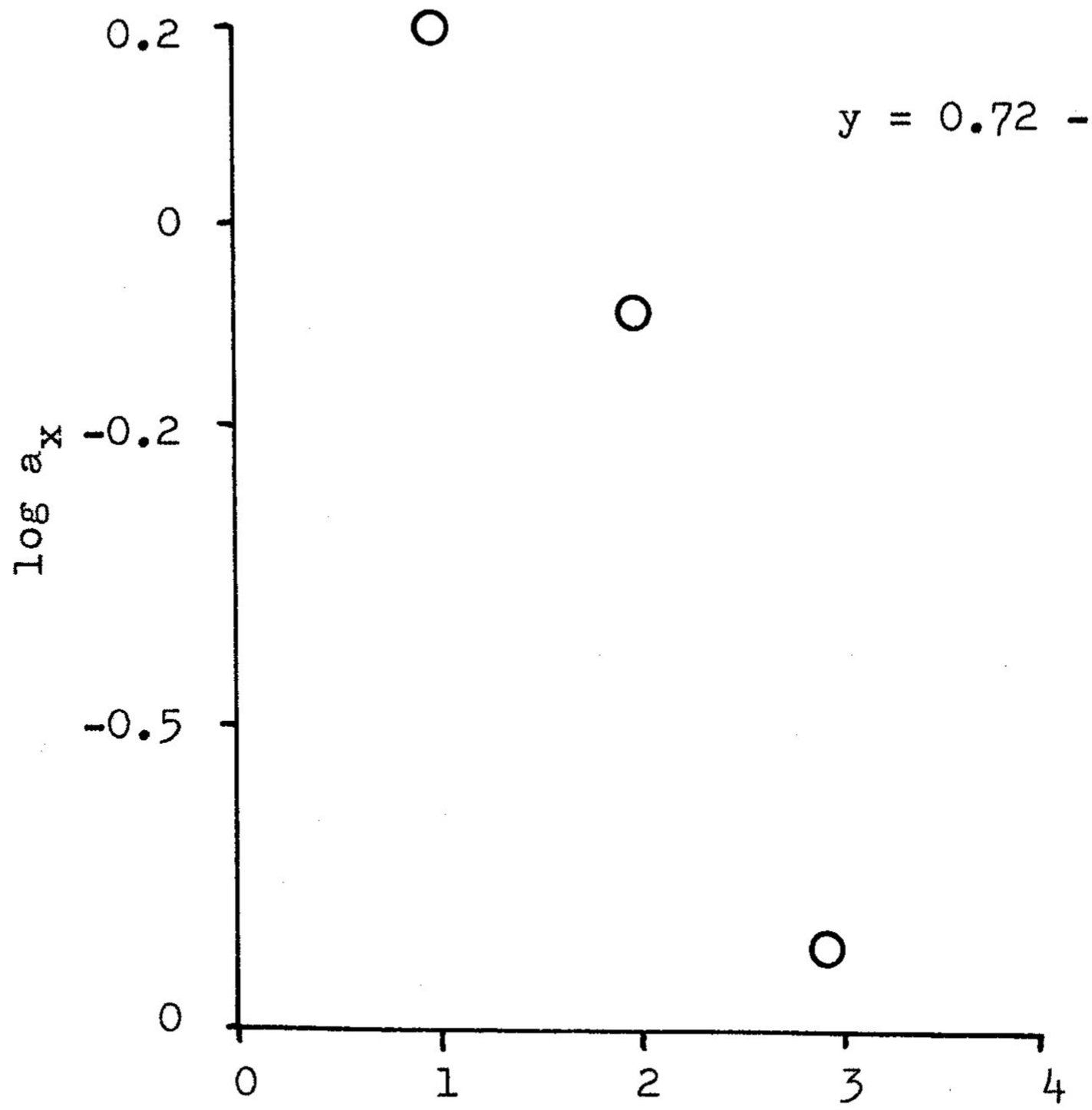
Nominate Blackcaps visited Gibraltar while on passage and also for the winter (Fig. 1.1.). The rate of recurrence after one winter was 8.86% and fits in well with recurrence rates published (Moreau 1972, Herrera & Rodriguez 1979). After two winters the recurrence rate was 4.42% and it dropped to 1.09% after three winters. The numbers of wintering Blackcaps at Gibraltar appeared to be dictated by the food supply there and possibly further north. The 1977/78 winter produced no Wild Olive berries at all and the proportion of wintering (= nominate) Blackcaps in the Blackcap population as a whole (i.e. nominate + local) was only 46%; the 1978/79 winter was better with 30% of the Wild Olives containing berries and the proportion of nominate Blackcaps that winter was 74%. The 1974/75 winter was even better and though the proportion of fruiting Wild Olives was not measured, it must have exceeded 80% (pers.obs.). Some of the recoveries of nominate Blackcaps (3.3.3.) show that changes in winter quarters do take place and some of these changes appeared to be related to the food supply at Gibraltar (compare 3.3.3. with above results). Changes in winter quarters occured to the north and south of Gibraltar.

Blackcaps may therefore not reach Gibraltar if conditions are good further north and others may move further south if the conditions they meet at Gibraltar are unfavourable. The term winter quarter is therefore a loose one, and although many

TABLE 3.48. Recurrence of nominate Blackcaps in winter quarters at Jews' Gate.

Retrap Interval (years)	Number Ringed	Number Retrapped	% Retrapped a_x	% Retrapped log a_x
1	1329	21	1.58	0.20
2	1241	10	0.81	-0.09
3	1041	2	0.19	-0.72

FIGURE 3.39. Recurrence in winter quarters of nominate Blackcaps at Gibraltar.



birds return to the same winter quarter the following year, they are by no means confined to it. The advantages of returning to a wintering area with a known food supply must be great but at the same time a certain degree of flexibility is necessary to cater for year to year variations in the food supply so that alternative wintering sites may be sought.

3.5.6. Habitat Impact

The impact which the two warbler species have on the habitats at Gibraltar can be calculated knowing their consumer biomass values. Garigue is the least important habitat and the main impact there is from Sardinian Warblers in summer (Tables 3.49., 3.50.). High Maquis is the most important habitat in the autumn but low Maquis takes over in winter. Low Maquis is still more important than High Maquis in spring but towards the summer both are equal in importance to the warblers.

Maquis is therefore the main habitat for the two resident Sylvia species but especially so for the Blackcap (Table 3.49.). All three forms appear to be able to change habitat quickly, presumably as the food supply changes (Frochot 1971).

TABLE 3.49. Habitat Impact by Blackcaps and Sardinian Warblers at Gibraltar.

(a) Blackcap (local)

Habitat	Season			
	Autumn	Winter	Spring	Summer
Garigue	0	0	0	0
low Maquis	9.03	6.90	5.81	16.80
High Maquis	14.26	3.07	3.63	9.87

(b) Blackcap (nominate)

Garigue	1.69	0.03	0.59	0
low Maquis	16.87	49.75	21.95	0
High Maquis	25.31	22.39	13.64	0

(c) Sardinian Warbler

Garigue	7.85	6.17	6.41	14.96
low Maquis	8.79	7.40	6.82	43.37
High Maquis	14.75	6.99	7.44	16.45

all figures are in g/ha

TABLE 3.50. Total Sylvia consumer biomass at Gibraltar.

Habitat	Season			
	Autumn	Winter	Spring	Summer
Garigue	9.54	6.20	7.00	14.96
low Maquis	34.69	64.05	34.58	24.71
High Maquis	54.32	32.45	24.71	26.32

all figures are in g/ha

CHAPTER 4

THE ECOLOGY AND BEHAVIOUR OF THE PALLID SWIFT AND THE SWIFT AT GIBRALTAR.

" ...., but though the common and pallid swifts look so similar they are distinct species, they do not intergrade in their characters and there is no suggestion that they ever interbreed, though there are places where they breed side by side. "

David Lack 1956, Swifts in a Tower.

4.1. INTRODUCTION

The Swift Apus apus and the Pallid Swift A.pallidus are numerically the two dominant aerial arthropod foragers at Gibraltar for most of the year (Fig. 1.19.). Neither species is resident, but Pallid Swifts are present at Gibraltar from mid-February to mid-November; the Swift is present between April and October, but the last nesting individuals leave by the first week of August.

The Pallid Swift breeds in the West and Central Mediterranean Basin, in the Middle East into Pakistan, and over a wide area of East Africa (Voous 1960). Recently it has been found nesting in tropical West Africa (Thiollay 1974). The West Mediterranean sub-species is A.p.brehmorum (Hartert). Very little is known about the ecology and behaviour of this species in the breeding grounds (Heim de Balsac 1951, Hue 1951, Hoffmann et al. 1951, Castan 1955, Affre & Affre 1967, Bernis 1970) and the winter quarters are imprecisely known (Lack 1958 c, Moreau 1972). The Swift is common and widespread in the Palaearctic and its life history, both on the breeding grounds (Weitnauer 1947, Koskimies 1950, Lack & Lack 1951, Lack 1956 a) and in the winter quarters (Brooke 1975) are well-known.

Gibraltar is in the zone of sympatry of

the two species. Both are abundant nesting species in Gibraltar and they often nest in close proximity. This situation may be found elsewhere in the Mediterranean but the relationships of the two species when they are in direct contact have not been studied at all.

This chapter will, as far as possible, have a similar infrastructure as the previous one. As much as possible the approach will be comparative. However when dealing with two very different species pairs such as the Sylvia warbler pair and the Apus swift pair, the methodology and results obtained have sometimes been very different.

4.2. TAXONOMY

Individuals of both species were measured at Gibraltar but no differences were found which would require taxonomic re-assessment (Lack 1956 b). This is not at all surprising as swifts are highly mobile and there must be considerable gene-flow between populations in the area. The morphological characteristics of the two species at Gibraltar are given in Table 4.1. The significance of these will be discussed in 4.4.6.

4.3. COMPARATIVE LIFE HISTORIES

This section, like 3.3., summarises the

TABLE 4.1. Morphological characteristics of Pallid Swifts and Swifts trapped at Gibraltar during the breeding season.

Character	Pallid Swift			Swift			
	N	Mean	s.d.	N	Mean	s.d.	P
Wing length	100	172.2	3.62	27	174.5	5.38	>0.05
Bill length	19	11.3	1.13	10	11.1	0.78	>0.05
Bill depth	13	2.9	0.25	10	2.7	0.19	>0.05
Bill gape	13	11.7	1.08	10	9.6	0.31	<0.001
Tarsus length	19	13.1	1.58	10	12.1	1.37	>0.05
Tail length	19	72.0	2.72	7	72.0	4.01	>0.05
Weight	100	41.3	3.63	24	44.9	4.90	<0.001

main features of the ecology of the two Apus species studied during the time they were present at Gibraltar. The main difference from 3.3., is that the swifts are only summer residents at Gibraltar whereas the warblers are completely sedentary.

4.3.1. The Breeding Season

The problem of finding nests was, in part, simpler than with the warblers. Thousands of Swifts and Pallid Swifts nested on Gibraltar, especially in buildings. As both species were colonial, finding a colony meant finding at least several nests. The main disadvantage was that the majority of the nests were in inaccessible situations (Bannerman 1963). This was particularly the case for the Swift which nested almost exclusively in holes in walls. These holes were sometimes close to the ground (in one case only 1 metre above the surface of a road) but they were very long and narrow making the eggs and young unreachable. The Pallid Swifts were just as difficult but a colony with about 30 accessible nests was found between the rafters in the attic of the Gibraltar Museum, a nesting situation which appears to be common in the Pallid Swift (Hue 1951, Hoffmann et al. 1951, Lack & Lack 1951, Laferrere 1972). Basic breeding information was gathered at this site in 1976 and 1977. The information in this area of the study is therefore more complete for the Pallid Swift

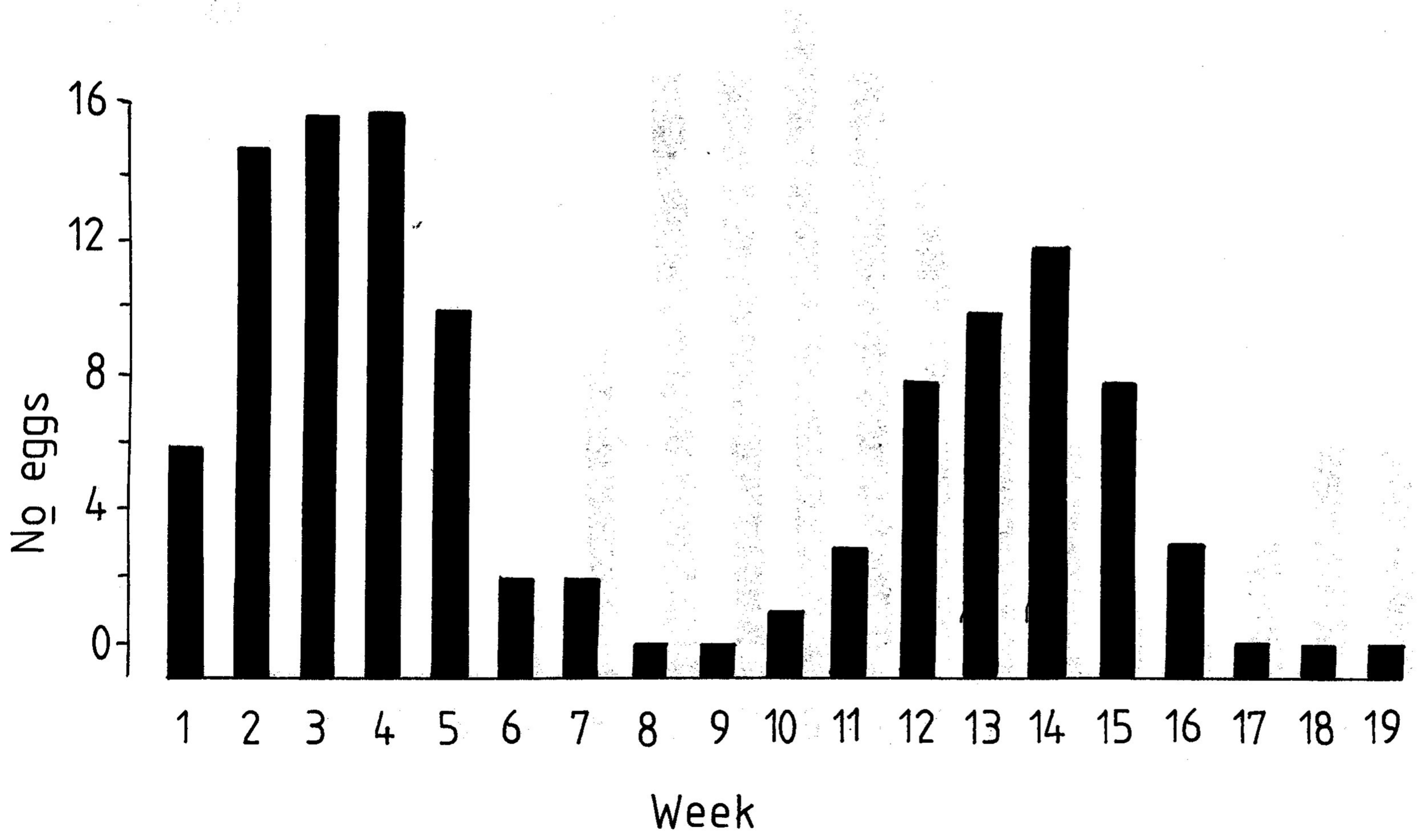
than it is for the Swift. Data obtained from nestlings found dying outside nests and from occasional accessible nests, have been used to supplement these results.

The breeding season of the Pallid Swift was studied partly in 1976 and completely in 1977. Even though Pallid Swifts were seen circling in large groups above Gibraltar as from the end of February, the first eggs were not laid until the second half of April (Fig. 4.1.). The peak in egg-laying was around the third week of May and a gradual decline followed until the second clutches started to be laid at the end of July (Fig. 4.1.). Chicks hatched three weeks after the eggs were laid so that peaks in the number of nests with chicks came about three weeks after the egg peaks (Fig. 4.2.). The incubation period was estimated at 21.4 $\pm$ 1.4 days (n = 8). The young took 46.4 $\pm$ 2.18 days to fledge (n = 10) The first young Pallid Swifts left the colony during the third week of June and most did so during the first week of July. The second brood young (see also Fig. 4.3.) started to leave the nests around the middle of September, 11th October being the latest date young were found in the nest. An almost completely fledged nestling was brought to me on 15th October, 1979. It was successfully released after four days. This is the latest record of unfledged Pallid Swifts at Gibraltar.

The nesting period of the Swift appeared to coincide with that of the first broods of the Pallid Swift. There were insufficient data to firmly

FIGURE 4.1. Number of Pallid Swift eggs present at weekly intervals at the Museum colony during 1977 spring, summer and early autumn.

Week 1 is the last week in April



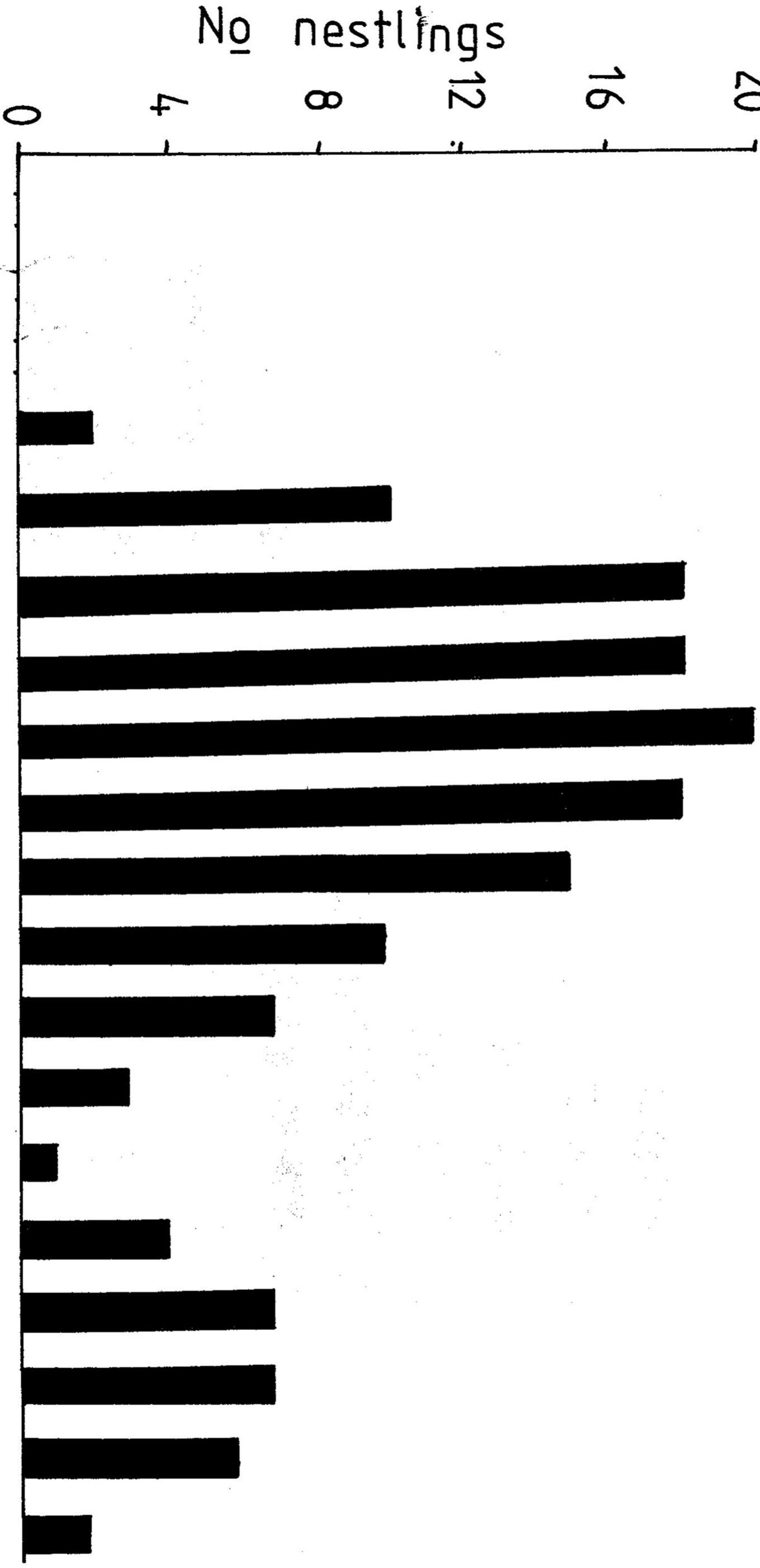
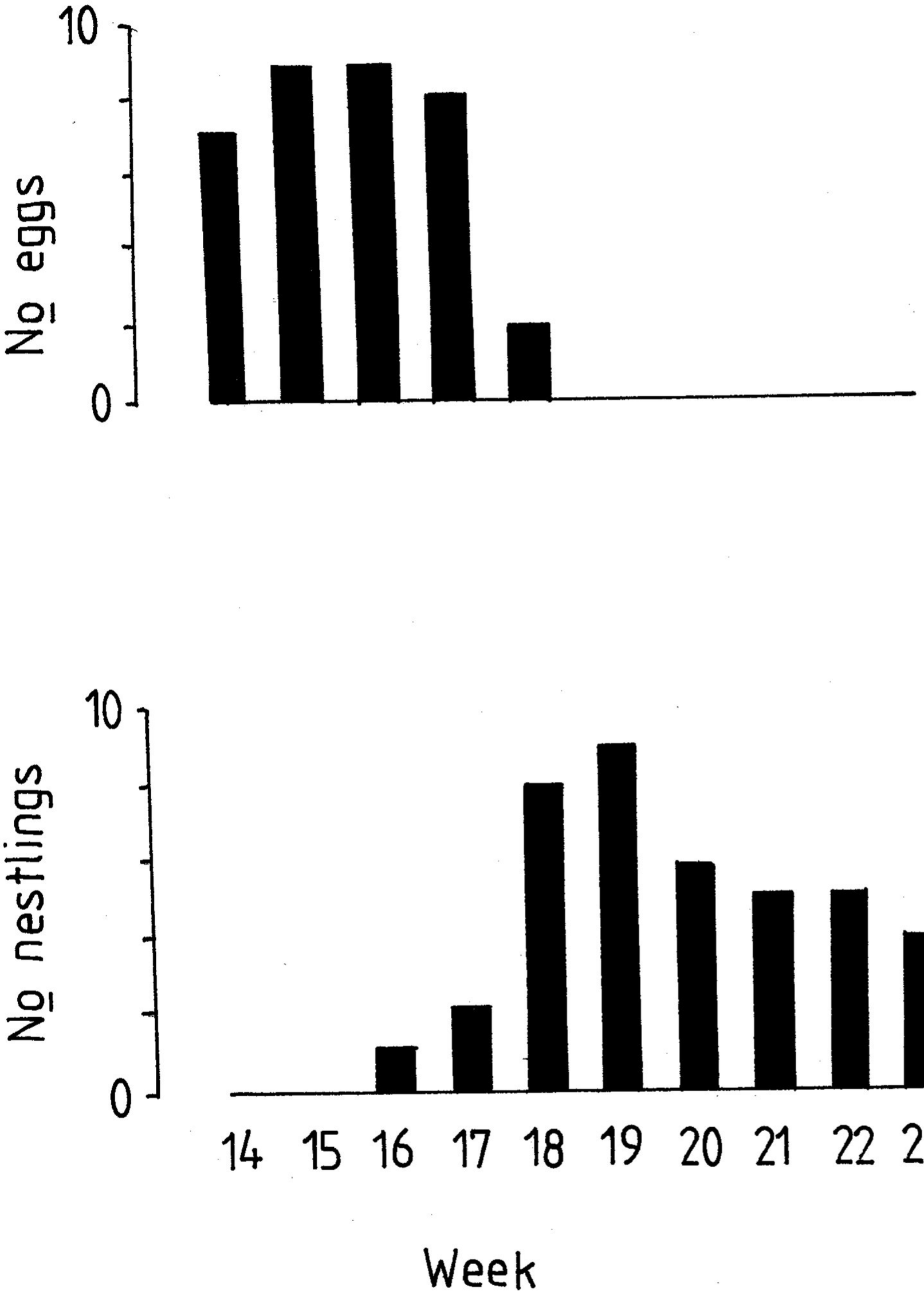


FIGURE 4.2. Number of Pallid Swift nestlings present at weekly intervals at the Museum colony during 1977 spring, summer and autumn.
Week 1 is the last week in April.

FIGURE 4.3. Number of Pallid Swift eggs and nestlings present at the Museum colony durin 1976 summer and autumn.

Week 1 is the last week of April.



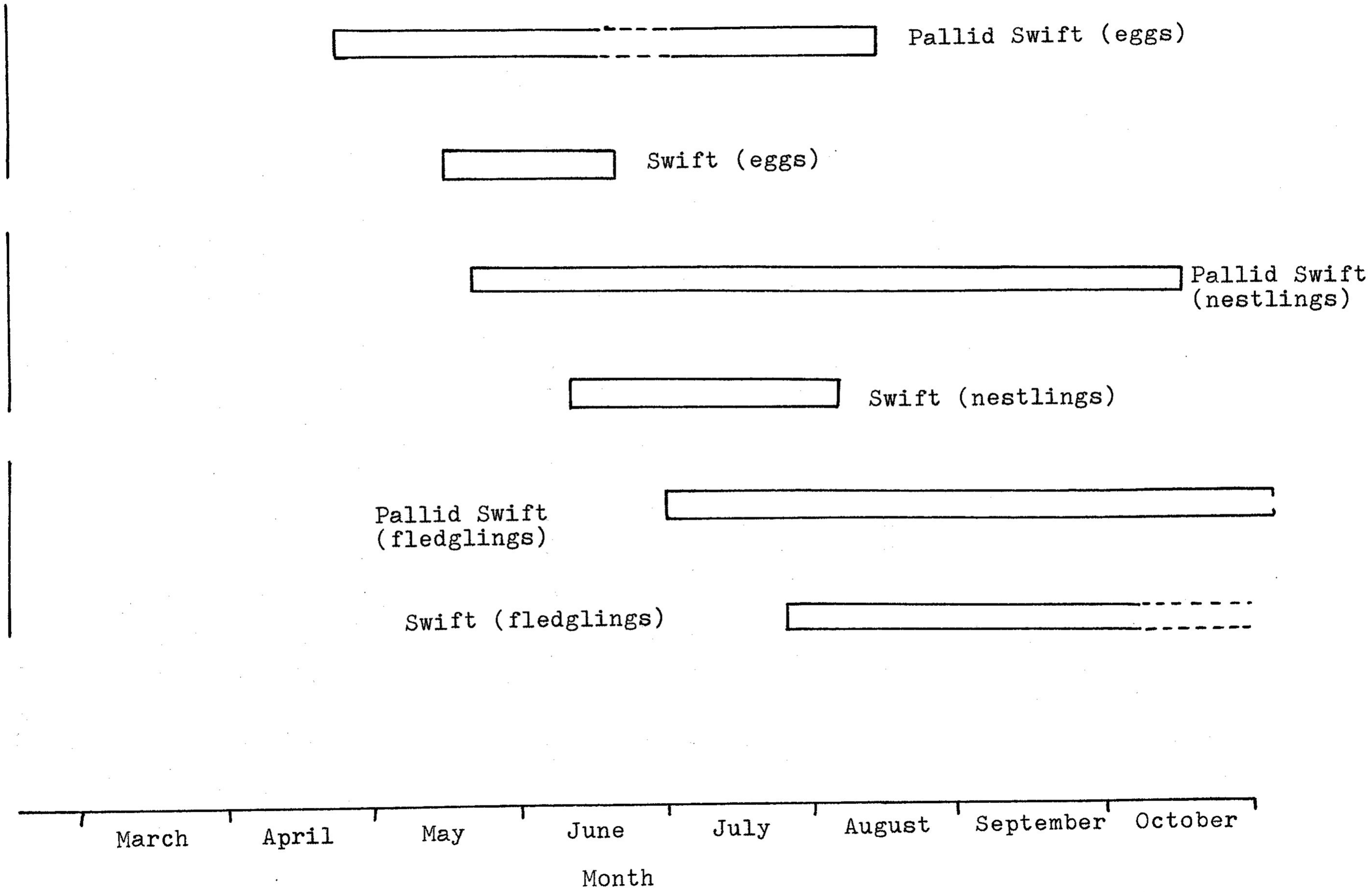


FIGURE 4.4. Main events in the breeding season of Swifts and Pallid Swifts at Gibraltar.

establish the breeding season of the Swift but adults with food balls were observed as late as 29th July, 1978 and young could be heard calling inside nests at the end of July in 1977 and 1978. Five young Swifts ringed at nests during the second week of July in 1977 had wing lengths corresponding to week 5 Pallid Swift young. Swifts must commence laying around the middle of May. As they arrive at Gibraltar in April, the period of pre-breeding activity is shorter than in the Pallid Swift.

4.3.2. The Moult

Adult Swifts have a single complete moult in the winter quarters (Niethammer 1938, de Roo 1966) and the process starts as soon as they arrive in Africa in mid-August (Herroelen 1953, de Roo 1966). The moult is slow and lasts between 6 and 7 months (de Roo 1966); most swifts take a long time to moult and this must be related to their aerial existence (Naik & Naik 1965). Most species which have been studied take from 6 to 8 months to moult the primaries (Medway 1962, Naik & Naik 1965, de Roo 1966). The migratory Chimney Swift Chaetura pelagica is said to moult in only 4 months (Johnston 1958).

Pallid Swifts remained much longer than Swifts on the breeding grounds and they commenced moulting while raising the second brood. The moult was suspended (Snow 1967) when they finished breeding and migrated south in October and November. The pattern is therefore very similar to that of the

Alpine Swift A.melba which starts moulting in the breeding grounds in june and interrupts the moult before migrating south in September (Stresemann 1965, in Naik & Naik 1965). The only difference is that the Alpine Swift is single-brooded (Bartels 1931, Arn 1945).

Of 38 adult Pallid Swifts examined at Gibraltar in July 4 were moulting primaries. Of 31 examined in August 8 were moulting primaries. A single adult examined in September was also in primary moult and one in October had renewed four primaries on each wing and had stopped moulting. No Pallid Swifts were found moulting before July. The moult was descendant, in contrast to the wing moult in other Apodidae (Stresemann 1963). In all cases the primaries which were moulted were numbers 9 and 10 (numbered ascendantly, Snow 1967). The bird which had moulted 4 primaries on each wing in October, had replaced numbers 7 to 10 on each wing. Most individuals were also moulting some body feathers but there was no evidence of tail moult.

Of 16 adult Swifts examined in July, only one showed any indication of moult (primary 10 at stage 3 on both wings) and none of the five examined in August were moulting. The 10th primary in some adult Swifts is moulted independently in the winter quarters in September and October (de Roo 1966). It is therefore possible for some Swifts to commence wing moult in southerly latitudes while ending the breeding season. Since they depart much sooner than

the Pallid Swifts, they moult much less of the plumage. Fewer individuals in the Swift population enter moult before migration than in the Pallid Swift population. Only 1 out of 29 adult Swifts at Gibraltar commenced moult before migrating (5.25%) but at least 14 out of 71 adult Pallid Swifts did so (24.56%). The figure for Pallid Swifts may be higher still as some of the ones not moulting in July may have entered moult later while still breeding. It must be very important for Pallid Swifts to be able to moult partly while breeding. Assuming the rate of moult is as in the Swift (indeed the adult trapped in October must have taken about 3.5 months to moult 4 primaries), then an individual starting the moult in mid-August would end it at the end of February or the middle of March. If it delayed the start of the moult until its arrival at the wintering grounds in November, then it would not be able to moult fully before the next northwards migration.

It is interesting that in the more southerly parts of its breeding range, the Pallid Swift arrives earlier in spring and leaves earlier in autumn than further north. In Tunisia, Pallid Swifts abandoned the colonies by the end of September (Castan 1955) and they arrive usually in North Africa in January (Heim de Balsac 1951). Further south, in the Canary Islands, they commence breeding as early as the first week in January and leave in September (Bannerman 1963). Occasionally they remain into the winter. At Gibraltar, they arrive in late February but do not

commence to breed until April; they leave in mid-October but some are about into November. In the south of France, the first birds arrive during the first week of April but most do so at the end of the month (Hue 1951). They remain nesting at this latitude into the middle of November (Affre & Affre 1967) and some may remain there all winter (Hovette 1972, Laferrere 1974).

Clearly then the south of France must be the limit of tolerance for this species if it is to be double-brooded. It would arrive so late further north that it would effectively have to be single-brooded, which is what the Swift does.

4.3.3. Movements

Swift movements in the Gibraltar area are complex. They can be divided into three broad categories.

1. Migration
2. Weather Movements
3. Foraging Movements

The first two types will only be treated briefly below. Because of their magnitude and duration these would repay more detailed study. Such a study could not be undertaken during the years at Gibraltar as it would have taken up most of the available time in the field, and it was not considered important

or relevant enough for this.

Massive movements of Swifts and smaller ones of Pallid Swifts and Alpine Swifts were in evidence during the spring (mainly in May) and in the autumn (mainly in late July and early August). The migration of the Swift was the most obvious because of the large numbers of birds involved. It was not always easy to decide whether swifts were migrating or whether the movements which were being observed were of local birds which were feeding. This was especially the case with the Pallid Swift which was less abundant as a migrant. The Swift usually formed huge flocks while on migration and these could rarely be confused with feeding groups. Pallid Swifts were seen moving north in March and April but there was no evidence of migration in May; Swifts started in late April and peaked in May. In autumn, Swifts passed from mid-July until October. Alpine Swifts often accompanied Swifts, especially in September. There was no notable Pallid Swift passage in autumn, but some were seen as late as the first week of November (Garcia Rua 1975).

The rate of passage of migrating Swifts was recorded on 6 occasions in spring and on 6 in autumn. The mean rate in spring was 9.98 birds/minute (s.d. 8.03) and in autumn it was 26.18 birds/minute (s.d. 15.95). The number of visible Swifts passing during 12 hours daylight (assuming a constant rate)

would therefore be 7,186 (2,556 - 11,815) in spring, and 18,849 (9,662 - 28,036) in autumn. These are crude measures and are probably underestimates. For example, on 3rd August, 1973 the rate of passage at Gibraltar was 10,000 Swifts per hour of daylight. In another part of the Strait in autumn, Garcia Rua (1975) counted 100,000 Swifts during the first hour of daylight on one day. Assuming a constant rate of passage for six weeks in the autumn, the number of Swifts entering Africa through the Strait per 1 kilometre of coastline would be 791,658 (405,804 - 1.18×10^6). The numbers of Swifts entering Africa in autumn are probably at least 150 millions (Moreau 1972). The number entering per kilometre of coastline should then be about 40,000, which is well below the figure for the Strait of Gibraltar. Even though the data are crude, they do suggest that a more detailed study of Swift migration is needed as there may be important concentrations in the area of the Strait of Gibraltar which will have to be explained.

At Gibraltar, visible Swift migration was confined to periods when winds blew from the west. In easterlies, groups of Swifts could be seen foraging over unusual places over the western slopes of the Rock, but these birds did not appear to move with the determination of others during westerlies. In periods when visibility is poor (as when easterlies prevail over Gibraltar) Swifts may not cross the Strait as readily as when conditions are good. The concentration of Swifts at Gibraltar in westerlies suggests some form

of downwind movement analogous to that of migrating soaring birds at Gibraltar (Finlayson et al. 1976) although the reasons may not be the same (Bernis 1951).

On several occasions in May 1977 and May 1978, there were large movements of Swifts over Gibraltar, but the birds were flying south. In all these cases the weather conditions were poor, either heavy rain or a sudden temperature drop, and so movements were probably similar to the weather movements performed elsewhere (Svardson 1950, Lack 1954, Udvardy 1954, Lack 1958 b). The movements at Gibraltar only took place in May as later on the weather was stable. The most spectacular movement of this kind took place on 19th May, 1977. There was a flow of cold air at Gibraltar from the north (rare even in winter) caused by an anticyclone over the Azores and a low pressure system over the Gulf of Lyon. Between 1830 and 1845 hrs 10,000 Swifts flew south over Gibraltar. By sunset, at least 20,000 Swifts had passed. As it became dark, many birds attempted to roost in buildings which were not used by the local birds (Lack 1956 a, Geroudet 1961).

Because of their relevance to resource partitioning, the local foraging movements of the swifts which nested at Gibraltar are considered in the next section.

4.4. RESOURCE PARTITIONING

Swifts are only present at Gibraltar for part of the year while they are breeding; they spend the rest of their time in the winter quarters in tropical Africa (Moreau 1972). Consequently, only mechanisms of resource partitioning which operate during the breeding season are described. Seasonal variations cannot be discussed.

4.4.1. Occupation of nest sites.

The Swift and the Pallid Swift nested in buildings and in old walls in Gibraltar and, in addition, the Pallid Swift and the Alpine Swift nested in caves and cliff ledges (Fig. 4.5., 4.6.). During the period May to July 1978, the entire town was surveyed and the distribution of colonies of the two species was plotted on a 1 : 2500 scale map of Gibraltar. Any group of swifts which nested in close proximity (e.g. in same cave or same building) and in which all the members appeared to forage together was considered a colony. Cliff colonies were included in the survey. Although it is unlikely that all the colonies at Gibraltar were found, a large proportion must have been, as each building in the town was checked on several occasions in the morning and in the evening. In all, 114 Pallid Swift colonies and 58 Swift colonies were found. The following data were

FIGURE 4.5. Distribution of Swift nesting colonies at Gibraltar in 1978.

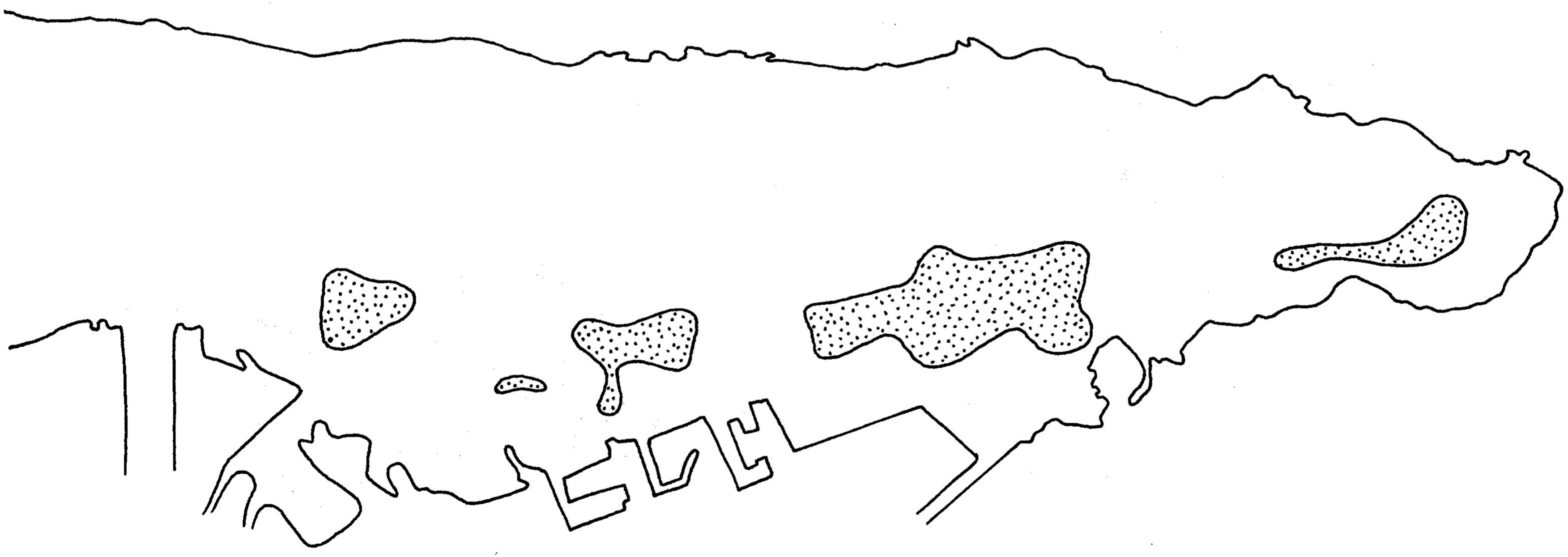
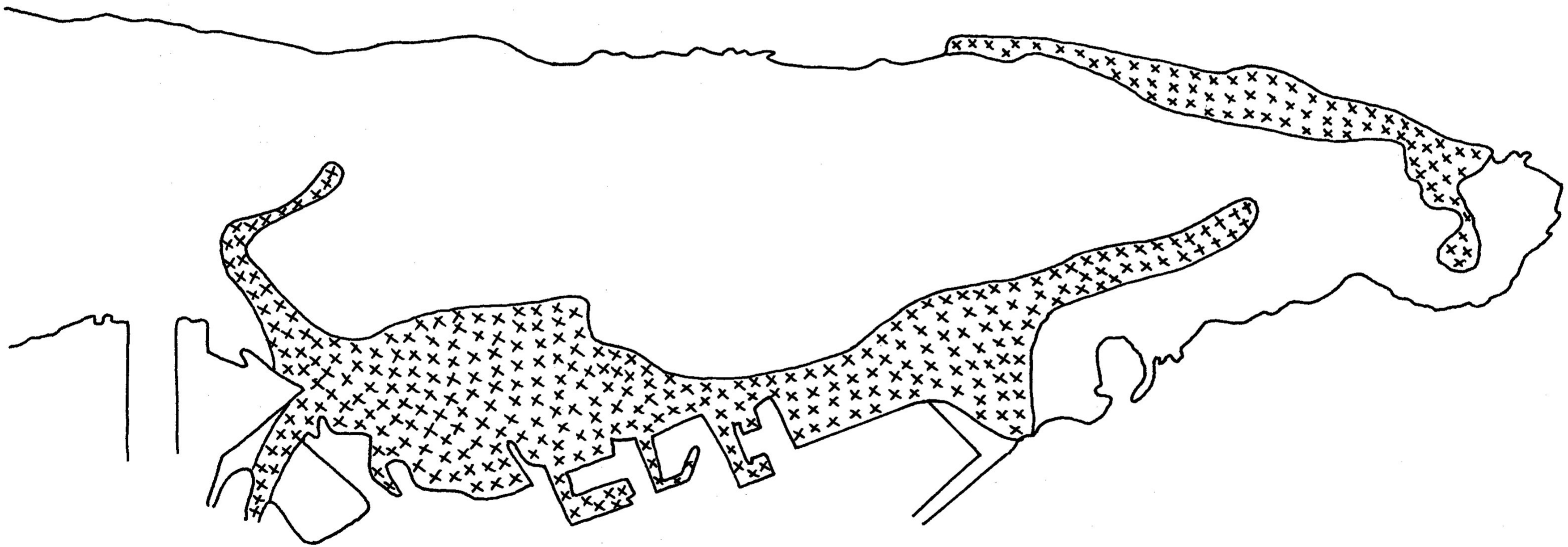


FIGURE 4.6. Distribution of Pallid Swift nesting colonies at Gibraltar in 1978.



were gathered at each colony : approximate size of colony (number of pairs), altitude, horizontal distance from the sea, true distance from the sea (from altitude and horizontal distance), orientation, type of nest site, height above the ground, and approximate age of the building.

The distribution of the nesting colonies of the two species are given in Figs. 4.5., and 4.6. The Swifts had a more fragmented distribution than the Pallid Swifts and they overlapped relatively little in the areas that they occupied. Extending the argument used in 3.4.10 for the amount of overlap in breeding territories of the Sylvia warblers, the nature of the overlap, whether more or less than random expectation, can be obtained. The areas were divided into 12.5 X 12.5 metre squares and each square was scored for presence or absence of the two species. The difference between the observed and expected values was highly significant ($X_1^2 = 5.90$ $p<0.05$). Pallid Swifts overlapped with Swifts on 43.24% of the squares, but they ought to have overlapped on 66.37% of the squares. Swifts overlapped with Pallid Swifts on 14.35% of the squares, but they were expected to overlap on 22.02% of these. The mean spatial overlap between the two species was 0.29. The mean habitat (= nesting site) overlap, calculated from the 5 values in Table 4.5 (see later) was 0.84. By subtraction, then 0.55 of the separation cannot be accounted for by differences in habitat occupation.

It is probably due to behavioural interaction between the two species (4.4.5.).

What are the differences in the types of nesting sites used by the two species ?

Age of Buildings

Colonies of Swifts are located in the old town (Appendix 4) but those of Pallid Swifts extend more into the modern parts of the town and into natural sites. Some of the buildings in which swifts had colonies could be divided according to age of construction into 20th Century or pre-20th Century. Of 82 Pallid Swift colonies in buildings of approximate known age, only 19 (23.17%) were in pre-20th Century buildings, but of 36 Swift colonies, 29 (80.56%) were in pre-20th Century constructions. Colonies in walls were also included. The difference between the two species is highly significant ($X_1^2 = 34.16 \quad p < 0.001$).

Distance from the sea

The mean distance from the sea of Swift colonies was 274 $\pm$ 109 metres, and for Pallid Swift it was 240 $\pm$ 159 metres (Fig. 4.7., Table 4.2. a). There were therefore no significant differences between the two species.

Altitude

Swift colonies were situated on higher ground than Pallid Swift colonies (Fig. 4.8., Table 4.2. b).

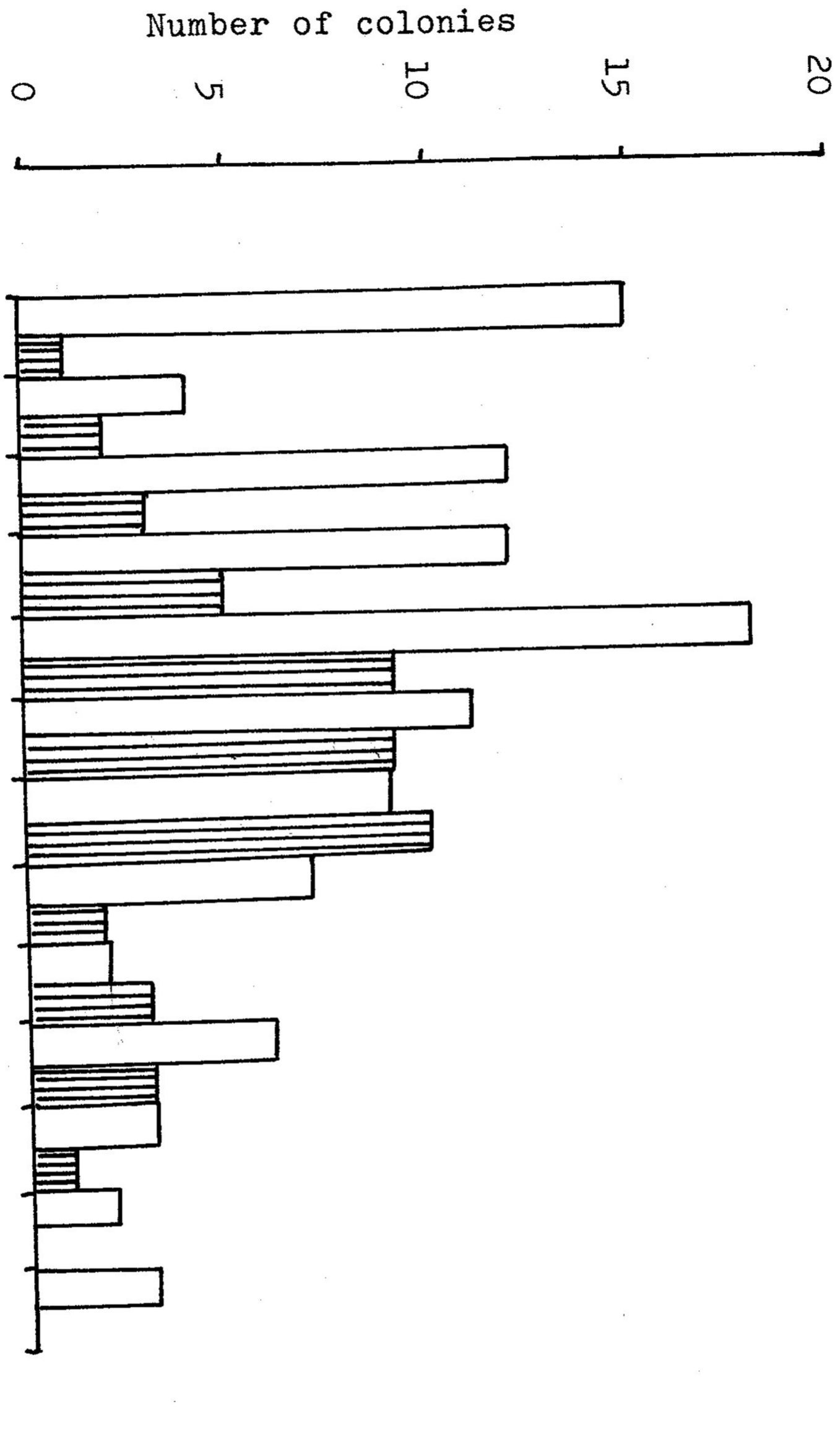


FIGURE 4.7. Distribution of Pallid Swift (unshaded bars) and Swift (shaded bars) nesting colonies at various distances from the sea at Gibraltar.

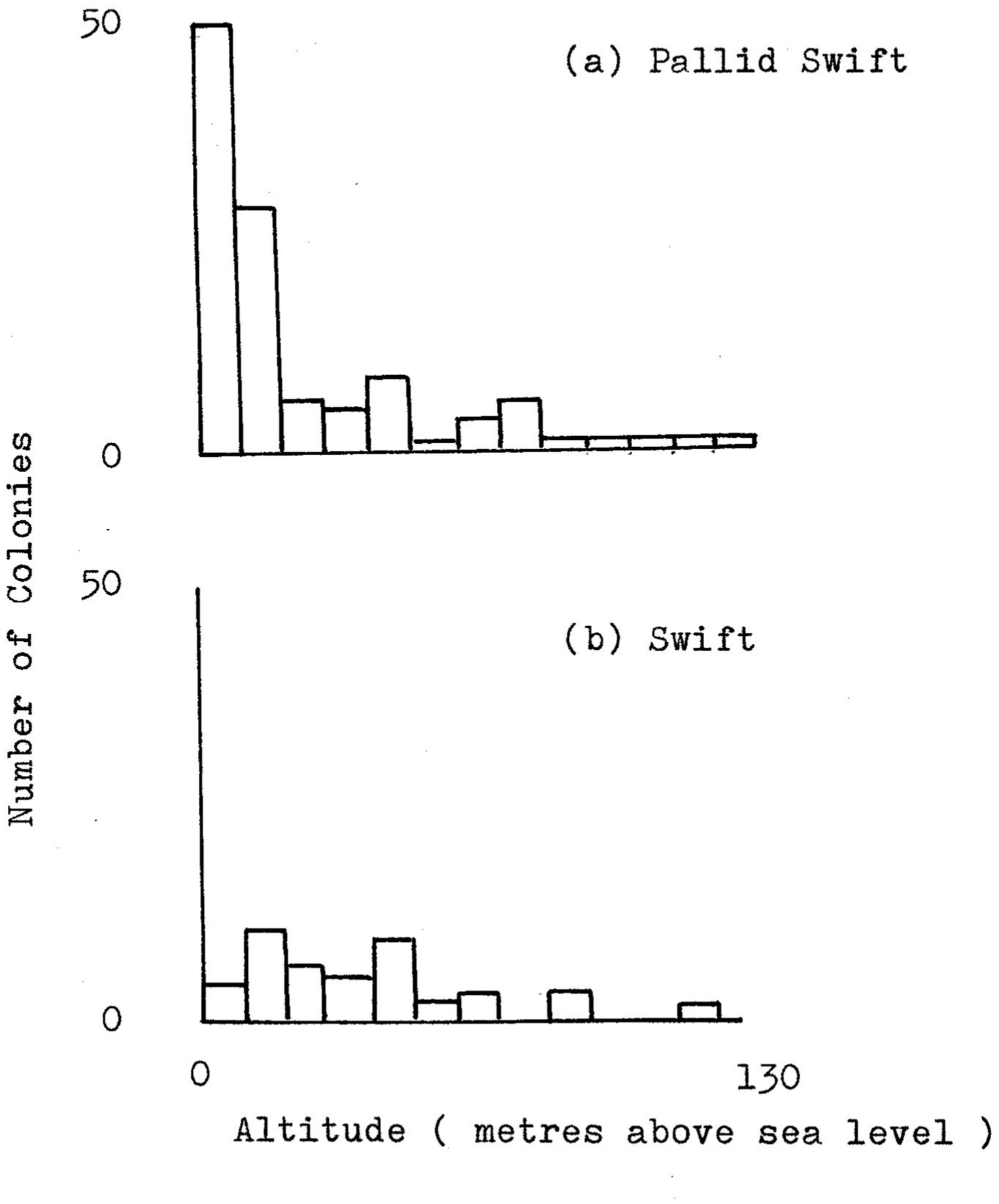
TABLE 4.2. Position of Pallid Swift and Swift nesting colonies in relation to distance from the sea and altitude above sea level.

(a) Distance from sea (metres)

Distance	Proportion	
	Pallid Swift	Swift
0 - 49	0.14	0.02
50 - 99	0.04	0.04
100 - 149	0.12	0.06
150 - 199	0.12	0.10
200 - 249	0.17	0.19
250 - 299	0.11	0.19
300 - 349	0.09	0.21
350 - 399	0.07	0.04
400 - 449	0.02	0.06
450 - 499	0.06	0.06
500 - 549	0.03	0.02
550 - 599	0.02	0.00
600 - 649	0.03	0.00
(b) Altitude		
0 - 9	0.44	0.08
10 - 19	0.26	0.21
20 - 29	0.05	0.15
30 - 39	0.04	0.15
40 - 49	0.07	0.23
50 - 59	0.01	0.04
60 - 69	0.03	0.06
70 - 79	0.05	0.00
80 - 89	0.01	0.06
90 - 99	0.01	0.00
100 - 109	0.01	0.00
110 - 119	0.01	0.02
120 - 129	0.01	0.00

Sample sizes : Swift, altitude = 48, distance = 48
Pallid Swift, altitude = 113, distance = 104.

FIGURE 4.8. Distribution of Pallid Swift and Swift nesting colonies with altitude at Gibraltar.



The mean altitude of Swift colonies was 36 $\pm$ 23 metres and of Pallid Swift colonies it was 23 $\pm$ 27 metres. Although the differences are significant, it seems unlikely that highly mobile species like swifts should segregate by altitude, when the differences are only of a few metres. The old town is situated on higher ground than the rest of the town of Gibraltar and the altitude difference may be a reflection of the difference in the ages of the buildings chosen.

Height

There was no difference in the heights of the constructions occupied by the two species for nesting in. Swifts nested 6 $\pm$ 3 metres above the ground and Pallid Swifts nested 6 $\pm$ 2 metres above the ground (Table 4.3.).

Orientation

There was no difference in the orientation of the colonies of the two species (Table 4.4. a). The commonest type was the colony with west-facing entrances and the least so was that with north-facing entrances. Little can be concluded from this as there is no data on the availability of each kind of entrance. The difference between the two species was not significant ($X^2_3 = 7.54$ $p > 0.05$).

Position of nests

Nests were placed in a variety of sites. The main

TABLE 4.3. Height of colonies of Pallid Swifts and Swifts in Gibraltar.

Height (m)	proportion	
	Pallid Swift	Swift
1	0.01	0.00
2	0.02	0.09
3	0.14	0.09
4	0.17	0.23
5	0.13	0.13
6	0.12	0.15
7	0.17	0.09
8	0.13	0.09
9	0.09	0.11
10	0.01	0.00
11	0.00	0.00
12	0.00	0.04

Pallid Swift N = 92. Swift N = 47

TABLE 4.4. Location of Pallid Swift and Swift nesting colonies in relation to building orientation and position of the nests.

(a) Building Orientation

Orientation	Pallid Swift	Swift
North	0.07	0.10
South	0.24	0.28
East	0.27	0.09
West	0.41	0.53

(b) Position of Nests

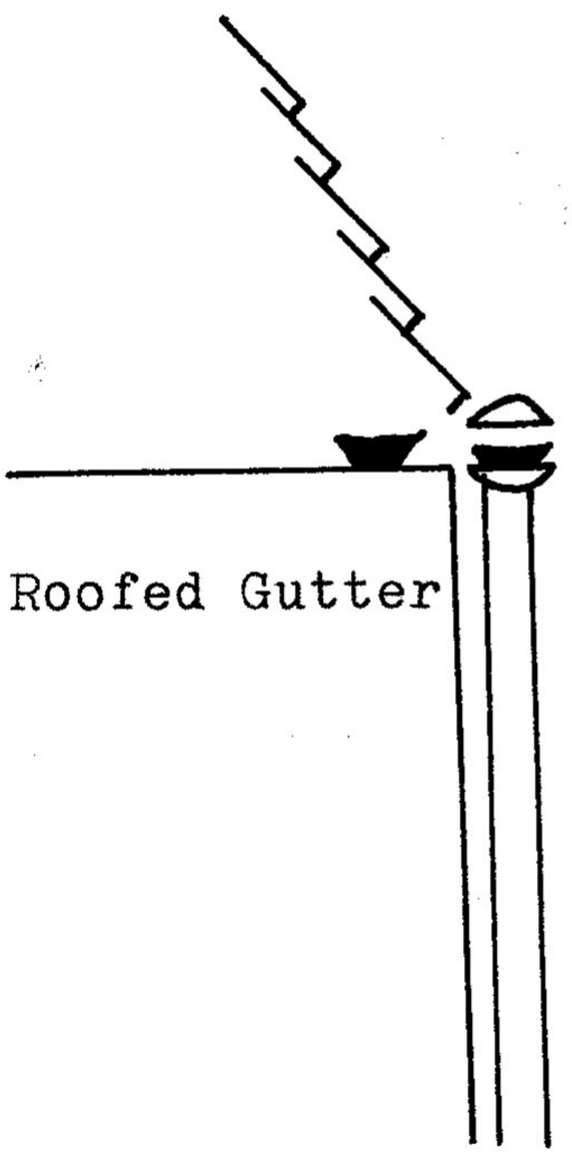
Position	Pallid Swift	Swift
under gutters	0.07	0.08
under eaves	0.70	0.63
holes in walls	0.03	0.27
holes in buildings	0.12	0.02
caves & cliffs	0.07	0.00

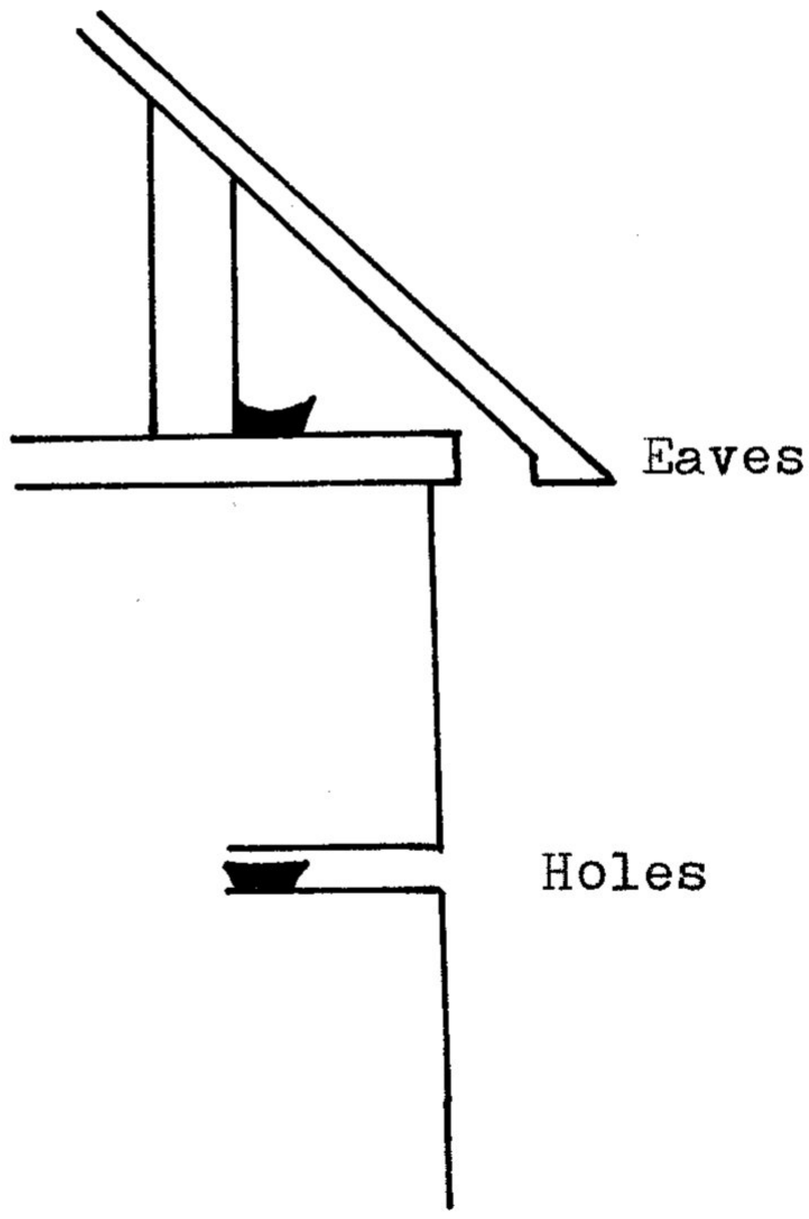
All values are proportions.
Sample sizes: Pallid Swift orientation = 114, position = 58, Swift orientation = 58, position = 48.

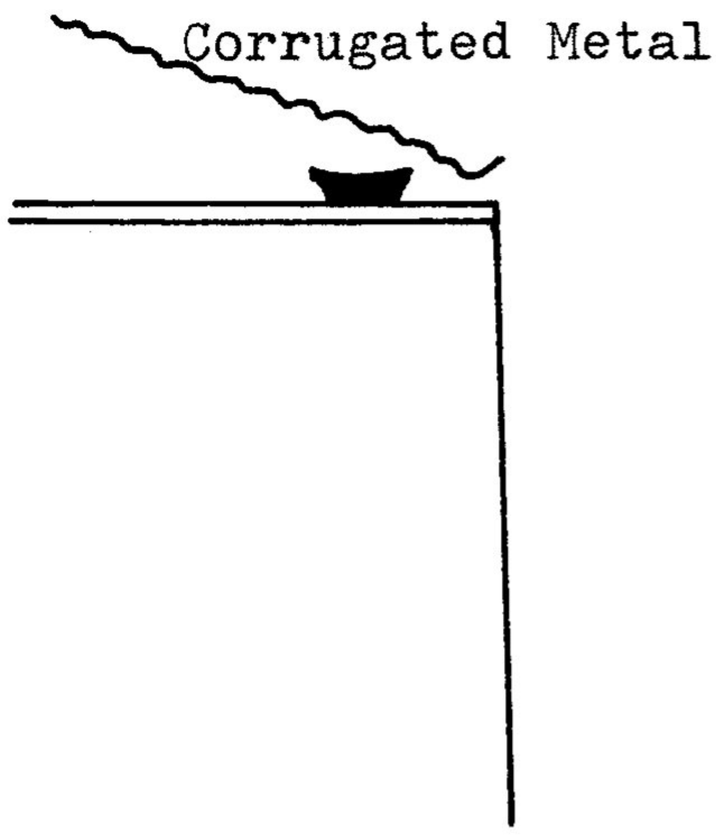
ones are summarised in Table 4.3 b and Fig. 4.9. If the data are lumped into (1) under guttering /under eaves and (2) holes, then the differences are significant. Natural sites have been ignored because X^2 values are then below 5 (for expecteds). For the (1)/(2) comparison $X_1^2 = 8.13$ $p < 0.01$. Only Pallid Swifts nested in natural sites. The earlier difference of age of buildings could be in part due to the different preferences in nest sites.

Colony Sizes

It was not possible to count the exact number of nests in each breeding colony as this would have been very time-consuming and anyway inaccurate. The approximate colony size was estimated; colonies were divided into small ones (with less than 10 pairs) and large ones (over 20 pairs). Intermediate ones were ignored because the method was not accurate enough to make the distinction possible. Of 92 Pallid Swift colonies, 44 (47.83%) were small, and of 46 Swift colonies, 14 (30.43%) were small. The difference is not statistically significant ($X_1^2 = 3.80$ $p > 0.05$). From these data, the breeding populations of the two species at Gibraltar have been estimated roughly at 2,030 pairs of Pallid Swifts and 1,110 pairs of Swifts. The true values are probably between 2,000 and 2,500 Pallid Swift pairs, and between 1,000 and 1,500 Swift pairs.







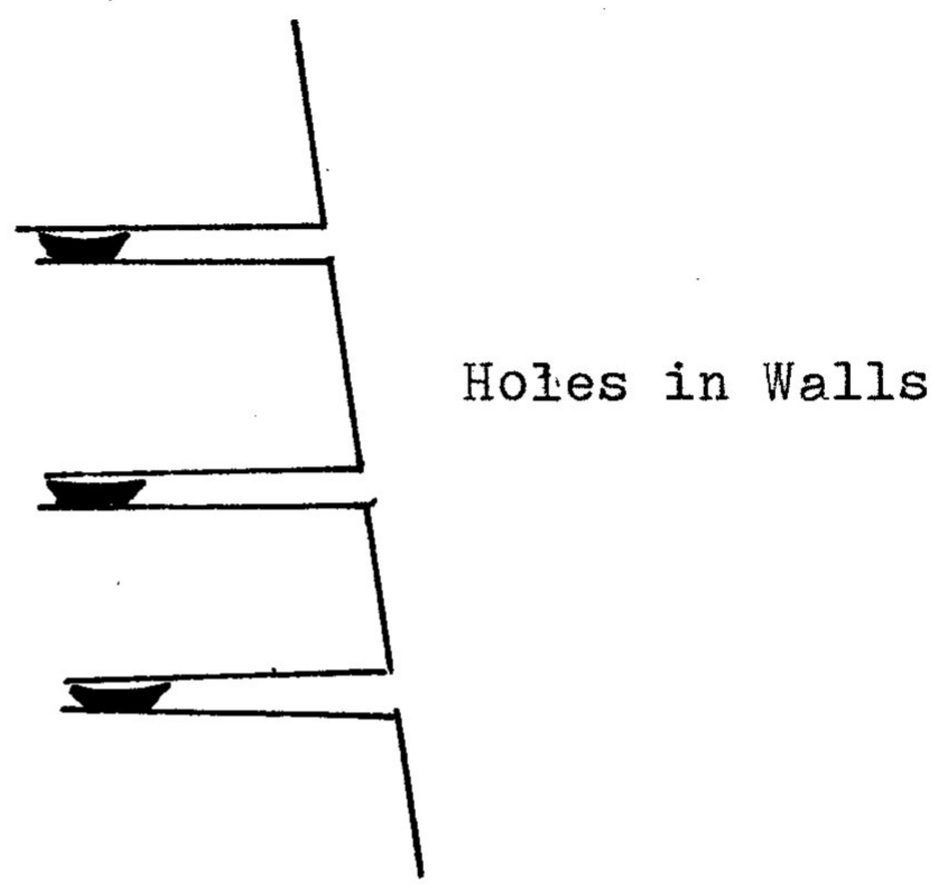


FIGURE 4.9. Types of nesting sites used by town-dwelling Pallid Swifts and Swifts at Gibraltar.

TABLE 4.5. Overlaps and nest site Niche Breadth for Swift and Pallid Swift at Gibraltar.

Dimension	Niche Breadth	
	Pallid Swift	Swift
colony orientation	3.29	2.65
altitude	3.65	6.35
distance	9.07	7.09
height	7.45	7.23
position	1.94	2.10

	Niche Overlap
colony orientation	0.93
altitude	0.59
distance	0.83
height	0.92
position	0.92

4.4.2. Foraging areas

The two species foraged in a similar way. In the early morning and late evening, most of the foraging was done near the colony; during the middle of the day the swifts flew north and west into the Spanish hills to feed. Early in the season, in February and March, Pallid Swifts formed noisy groups over Gibraltar in the mornings and these groups gradually moved into Spain as the day advanced. They could be seen returning late in the evening. Later in the season, once the young had hatched, there was a daily exodus of breeding adult swifts into Spain in mid-morning and a large return in the evening. During the middle of the day these birds moved to and from the foraging grounds and the colonies. On calm mornings feeding activity lasted longer near the colony; on calm evenings the return to feed near the colony was earlier.

Since Gibraltar is a small peninsula which protrudes into an area of sea where strong winds from east and west prevail, it is likely that large concentrations of aerial arthropods are only to be found when conditions are calm and the arthropods are not blown out to sea. When winds are strong it is probably best for swifts to feed over the mainland.

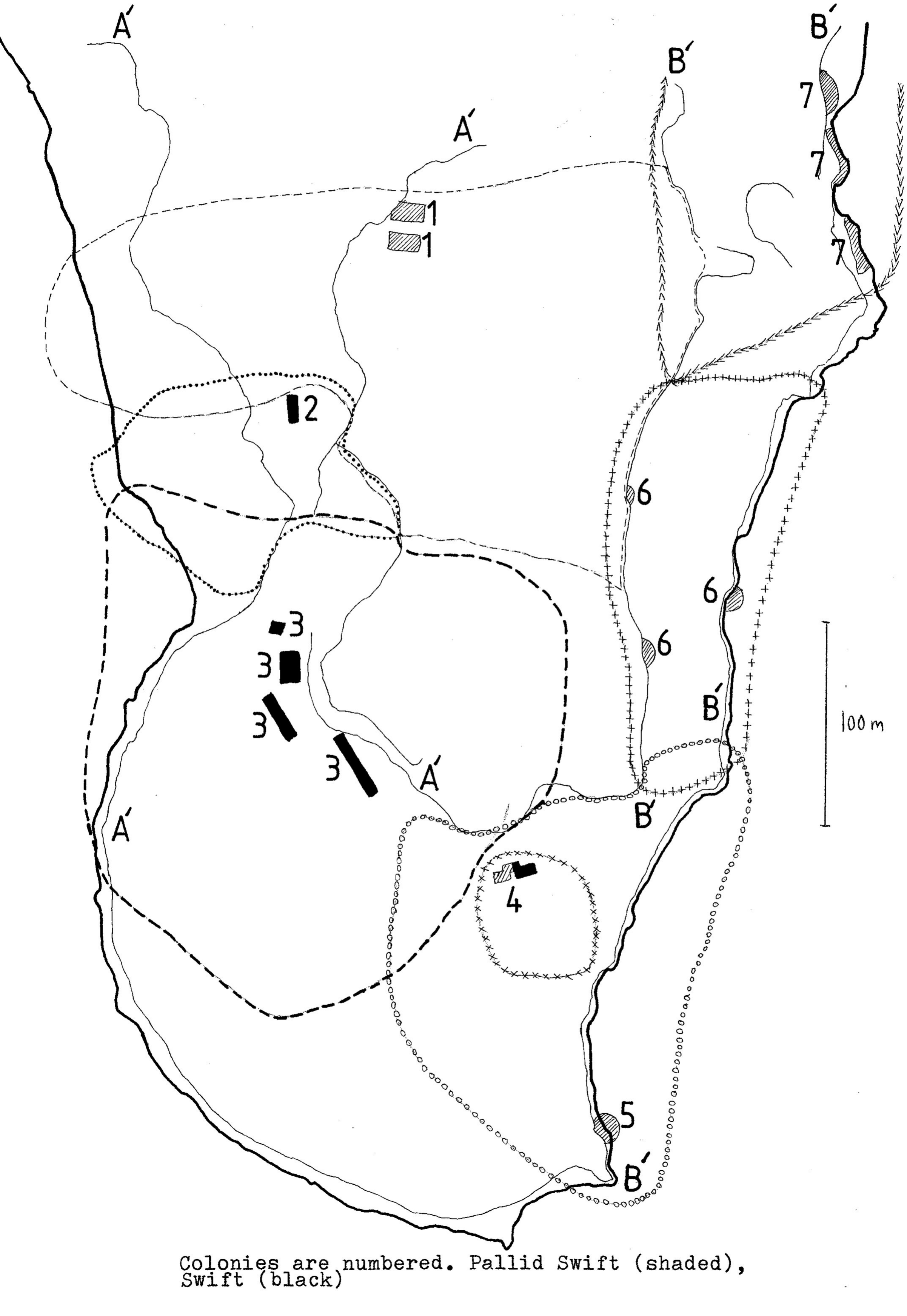
Foraging behaviour near the nesting area

Swifts and Pallid Swifts foraged around their colonies

in the morning and in the evening. A small area, centred over Windmill Hill (Fig. 1.2.) was studied in July 1978. This area was chosen because it had colonies of the two species (including Pallid Swift colonies in cliffs, caves and buildings) but at a lower density than in the main town area. Groups belonging to different colonies could therefore be followed easily. It was also the most southerly area in Gibraltar and was surrounded by sea on three sides, making it a very windy area. In calm weather, large clouds of Swifts and Pallid Swifts foraged noisily over the entire area (Fig. 4.10.). Groups could be separated easily and their colonies could be identified by following individuals for long periods, as they eventually returned to their nests. When winds blew from the west, birds from colonies 4 to 7 foraged in large groups over the sea to the east of the study area, and those from colonies 1 to 3 foraged along the tops of the west - facing cliffs (line A' - A', Fig. 4.10.). Those from colonies 4 to 7 were presumably taking arthropods which were being blown out to sea, and the others must have been taking ones concentrated by the westerlies blowing onto the cliffs. In easterlies birds from colonies 4 to 7 foraged along the tops of the east-facing cliffs (B' - B', Fig. 4.10.) and they were sometimes joined by birds from colony 1. Those from colonies 2 and 3, and sometimes 1, foraged over the sea to the west of the study area.

The foraging areas around the colonies appear

FIGURE 4.10. Main foraging areas near the colony of Swifts and Pallid Swifts nesting in the Windmill Hill area. See text for details.



Colonies are numbered. Pallid Swift (shaded), Swift (black)

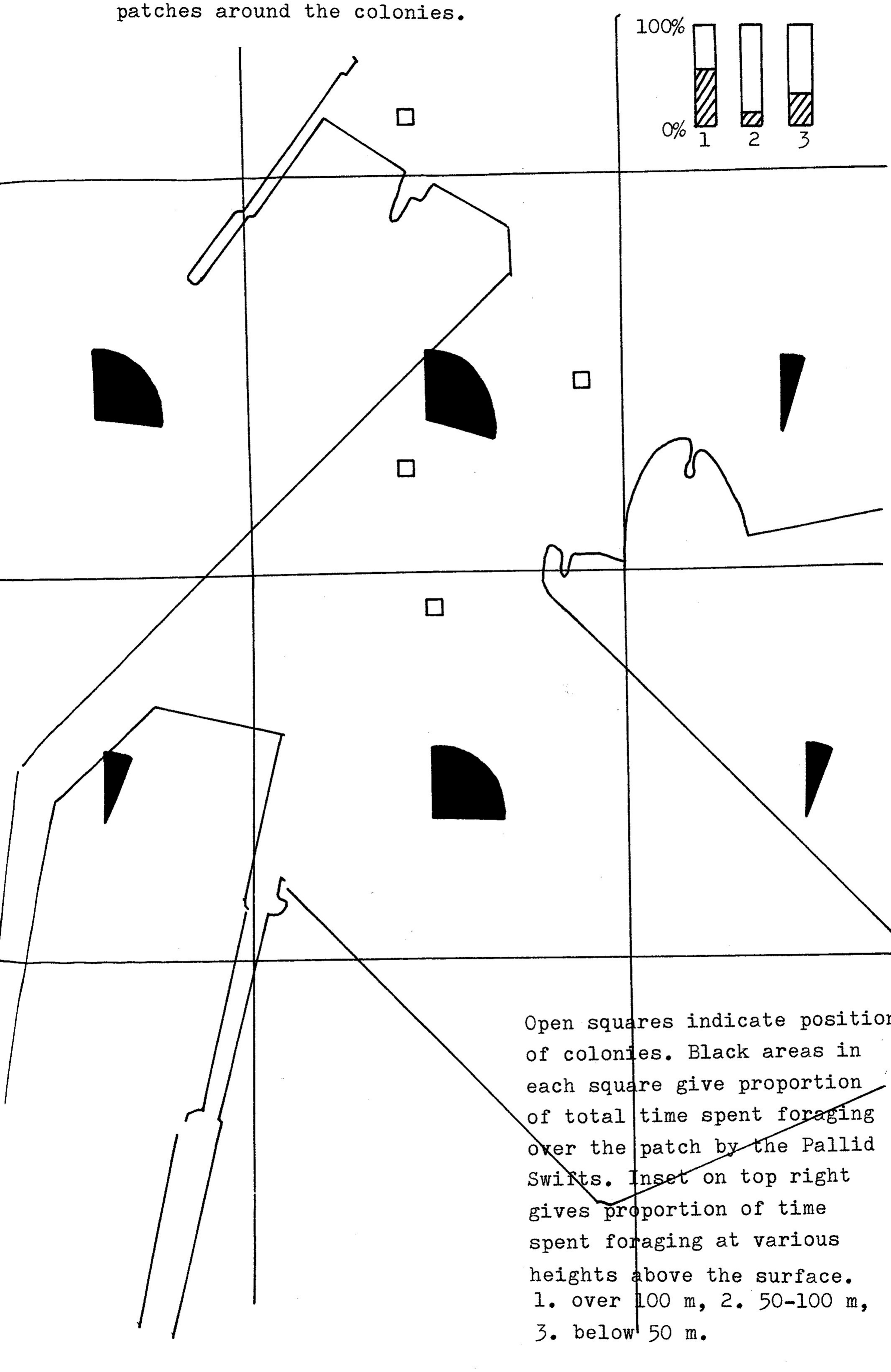
to be exclusive (Fig. 4.10.). This is even greater than appears because the colonies are separated by altitude as well. Pallid Swifts from colony 1 foraged along the top of the cliff line A' - A', but the Swifts from colony 2 did so below the same cliff line.

In the centre of the town, colonies were tightly packed and it was difficult to observe the foraging areas of the different groups. Despite the apparent chaos, groups which were followed appeared to remain together and separate from other groups.

Swifts foraged unevenly over any area. Within their foraging area, there must have been concentrations of food and presumably the swifts concentrated their activity on such patches. From the food the two species took, there is strong evidence that they frequently took swarming insects, particularly social Hymenoptera (4.4.4.). Swifts did not remain over any one patch all the time presumably as the disturbance caused by the flock would deplete the insect supply. The behaviour of the flock within an area was to move around the area, allocating more time to certain patches, those which presumably had more food (Fig. 4.11.). The average time taken for a group to return to forage over the same 100 X 100 metre patch was estimated at 38.9 $\pm$ 18.7 seconds for Swifts, and at 27.3 $\pm$ 19.0 seconds for Pallid Swifts.

. Nevertheless,

FIGURE 4.11. Amount of time spent foraging in 1 hectare patches around the colonies.



Open squares indicate position of colonies. Black areas in each square give proportion of total time spent foraging over the patch by the Pallid Swifts. Inset on top right gives proportion of time spent foraging at various heights above the surface. 1. over 100 m, 2. 50-100 m, 3. below 50 m.

TABLE 4.6. Occupation of 100 X 100 metre Squares by swifts at Gibraltar.

Number of birds in patch	Number of times Observed	Expected	
0	358	168.46	
1	60	210.58	
2	58	131.61	
3	21	54.84	
4	19	17.14	
5	13	4.28)	
6 ++	59	0.89)	5.17

Pallid Swift & Swift data combined.

$X^2_5 = 1247.07$ $p < 0.001$

Expected calculated from Poisson distribution

for large patches individual birds were rarely seen on their own. Large patches were unoccupied for long periods and were occupied during the rest of the time by flocks. Although the differences were not quite significant, flocks of Swifts appeared to be larger than those of Pallid Swifts for colonies of similar size. Thus for colonies with about 30 pairs, the average flock size for Swift was 8.53 $\pm$ 4.6 birds, whereas for Pallid Swift it was 7.29 $\pm$ 3.86 birds. Within feeding flocks, Swifts appeared to be more spaced out than Pallid Swifts. The average duration between observed contacts between individuals within a foraging group was 37.17 $\pm$ 20.68 seconds for Pallid Swifts, and 73.42 $\pm$ 79.07 seconds for Swifts. Flock size was related to duration in 100 X 100 metre patches (Figs. 4.12., 4.13.). The larger the flocks, the longer they remained in an area and the longer the individuals in the flock remained.

Foraging behaviour away from the nesting area

It was not possible to observe the behaviour of swifts over the Spanish hinterland in detail but some observations in the vicinity of Gibraltar suggested that large concentrations occured along the edges of woods, along hill tops, etc (Lack 1956 a). There is also some evidence of large concentrations of Swifts at the western end of the Strait during strong easterly winds (Garcia Rua 1975). By observing swifts from the northern end of Gibraltar (Figs. 1.2., 4.14.), some

FIGURE 4.12. Relationship between Flock Size and Amount of time spent over a 1 hectare patch by the flock.

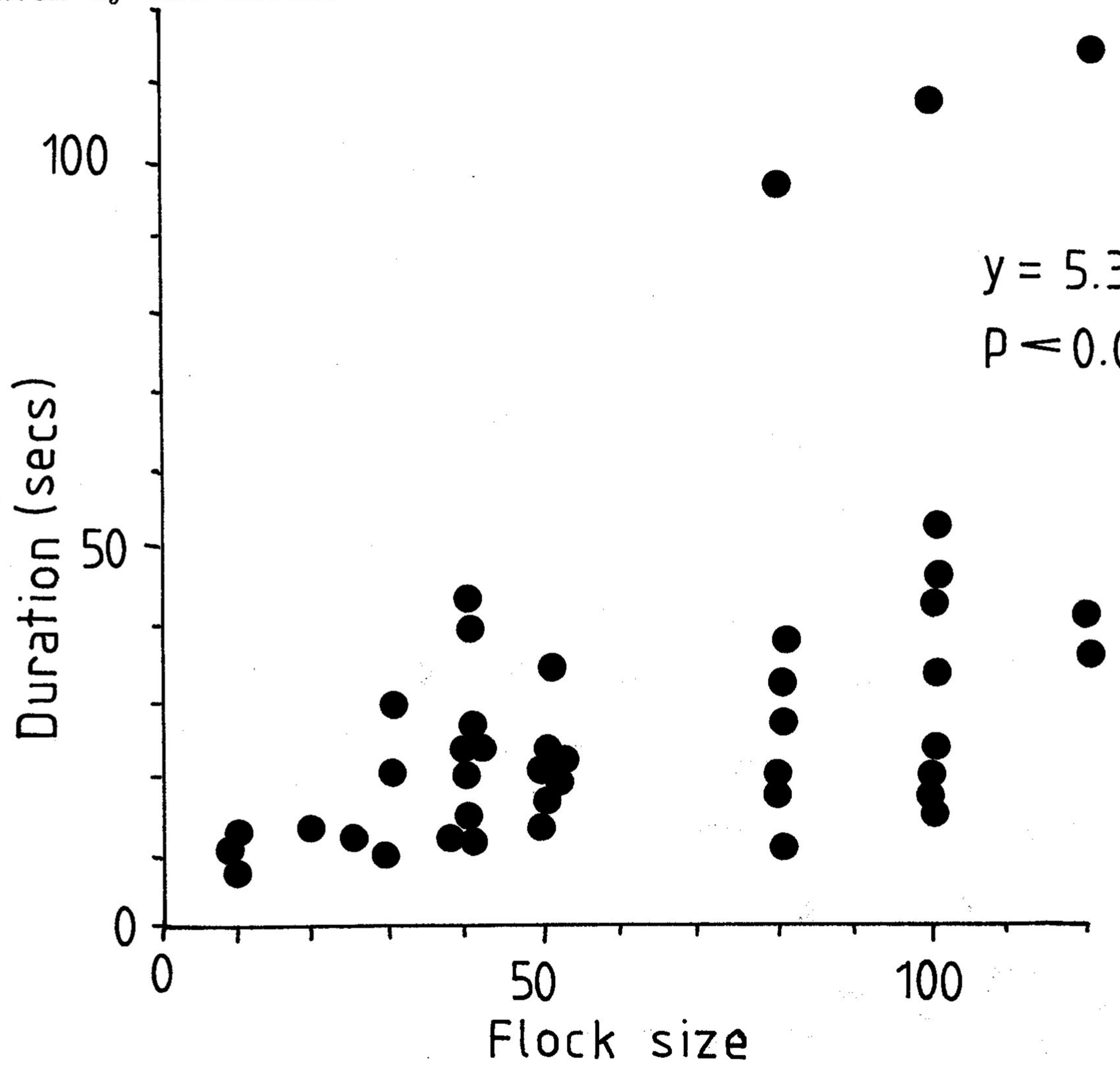


FIGURE 4.13. Relationship between Flock Size and Amount of time spent over a 1 hectare patch by individuals in the flock.

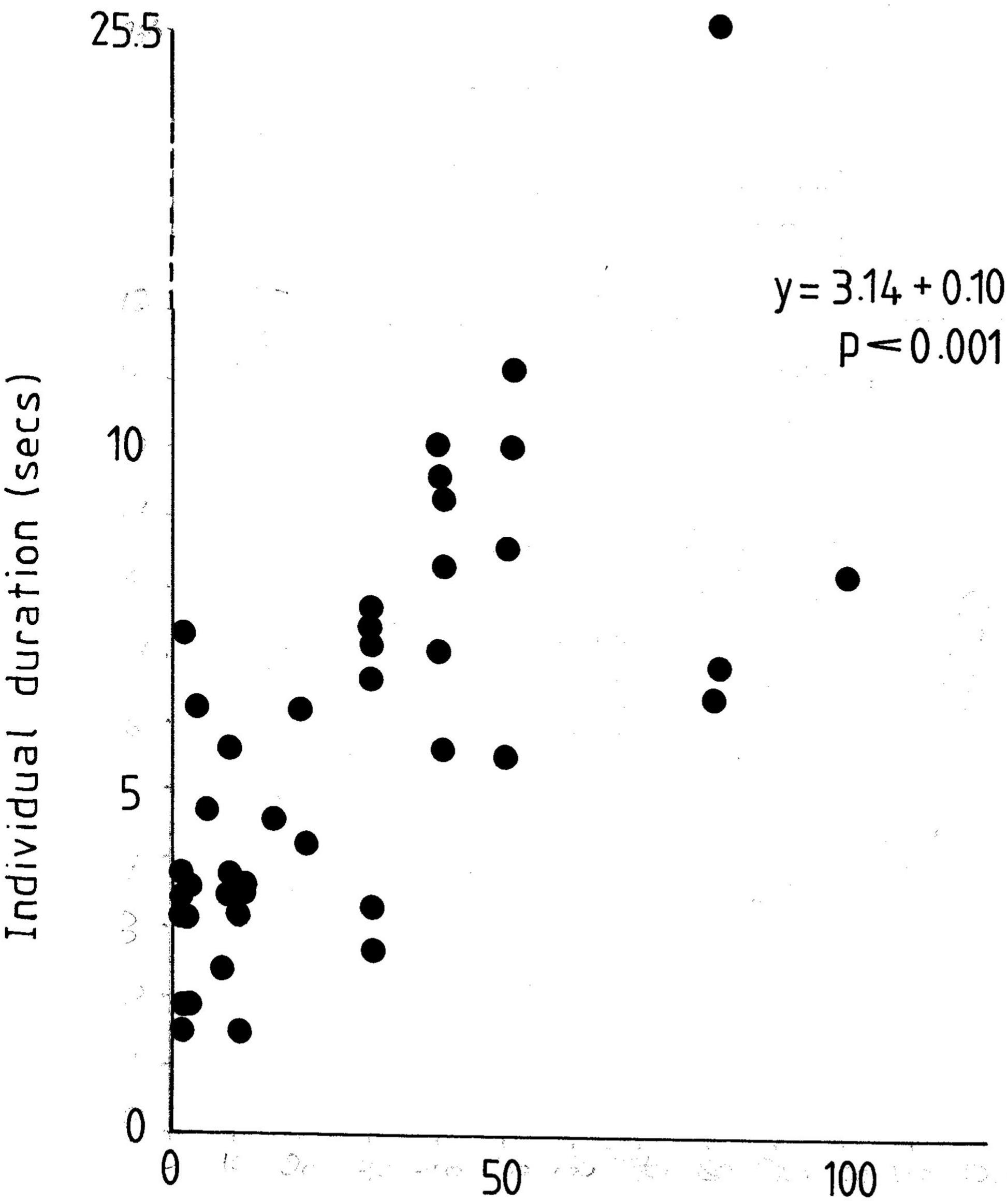
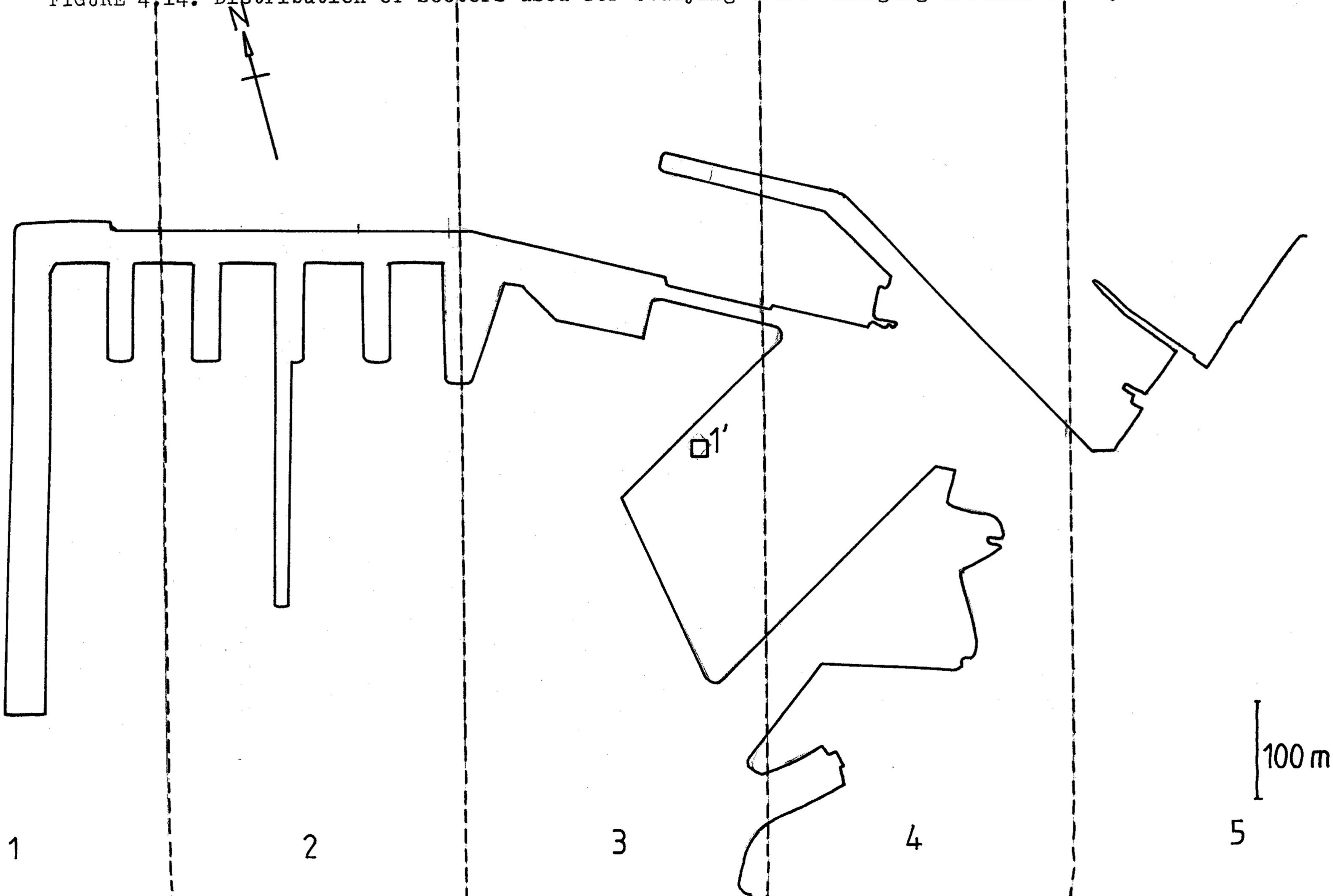


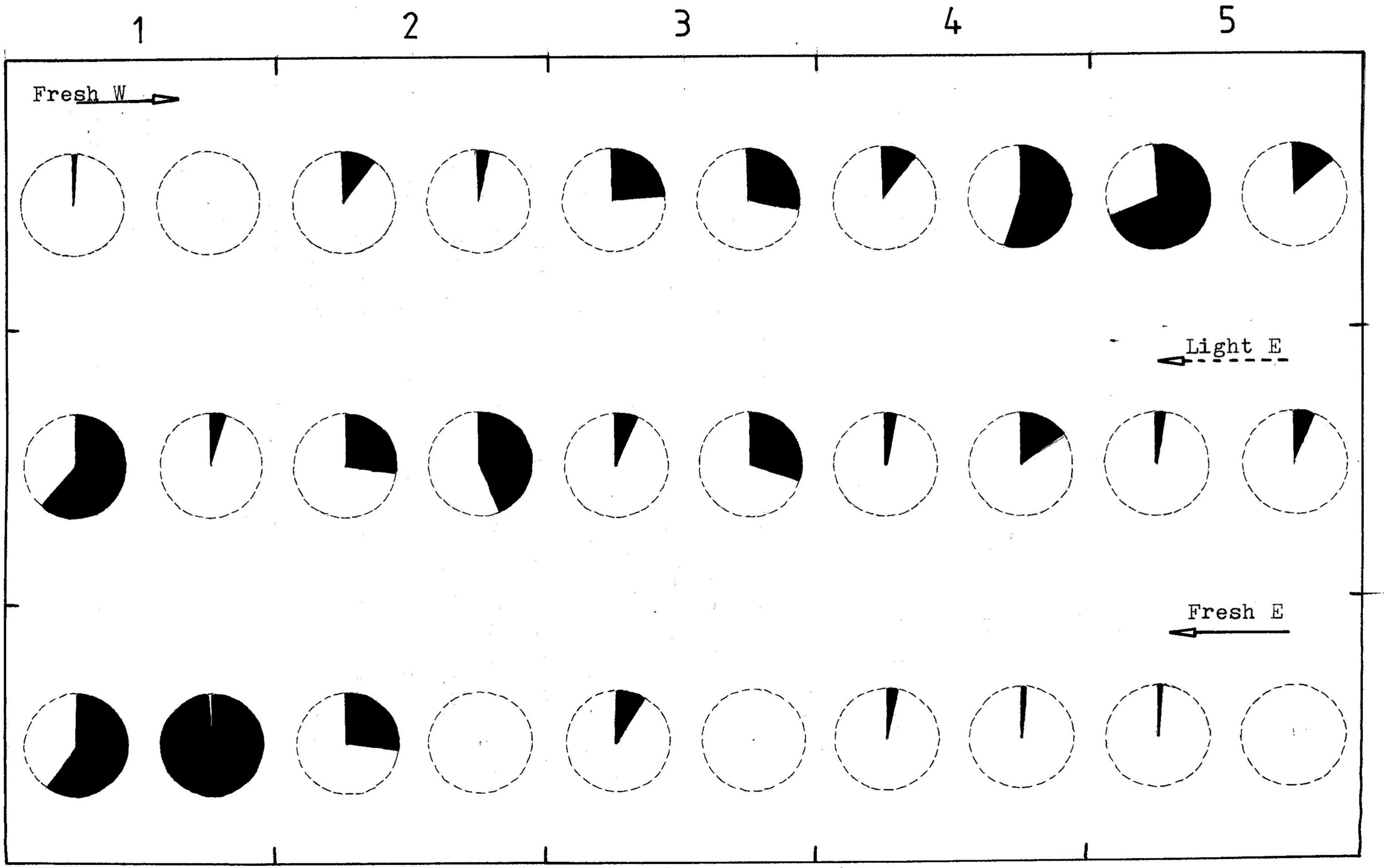
FIGURE 4.14. Distribution of sectors used for studying swift foraging movements away from the colonies.



idea was obtained of their behaviour in different wind conditions. Observations made in other parts of Gibraltar confirmed that all the birds from the town (even those at the extreme south) flew north along the Gibraltar peninsula and into Spain over the observation site. The Pallid Swifts nesting in caves at the eastern side of Gibraltar flew north over the eastern side of Gibraltar and sometimes they approached these colonies from the north-east (Fig. 4.6.).

The movements of the town swifts were influenced by prevailing winds (Fig. 4.15.) Data for the two species have had to be lumped as many of the distant birds seen could not be identified . The area around the observation point was divided into five sectors, from west to east , and these covered the whole of the swift flypath (Fig. 4.14.). The numbers of swifts moving north into Spain over each of these sectors depended on prevailing winds. West and east winds prevailed and caused swift concentrations at the downwind sectors (Fig. 4.15.). In calm weather, swifts flew over the central parts of the area. This behaviour must lead swifts to where the aerial plankton is densest (Lack 1956 a). The swift concentrations may be the result of an active process or they may be due to the birds drifting with the wind. Since the route used to return to the colonies appears to be different from that used to leave the colonies in the same winds, it is probable that swifts actively chose downwind areas to feed in.

FIGURE 4.15. Distribution of swifts in different sectors depending on wind conditions.



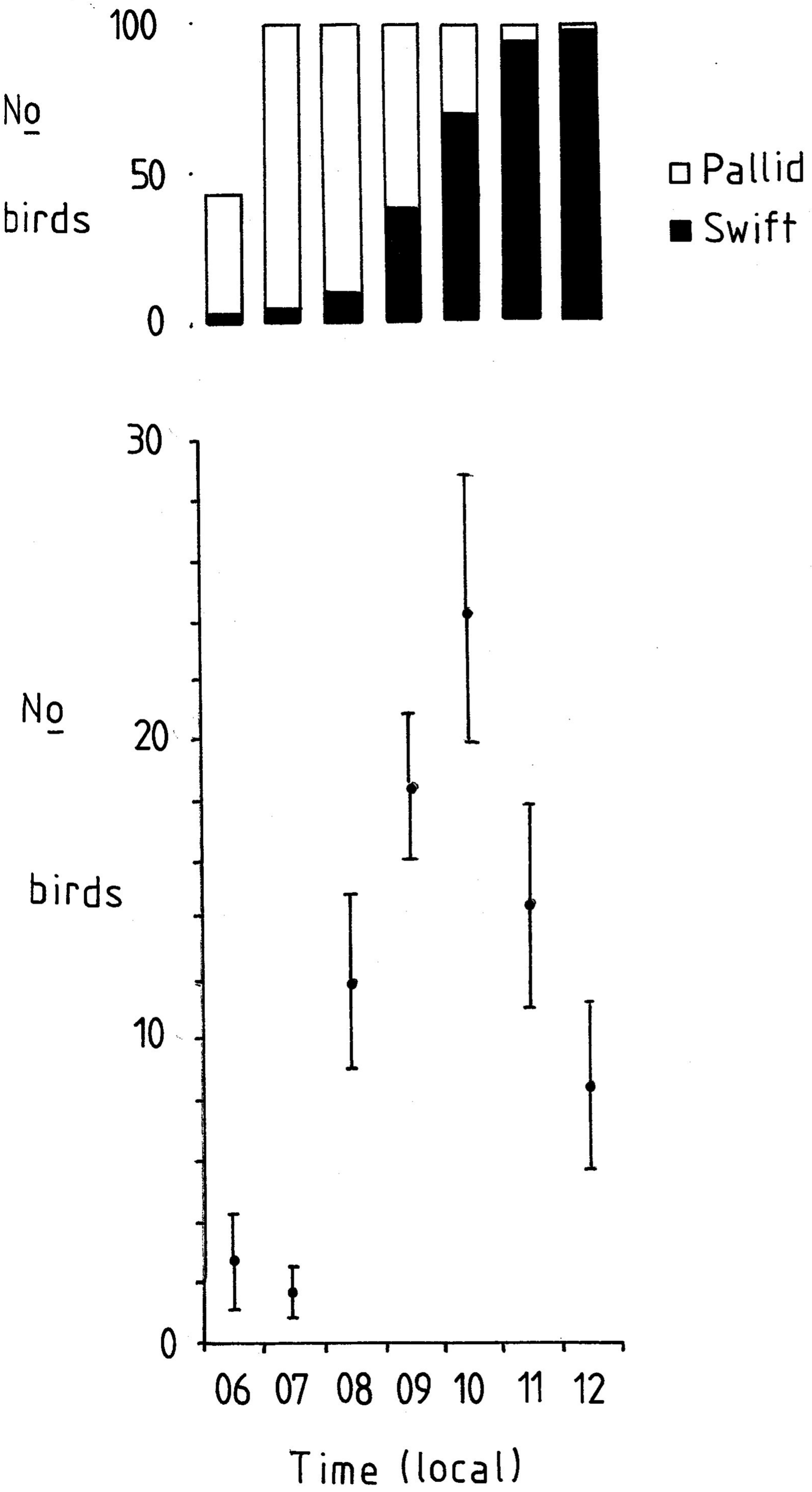
For each sector, first circle represents northward movement and second circle represents southward movement.

4.4.3. Temporal separation of foraging activities

The rate of movement (birds/minute) and the specific identity of swifts flying north to feed over Spain was recorded in detail on one morning (18th May, 1978) to see if the two species departed at different times of day. Less-intense observations on other mornings confirmed the results obtained. The departure of swifts in the morning followed a clear pattern (Fig. 4.16.). There was little movement for the first two hours after sunrise, but there was then a sudden increase in the number of birds flying north with a peak at 1000 hrs. Birds started returning as early as 1100 hrs and for the rest of the day there was a constant north-south movement. Most of the swifts which departed before 0900 hrs were Pallid Swifts. There was then an increase in the proportion of Swifts so that by 1200 hrs nearly all the swifts flying north were of this species (Fig. 4.16.). Swifts therefore remained feeding near the colony for longer than Pallid Swifts. The overlap in the time of departure was very low, 0.193.

The evening return was similar for the two species. Of 148 swifts identified 3 hours before sunset 77 (52,03%) were Pallid, 72 out of 122 (59.02%) were Pallid 2 hours before sunset, and 24 out of 40 (60.00%) were Pallid in the last hour of daylight. The differences were not significant ($X^2_1 = 1.67$ $p > 0.05$).

FIGURE 4.16. Swift and Pallid Swift departures from the colonies during the morning.



4.4.4. Food

Only the food brought to the nestlings could be studied and the data were obtained from food balls brought back by the parents for the nestlings (Lack & Owen 1955). Two methods were used to collect the food balls. In one, a collar (pipe cleaner) was placed around the neck of the nestling ; when the parent returned it fed the nestling but this was unable to swallow the food. Once the adult had left, the food was forced out of the nestling's mouth. In no case was any damage observed on the nestling and rarely was more than one food ball taken from a nestling. The method could only be used for Pallid Swifts as Swifts' nests were not accessible. The second method was preferred as it was quicker and just as effective. Adults were trapped in mist nets as they entered the colony and the food balls they were carrying were removed. There was no effect on the adult as many of the birds treated in this way were later retrapped at the colony with food. On one occasion an adult Pallid Swift was trapped twice in 30 minutes and it had food on both occasions.

Individual food balls were examined and insects classified down to order and measured to the nearest millimetre. Most food balls contained over 200 arthropods (one contained 427 insects). In England, Swift food balls contain between 300 and 1,000 insects depending on the size of the prey. The

larger the prey the smaller the food ball (Lack & Owen 1955). In order so as not to bias the results in favour of those food balls with most insects, only 50 individuals were classified and measured from most food balls. These individuals were selected at random by placing all the insects in the sample in numerical order and selecting 50 from a random number generator. Four food balls belonging to Pallid Swifts weighed 1.1 g, 1.1 g, 1.2 g, 1.1 g. No Swift food balls were weighed. Swift food balls in England weighed, on average, 1.1 g (Lack & Owen 1955). All the food balls used in the analysis were collected at Gibraltar during June and July 1978.

Under the conditions examined, Pallid Swifts took a much wider range of prey items than Swifts (Table 4.7.). Diet overlap was nevertheless high. Pallid Swifts took larger prey than Swifts, which never took prey over 12 mm long (Fig. 4.17.). Most of these large prey were moths (Lepidoptera) and dragonflies (Odonata), the largest recorded being 27 mm long (a moth). In England, Swifts take prey between 5 and 8 mm long in good weather, but in poorer conditions they include smaller prey (2-5 mm). Swifts in England rarely take very small or very large items, below 2 mm or above 10 mm (Lack & Owen 1955). Swifts are known to take moths occasionally in Britain when the latter are swarming. Hale Carpenter (1938) records Swifts taking swarming <u>Arctia plantaginis</u> near Coniston. In Lack & Owen's (1955)

TABLE 4.7. Numbers and proportions of insects of different taxa and sizes taken by Swifts and Pallid Swifts at Gibraltar.

(a) Pallid Swift

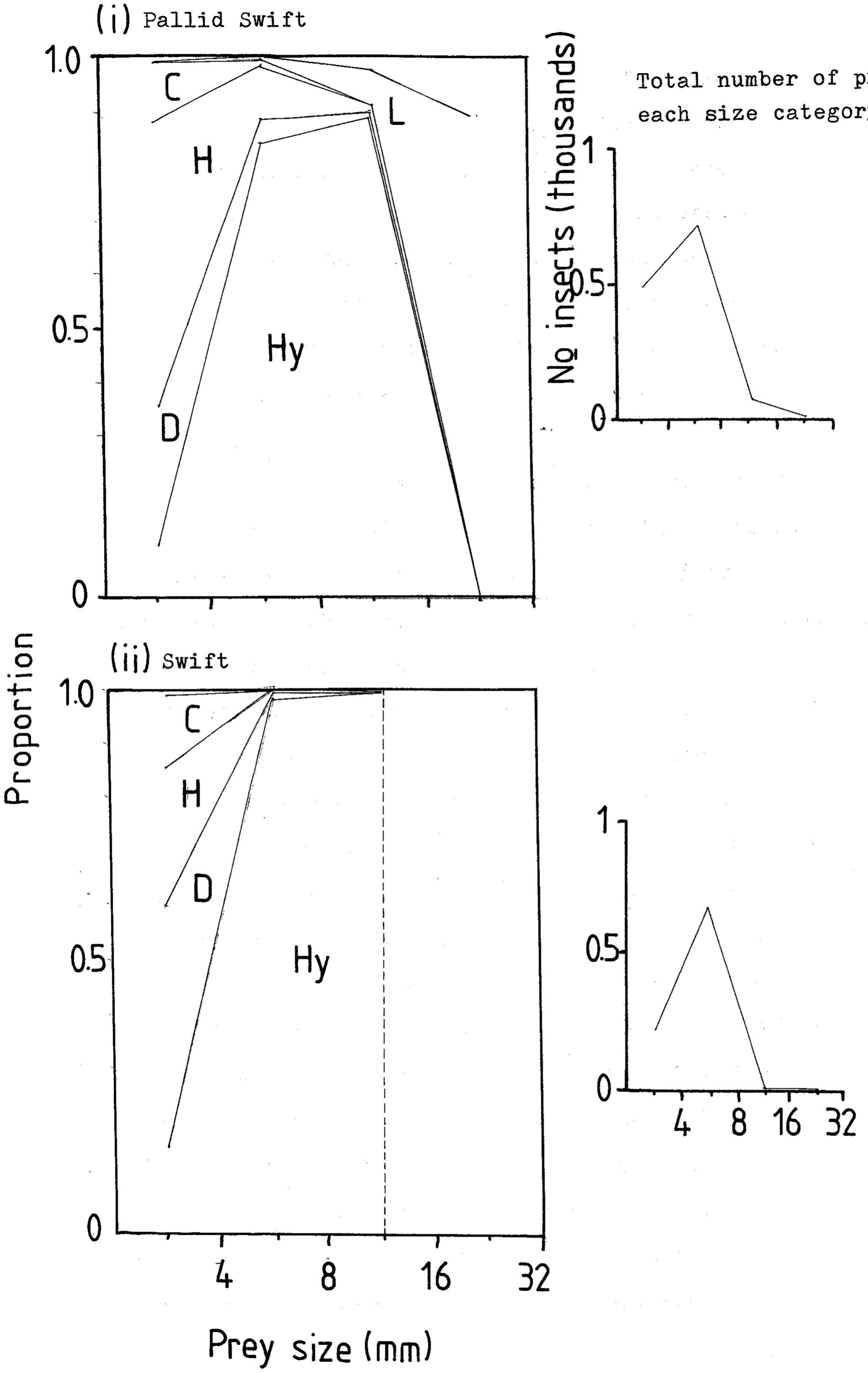
Size (mm)	Hymenoptera	Diptera	Hemiptera	Coleoptera	Lepidoptera	Others
0 - 4	46	125	255	54	0	5
	.036	.097	.197	.042	0	.004
5 - 8	602	29	70	8	1	2
	.466	.022	.054	.006	.001	.002
9 - 16	78	1	1	0	6	1
	.060	.001	.001	0	.005	.001
17 - 32	0	0	0	0	8	1
	0	0	0	0	.006	.001

(b) Swift

0 - 4	36	97	57	30	0	0
	.040	.108	.063	.033	0	0
5 - 8	661	6	2	2	0	0
	.734	.007	.002	.002	0	0
9 - 16	7	0	0	0	0	0
	.008	0	0	0	0	0
17 - 32	0	0	0	0	0	0
	0	0	0	0	0	0

Top value in each row is number of observations and lower value is proportion of total. Niche Overlap = 0.940, Noche Breadth, PS = 3.63 Sw = 1.79.

FIGURE 4.17. Summary of prey types and sizes taken by Swifts and Pallid Swifts at Gibraltar in spring.



C=Coleoptera, H=Hemiptera, L=Lepidoptera, Hy=Hymenoptera, D=Diptera.

study moths comprised only 1% of the diet of the Swift and these must have been small moths. Swifts appear to be selective of some of the prey types they take. Of 8 adult Swifts which were shot and examined around a beehive, all were found to be consuming only the stingless drones (Lacey 1910). Bees and wasps were never found in the diet of the swifts at Gibraltar even though other Hymenoptera were the commonest prey taken (Table 4.7.).

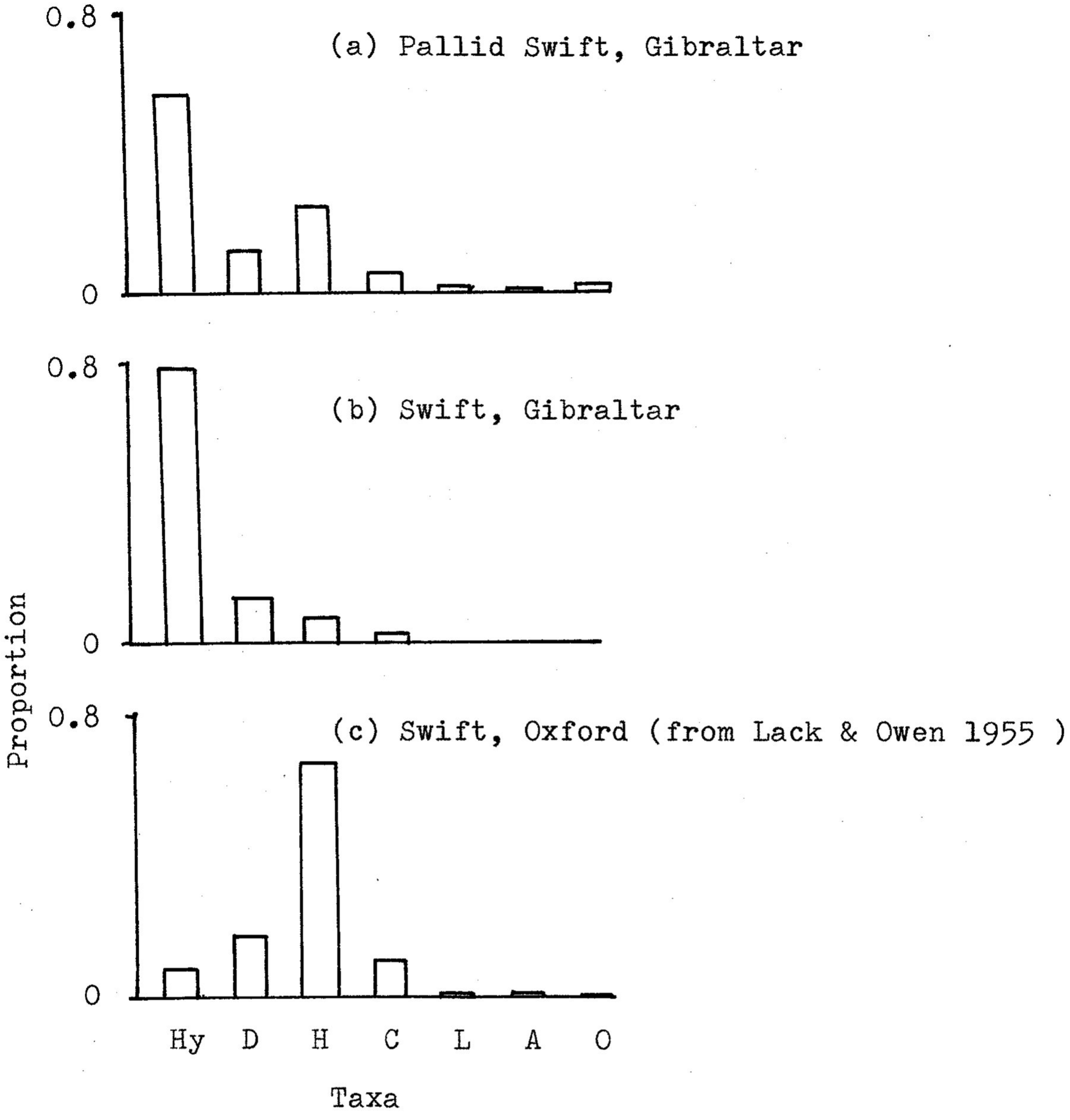
Swifts concentrated more on swarms of social Hymenoptera, especially winged ants, than Pallid Swifts. In West Africa, of 17 Swift stomachs examined, 5 had only termites (Isoptera), 11 had only ants (Hymenoptera), and the other had mainly ants (Chapin 1939). In Europe too, Swifts are known to feed around swarms of insects (Heyder 1927, Lack & Owen 1955). Pallid Swifts also took social insects but they were never as specialised as the Swifts. In neotropical swifts at least, it appears that as the larger species are wider ranging than the smaller species (Snow 1962), these former species feed more frequently on swarms of insects than the latter species (Hespenheide 1975 b). The Swift and the Pallid Swift, although small swifts in Europe, are large compared to some of the small neotropical swifts and feed frequently on swarming insects. In the Gibraltar area both species are wide-ranging. Lack & Owen have suggested that breeding adult Swifts feed near the colony at all times and that it

is the non-breeders which forage more widely. This is thought to be the reason why Swift colonies in Britain are evenly spaced out. At Gibraltar the colonies are close to each other so presumably the swifts may have to range more widely for pery to avoid overcrowding around the tightly-packed colonies.

Pallid Swifts therefore took different food types from the Swifts. They were less specialised than the Swifts and took larger insects. The differences in prey sizes taken were highly significant ($X^2_2 = 110.11$ $p < 0.001$). Similarly, they took a wider range of prey taxa than Swifts. Pallid Swifts included spiders (Araneae) in the diet but Swifts did not even though they do so in Britain (Owen & Le Gros 1954, Lack & Owen 1955). The difference in prey taxa taken by the two swift species was highly significant ($X^2_3 = 147.01$ $p<0.001$).

The diet of the Swift at Gibraltar was very different from that in Britain (Fig. 4.18., Lack & Owen 1955). In Britain Swifts are less-specialised than at Gibraltar and the main components of the diet are Hemiptera. Very few Hymenoptera are taken but these are the main prey at Gibraltar. The differences may be a reflection of the prey availability in the two areas or they could reflect specialisation by Swifts where they share an area with Pallid Swifts. Since Hemiptera were frequent in the diet of the Pallid Swift, it suggests that Swifts were avoiding them

FIGURE 4.18. Main prey types taken by Pallid Swifts and Swifts at Gibraltar and by Swifts at Oxford.



Hy=Hymenoptera, D=Diptera, H=Hemiptera, C=Cóleoptera, L=Lepidoptera, A=Araneae, O=Others.

in Gibraltar and its surroundings.

On average adult Pallid Swifts and adult Swifts returned with food once an hour, often more frequently. During the summer at Gibraltar, swifts have about 14 hours foraging time a day and so they must bring back at least 10 food balls to the nest each day, and probably much more than this. In England, one Swift brood received 42 meals in one day (Lack & Owen 1955). The average food ball contains about 300 insects so that each nest receives at least 3,000 insects a day. Assuming there are 3,000 pairs of swifts at Gibraltar (4.4.1.) and that the adults between them consume as much food as a brood in one day, then the swift population at Gibraltar must be taking a minimum of 18 million arthropods each day. To this figure must be added an unknown value of prey taken by non-breeders.

4.4.5. Aggression

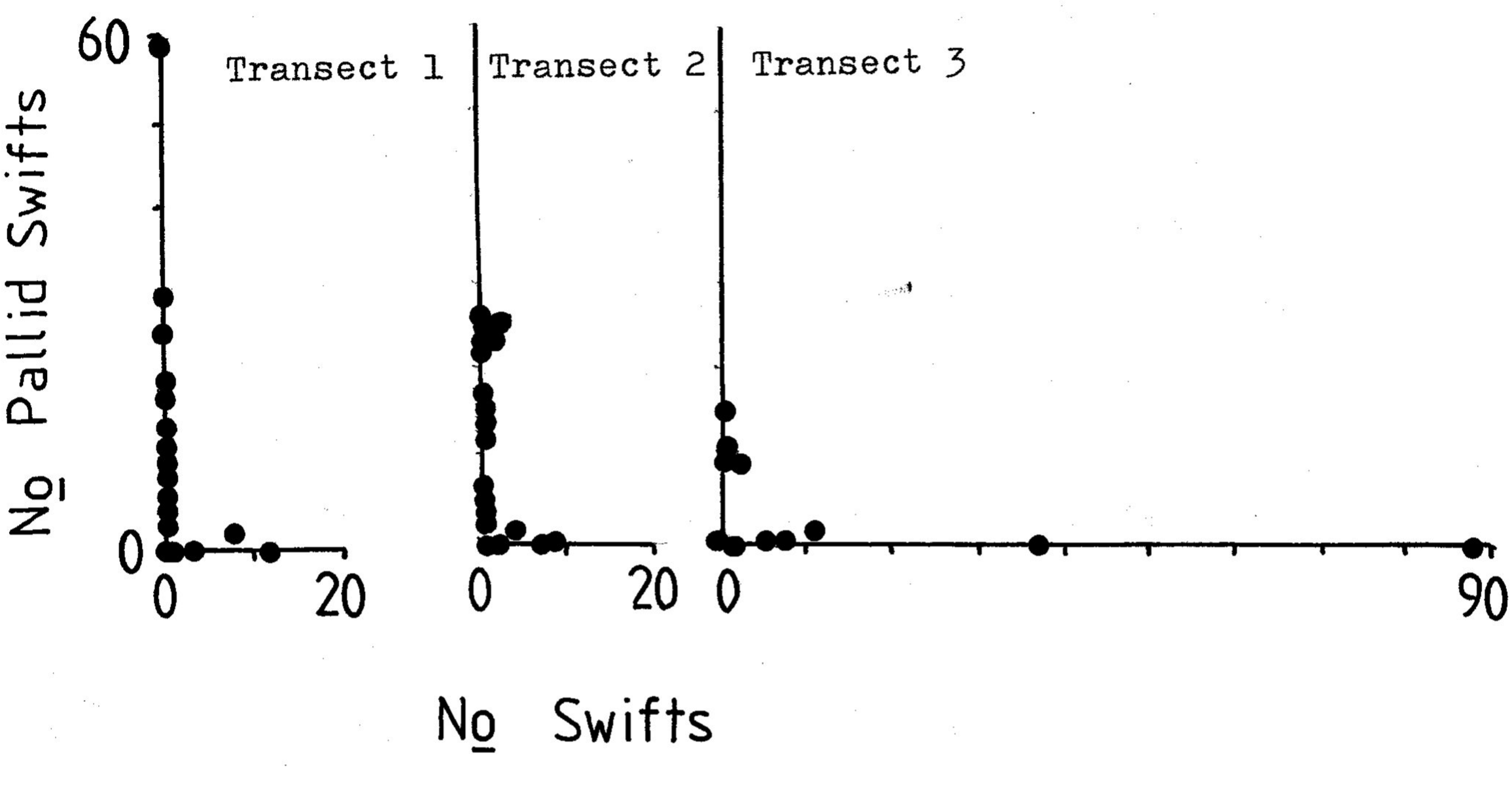
Lack & Owen (1955) have suggested that Swifts in England feed near the nests and that as a result colonies are evenly spaced out. At Oxford, colonies are spaced out at ¼ to ½ mile intervals and the spacing is not due to lack of available nesting sites in between. This implies that if colonies were closer together, there would be a great deal of inter-colony competition. Indeed there appears to be much aggression between Swifts in the immediate proximity of nests (Lack 1956 a). At Gibraltar, the colonies are tightly

packed in a small area and in the centre of the town, colonies may be as close to each other as 3 or 4 metres.

It has been pointed out earlier that swifts foraged over well-defined areas above their colonies and that swifts from different colonies foraged over different areas (Fig. 4.10.). In May 1978, the presence or absence of either species at 50 metre intervals over the town area was recorded. At 50 metre stops, the number and specific identity of swifts foraging overhead was recorded. This was repeated on three different mornings along three different transects in the town. Whenever Swifts were recorded foraging over a patch, there were very few or no Pallid Swifts (Fig. 4.19.); the converse was also true. Birds from different colonies appeared to avoid each other.

At the Windmill Hill Pallid Swift colony (colony 1 in Fig. 4.10.), individuals foraging above the colony were observed to approach other Pallid Swifts from the same colony when these were released after being ringed. On 22 out of 30 occasions when Pallid Swifts were released in this way, other Pallid Swifts from the same colony approached the released bird. The mean number of individuals approaching the released bird was 2.57 ± 1.47. In no case were the released birds chased and they rejoined the main flock at once. It was possible to trap Pallid Swifts from other colonies and release them at Windmill Hill on 9 occasions. On all of these, the

FIGURE 4.19. Number of Swifts and Pallid Swifts observed foraging together at 50 metre intervals over the town of Gibraltar.



released individuals were approached by colony members and in all cases they were chased off. As the number of chasers changed frequently it was not possible to decide on a mean figure but the minimum on any occasion was 2 and the maximum 10. On another occasion an Alpine Swift approached the colony and was chased off by the whole flock (over 30 birds at the time).

Pallid Swifts (and probably Swifts) probably defend foraging areas around the colony even though these areas may change from one day to the next. Colonies therefore act as discrete foraging entities. The phenomenon may be a colony one rather than a species one. In the two mixed colonies that were found at Gibraltar, Swifts and Pallid Swifts foraged side by side in the same flock and joined in screaming parties (Lack 1956 a). Screaming parties of Swifts in England take place mainly on calm mornings and they are thought to be a form of communal activity (Lack & Lack 1952). At Gibraltar screaming parties of Swifts, Pallid Swifts and Alpine Swifts also occur almost exclusively on calm mornings and evenings. The screaming parties are very obvious and are not confined to the area just around the colony as the noisy groups often circle high above the colony. It could be that the screaming parties advertise the possession of a foraging area over the colony and, as this changes from day to day, advertisement has to be continued throughout the breeding season. This could also explain why screaming parties, at Gibraltar

at least, are commonest on calm mornings as it is then that insects are most plentiful around the colony and foraging activity is prolonged over it. At Gibraltar, as in England (Lack & Lack 1952), screaming parties are rare early and late in the season when there are few swifts about. At Gibraltar, the likelihood of competition between colonies and the need for screaming parties may then be reduced. It is also true that early and late in the season calm days are rare.

4.4.6. Resource Partitioning - a discussion

At Gibraltar, Swifts and Pallid Swifts differ in their occupation of nesting habitat, in food, and in the timing of breeding and foraging activities (see 3.4.11.). Resource partitioning appears to be enhanced by inter-group spacing.

Historical background

Assuming that the nesting behaviour of the swifts has not changed at Gibraltar in recent times, it is probable that prior to the invasion and initial colonisation of Gibraltar by Tariq in 711, the only nesting swifts at Gibraltar were Pallid and Alpine in caves and cliff ledges. With the increase in the number of buildings, Swifts may have colonised the town, where they may have dominated numerically. The Swift may have been the main town-nesting species at Gibraltar as late as 1895 (Irby 1895). That Swifts nowadays nest only in old buildings at Gibraltar would seem to support this view. Pallid Swifts may have

commenced nesting in buildings later than the Swifts. The present-day distribution of the two swifts at Gibraltar might suggest that Pallid Swifts are encroaching into the traditional sites of the Swifts (Figs. 4.5., 4.6.). If so the situation at Gibraltar may not be in equilibrium.

Mechanisms of resource partitioning

During the breeding season the two swift species may be exploiting superabundant food resources and the critical periods of the year may be in the winter quarters (Lack 1956 a). This cannot be so for nesting sites as all potential sites appear to be occupied at Gibraltar at present.

Swifts and Pallid Swifts differed in the types of nesting sites occupied. Pallid Swifts nested in natural sites and buildings, and Swifts only in buildings. In the town Swifts occupied holes in walls and Pallid Swifts under eaves (Lack 1971). Nevertheless overlap was high.

Differences in feeding behaviour could not be detected but as individual colonies were separated spatially, the main differences may have depended on where the colonies were situated. As the overlap in the timing of the departure to feed away from the colonies was low, the total amount of time spent interacting must have been low.

Despite important differences in the food types taken by the two species, food overlap was high. It is a

logical outcome of this that when swifts foraged near the colony, and were not separated from each other temporally, avoidance was necessary since food and feeding behaviour were very similar.

Niche Breadth

Pallid Swifts were less-specialised than Swifts in the dimensions examined (Table 4.5., 4.7.). They were wider-niched in range of nesting sites and food. This may explain why the Pallid Swift appears to be a more successful species than the Swift at Gibraltar. It can use nesting sites which the Swift does not, especially in modern buildings. As Pallid Swifts take a wider range of foods, they may be able to remain in the Gibraltar area much longer than Swifts and so raise two broods. In the autumn, food availability will drop for aerial foragers and those which can take a wider range of prey types will be better able to cope with the decline by taking alternative prey.

Morphological adaptations

Morphologically, the Pallid Swift and the Swift differed in wing length, weight and gape size (Table 4.1.). The Swift was the longer-winged, heavier species but the Pallid Swift had a wider gape, which was also more variable between individuals. The wider gape of the Pallid Swift would seem to account for the larger range of pery types taken by this species.

4.5. OUTCOMES

Because of the difficulties in finding a suitable Swift colony initially; and because it could only be studied for one year, much of what will follow will only relate to the Pallid Swift.

4.5.1. Weight and Fat

Adult Swifts were always heavier than adult Pallid Swifts, probably because they were slightly larger (Table 4.1.). Neither species showed much weight variation during the breeding season though Pallid Swifts were heavier in April than later in the season (Table 4.8.). There was also little variation in the amounts of fat stored by adults; of 21 Swifts none had any fat in the tracheal pit, and of 21 Pallid Swifts, 17 had no fat, one had a trace (fat score = 1), and two had half the pit covered with fat (fat score = 2). This suggests that food at this time is not abundant enough to allow adult swifts to deposit fat, or they may not need to do so. Fat when conditions are predictable may be disadvantageous especially as it will reduce flight performance (Dick & Pienkowski 1979). Most of the food therefore goes to the nestlings. Data on young Swifts were scanty but there were sufficient data on young Pallid Swifts from the museum site (4.3.1.) for a comparison between first and second broods. 63.16% (12/19) of the pairs recorded in 1977 laid a second clutch. First clutches were

TABLE 4.8. Weights of Pallid Swifts and Swifts trapped at Gibraltar.

Month		WEIGHT Pallid Swift	Swift
Apr	$\bar{x}$	43.9	
	s.d.	3.69	
May	$\bar{x}$	41.5	
	s.d.	3.48	
Jun	$\bar{x}$	41.3	45.1
	s.d.	3.06	1.91
Jul	$\bar{x}$	40.9	44.8
	s.d.	3.59	2.43
Aug	$\bar{x}$	41.5	40.9
	s.d.	4.13	4.38
Sep	$\bar{x}$	36.5	
Oct	$\bar{x}$	40.0	

Mean weights in grammes

consistently larger than second ones, averaging 2.89 $\pm$ 0.46 eggs for the first and 1.95 $\pm$ 0.58 for the second (Table 4.9.). Hatching and fledging sucess was significantly higher for the first broods than for the second broods (Table 4.9.).

The rate of growth of the wing was the same for first and second brood young but those of the first broods were longer-winged at any stage (Fig. 4.20.). Second brood young, although lighter at first, put on weight faster than first brood young and were heavier on fledging (Fig. 4.21.). This was probably because most first broods had at least 2 young surviving to fledging which competed with each other for food, whereas second broods usually had only one surviving nestling which consumed all the food. The second brood fledgling probably had the advantage on leaving the nest in September and October, when aerial insects were scarcer than in June and July, that it could probably survive longer without food.

4.5.2. Mortality

47.27% of all the Pallid Swifts' first brood chicks that hatched died before leaving the nest and 69.77% of the second brood chicks died at the same stage. The survival of first year birds was 32.71%, comparing with a first year survival of about 30% for Swifts in England (Lack 1956 a). Adult mortality was calculated from the Windmill Hill colony which had been studied since 1973. Using the method in 3.5.4., an annual mortality rate of 26% was obtained (Fig. 4.23.). The annual

TABLE 4.9. Clutch size and breeding success in Pallid Swifts at Gibraltar.

(a) Clutch Size

	Brood 1	Brood 2
Mean	2.89	1.95
s.d.	0.46	0.58
N	19	22

(b) Hatching/Fledging Success

	Brood 1	Brood 2
No Eggs	55	43
No Hatched	48 (87.27%)	28 (65.12%)
No Fledged		
(i) of eggs	29 (52.73%)	13 (30.23%)
(ii) of young hatched	29 (60.42%)	13 (46.43%)

FIGURE 4.20. Growth of the wing in nestling Pallid Swifts of first broods (open circles) and second broods (closed circles).

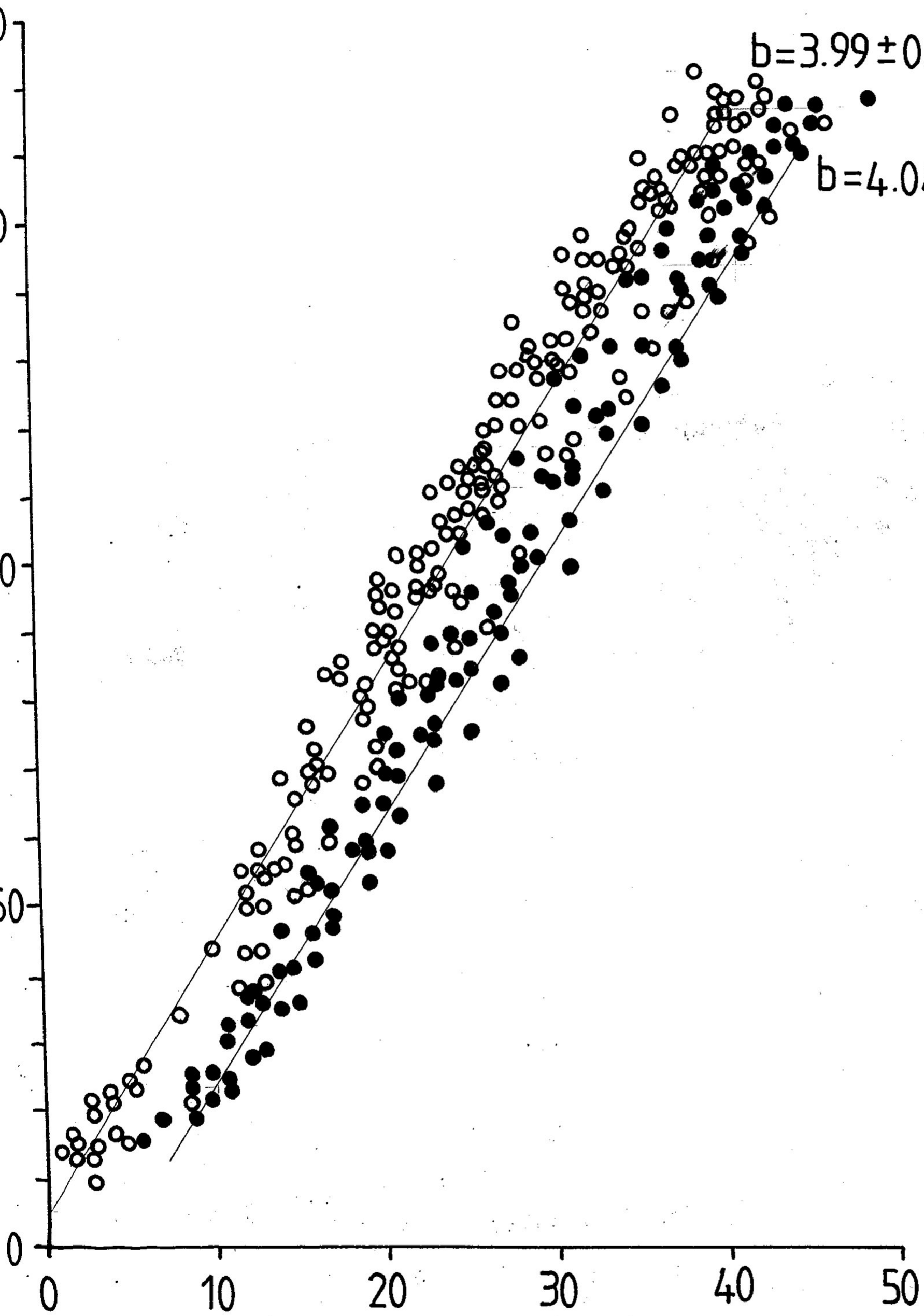


FIGURE 4.21. Increase in body weight with age in nestling Pallid Swifts from first broods (open circles) and from second broods (closed circles).

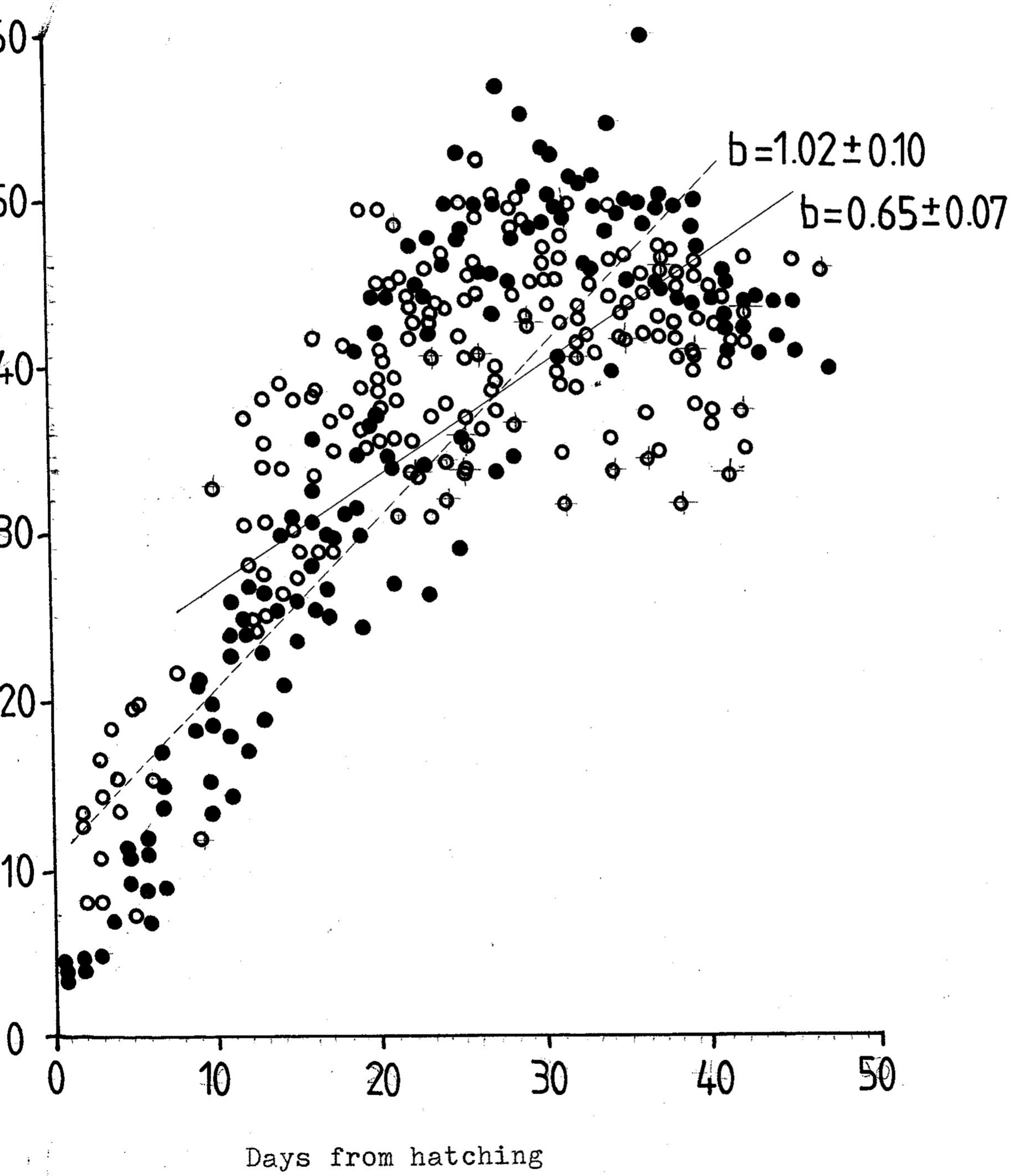


FIGURE 4.22. Relationship between wing length and Weight in first and second brood Pallid Swifts.

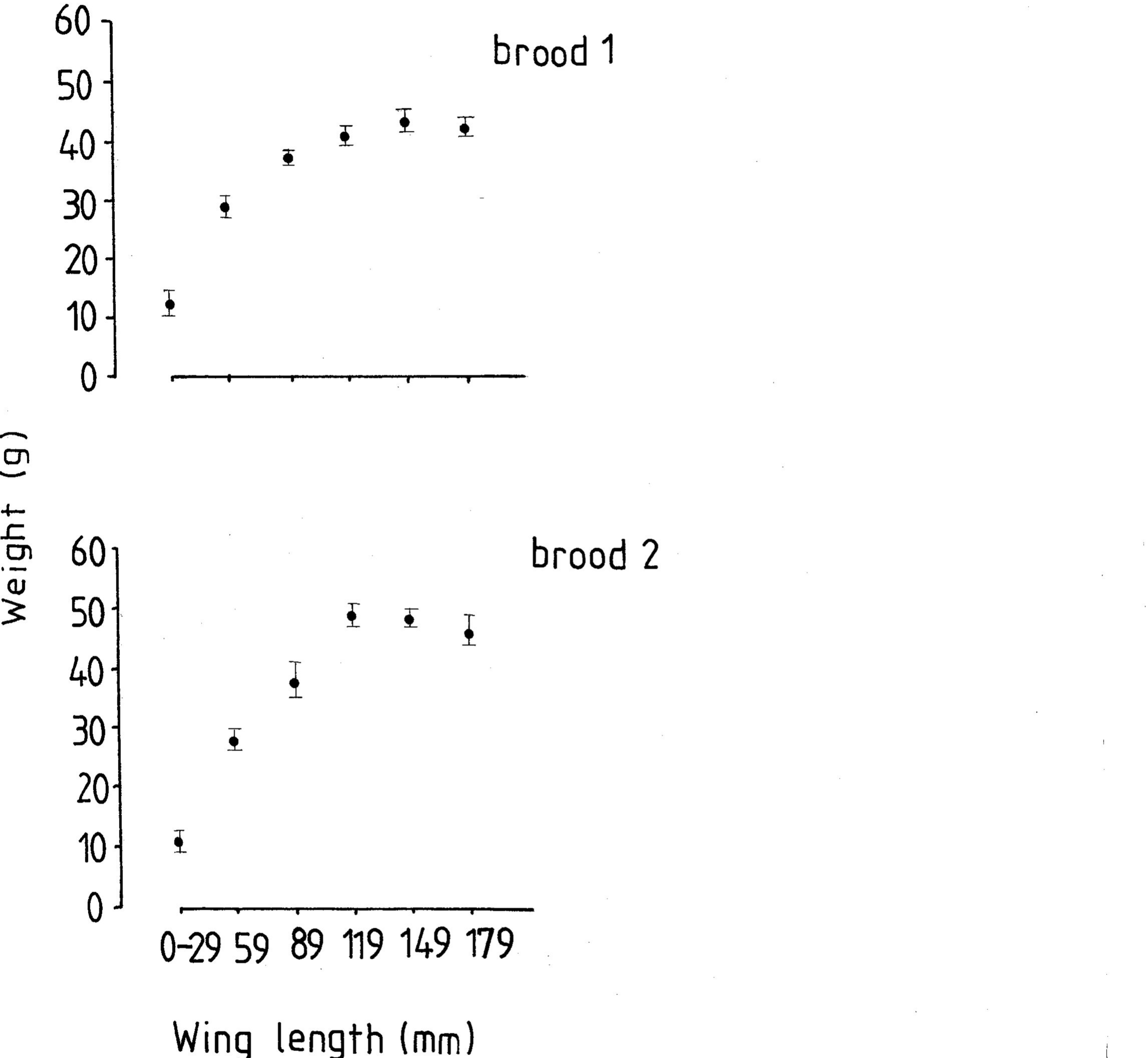
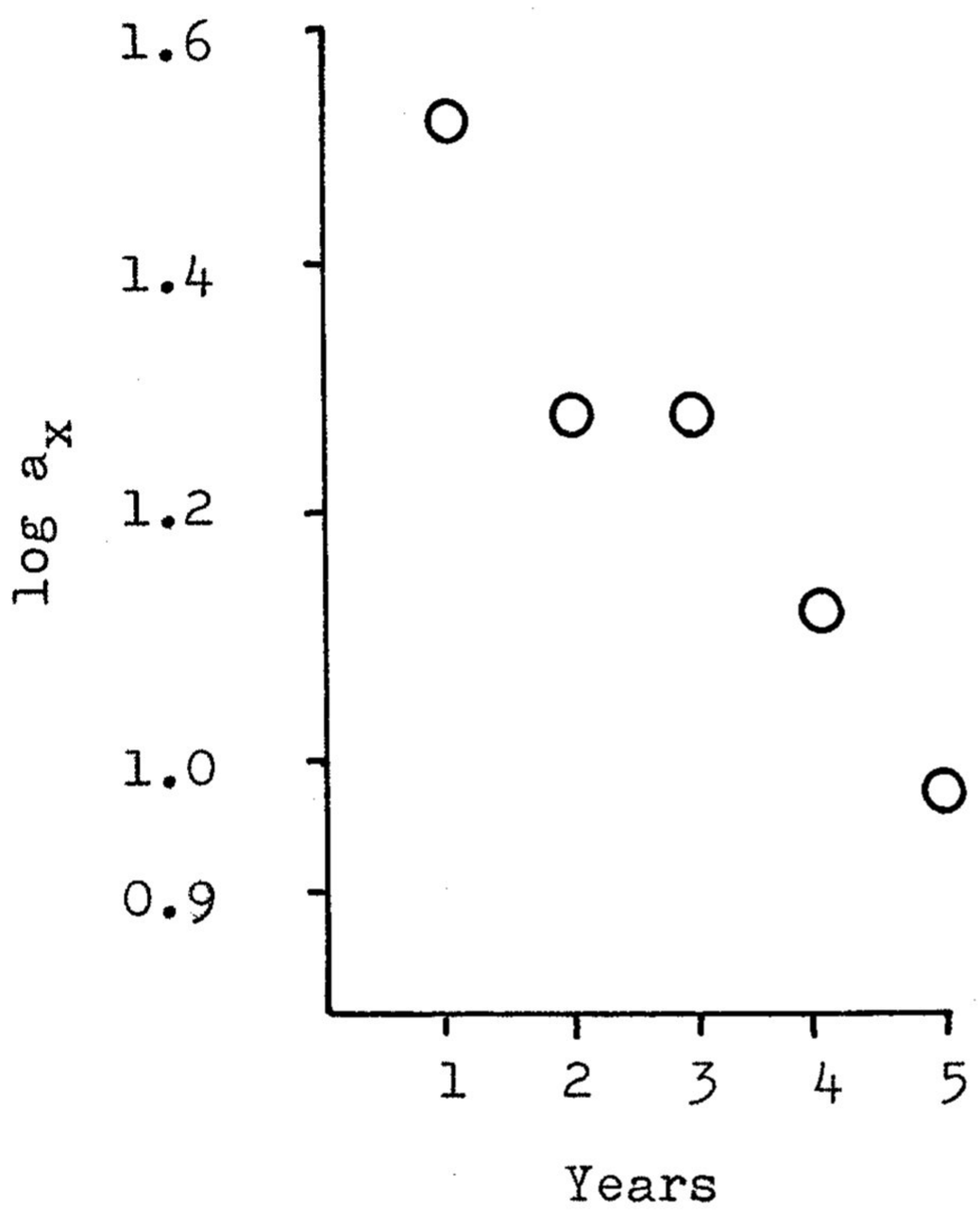


FIGURE 4.23. Survival of Pallid Swifts at Windmill Hill, Gibraltar.



$y = 1.612 - 0.126x$

mortality of adult Swifts in England is about 15 - 17% (Lack 1956 a, Perrins 1970).

Pallid Swifts produce about 2 young per year on average whereas Swifts probably produce less as they lay only once. In Britain, Swifts produce 1.3 young per year. Nevertheless Pallid Swift adult mortality is 26% per annum as opposed to only 15% per annum for adult Swifts (Perrins 1970). First year mortality is similar in both species.

CHAPTER 5

A DISCUSSION

" There is ample room, for any one with energy, to work out a great deal more information about the birds of the Straits (of Gibraltar) ; but it must be remembered that little can be done in hasty visits of two or three months....."

Howard Irby 1895,
The Ornithology of the Straits of Gibraltar.

5.1. INTRODUCTION

Until now, most studies of birds in the Mediterranean Basin have been focused on the migration of birds through the area (Moreau 1961, 1969, Casement 1966, Smith 1968, Moreau & Dolp 1970), occasionally on bird communities in some localities (Blondel 1969, Cody & Walter 1976, Herrera 1978 a), and sometimes on the habits of some species (Bergmann 1978). The three aspects are covered by this work. The bird communities in three habitats are examined with particular reference to seasonal variations in species and numbers in the habitats (Karr 1976 a). Two pairs of species which are numerically dominant in these habitats and which have similar ecological requirements are then looked at in detail.

5.2. HISTORICAL BACKGROUND

The Rock of Gibraltar is a small peninsula at the southern end of Iberia (Fig.1.1.). As in most parts of the Mediterranean Basin, its habitats have been largely altered by Man (Cody & Mooney 1978). The climax vegetation at Gibraltar was probably Oleo-ceratonium evergreen woodland (Cortes 1979). During the sieges of Gibraltar (1727), or even before that (1704), most of the trees there were cut down so that by the late 19th century the

main habitat of the western slopes of Gibraltar was steppe or at most Garigue (Fig.1.2.) and Cortes (1979). During this period, the vegetation was kept from developing towards a stable climax by animals which were grazed throughout the western slopes (Landsdowne in litt.). During the late 19th century, the nesting species at Gibraltar included some which are nowadays extinct there, such as the Black Wheatear Oenanthe leucura and the Dartford Warbler Sylvia undata (Irby 1895). During the first and second world wars, most of the Upper Rock was fenced and grazing animals were removed. Gradually, the present situation, with a dense olive-dominated carpet of vegetation over the larger part of the western slopes, developed. This dense vegetation or High Maquis which covers most of the Upper Rock (Fig.1.3.) is probably the present-day climax community (Cortes 1979). Among the changes in the breeding bird community which have taken place this century, the most noteworthy is the probable establishment of a breeding population of Blackcaps on Gibraltar. The present-day Blackcap resident population at Gibraltar is of the order of 300 pairs.

The other majoe habitat change has been the establishment and growth of the town at the base of the western slopes (Appendix 4). Most of the vegetation of these lower slopes has been removed and has been replaced by buildings, or at best by gardens with many exotic plant species. The town was founded in 711 and

has grown steadily since and now has a population of just under 30,000. As a result of the spread of the town, a new species of aerial-insect forager probably became established, the Swift. This must be so if it is assumed that before the town was built, the only nesting swift species at Gibraltar were those which still nest there in natural sites.

5.3. PRESENT-DAY BIRD COMMUNITIES

It is impossible to define and describe a typical community of any group of organisms in any major climatic or geographical area, especially if the area has been modified by Man. Recent studies of community convergence in different continents are inaccurate because they disregard the variation which exists between communities in the same or similar habitats within any one region (Cody & Mooney 1978).

The vegetation structure of the maquis on Gibraltar is very similar to that on Terrubia, Sardinia, even though many of the plant species are different (Cody & Walter 1976, Cody & Mooney 1978). However, the bird communities are very different (Table 5.1.). There are only 13 species in the Gibraltar habitat during the breeding season (March - June) whereas there are 24 species in Sardinia. The community structure, as defined by Pianka 1973, is very different. At Gibraltar there are only a few species but they reach very high

densities (Crowell 1962, Grant 1966, 1967, MacArthur et al. 1972, 1973, Cox & Ricklefs 1977). Of the 6 species shared by the two sites, 4 reached much higher densities at Gibraltar than in Sardinia and the other two were only slightly more abundant in Sardinia than at Gibraltar. Using Cody & Mooney's (1978) classification of foraging types (which differs from that used in chapter 2 of this work), there were 9 foliage insectivores in Sardinia and 5 at Gibraltar; 1 sallying flycatcher in Sardinia and none in Gibraltar; 6 ground foragers in Sardinia and 4 in Gibraltar; 3 seed eaters in Sardinia and 1 in Gibraltar; 1 aerial forager in Sardinia and 3 (the swifts) in Gibraltar. In the impoverished community at Gibraltar (except for the swifts) the trend is for one species in each foraging type to become numerically dominant; the rest usually contributed only an insignificant proportion of the total. The exceptions were the foliage insectivores which had two dominant breeding species, Blackcap and Sardinian Warbler, and the aerial foragers which also had two dominant species, Pallid Swift and Swift. Most of the breeding species at Gibraltar are plastic specialists (Morse 1971), see Table 5.1. Therefore two very similar habitats, at Sardinia and Gibraltar, had considerably different communities of birds in the breeding season. Cody (1978) found similar inter-country differences in similar habitats between England and Sweden.

As well as this geographical, inter-site variation, there is also a seasonal, within-site variation which is often ignored in community studies (Karr 1976 a). These changes are peculiar to each site (compare Gibraltar Garigue, 2.3.2., with Santa Fe Garigue, Blondel 1969) and are the result of a combination of factors, among which the most important are geographical location, including local geography, variability and predictability of climate and resources (Alerstam & Enckell 1979), and historical effects (Karr 1976 a). The bird communities at Gibraltar exemplify these factors very well. For a Mediterranean locality, the seasonal fluctuations in numbers and species are disproportionate, as a result of Gibraltar's position in an area which concentrates large numbers of migrating birds (Nisbet et al. 1961, Bernis 1962). The wet winters and the particular way in which Man has modified the habitats also make the communities peculiar to Gibraltar. The presence of a town near the habitats must mean that some species, such as House Sparrow Passer domesticus or Spotless Starling Sturnus unicolor, which would not normally occupy maquis vegetation, do so and can become important components at least at times. It therefore becomes very difficult to predict the composition of a bird community in a particular habitat in any region, especially if Man's influence has produced major alterations to the habitats or the areas around the habitats.

The three habitats studied at Gibraltar had a high species turnover and this was most pronounced in the simplest habitat, Garigue, and least so in the most complex, High Maquis (Fig.2.16.). Migrants accounted for up to 80% of the communities by biomass, 90% of the communities by numbers, and 79% of the communities by species. This is much higher than the proportion of migrants in other communities studied in several habitats in different parts of the world (McClure 1964, McClure & bin Ohthman 1965, Blondel 1969, Frochot 1971, Britton 1974, Karr 1976 b , Herrera 1978 a). Alerstam & Enckell (1979) and Willis (1966) suggest that migrants will be better competitors against residents in simple habitats, especially in two-dimensional habitats, because these simple habitats will be more open to environmental fluctuations, so that residents will not be able to exploit these habitats as successfully as more stable ones (Frochot 1971). Karr (1976 a) also found a decline in species turnover with season with increasing vegetation complexity in bird communities in tropical America. Despite the high turnover of species at Gibraltar, very few of these were dominant numerically or by biomass (Figs. 2.7., 2.8., 2.14., 2.15.). Morse (1971) has questioned whether the densities of resident birds in areas where large numbers of migrants go through are lower than in areas where fewer migrants pass. The few resident species at Gibraltar are, in fact, very numerous and reach higher densities than in similar

communities elsewhere (Blondel 1969, Cody & Mooney 1978). This increase in density appears to be a response to the reduced number of resident species present (density compensation, Cox & Ricklefs 1977, Cody & Mooney 1978). It may be that the low number of resident, especially summer resident, species is due to intense competition from transient species. Gibraltar's habitats have a number of features which must make it difficult for a large number of resident species to coexist. They are very seasonal, unpredictable and structurally simple (Karr 1976 b, Alerstam & Enckell 1979),

Some niches (e.g. that open to ground foragers in winter) are probably seasonal and so there may be some empty niche space at certain times of the year (Alerstam & Enckell 1979), but on the other hand the habitats cannot support a ground forager all year. These empty niches may be sufficiently predictable on a year to year basis to enable some species to return to the same site in consecutive winters (3.5.5.). There is no evidence that migrants stop at Gibraltar in successive seasons while on passage, but different species stopped each year at the same period (Moreau 1972, Morel 1973, Pearson & Backhurst 1976). The habitats are also in an area which probably has many more migrants than others with similar conditions because of local geography.

It is important to note that all the dominant

species (as defined by McNaughton & Wolf 1970) at Gibraltar are year-round residents or winter residents and that summer residents are of negligible importance. This contrasts with habitats further north where the bird numbers are lowest in winter when food availability is reduced (Frochot 1971), or in more stratified habitats in the Mediterranean region where the wintering community is composed almost exclusively by residents (Herrera 1978 a). The only important summer residents are the two swift species which exploit what must be the most seasonal, certainly the simplest, of Gibraltar's habitats. In summary then, the ,ore seasonal and less-complex the habitat is, the fewer resident species it can sustain, and the less-seasonal and more complex the habitat is, the ' fuller ' it is the year round and so the fewer the number of species which can enter to exploit temporary food sources. It will be the plastic (Morse 1971) species which will be the residents and the stereotyped ones will have to change area with season. The Gibraltar habitats are seasonal and so few species are resident but the seasonal variation in resources is probably predictable enough to allow a few plastic species to remain resident. Unpredictable and seasonal habitats should have even fewer resident species (MacArthur 1959, Herrera 1978 b).

5.4. DOMINANT SPECIES

In Garigue, Sylvia warblers do not attain high densities and they are not major components of the community in that habitat (Figs. 2.14., 2.15.). The dominant species numerically and by biomass are ground foragers, some resident polyphages (plastic) and some non-resident specialists. The low Maquis is different. Foliage insectivores dominate all year, among them two resident polyphages, Blackcap and Sardinian Warbler. The rest are non-resident specialists. The only other dominant resident species are two polyphagous ground species (Figs. 2.7., 2.8.). The aerial community holds two dominant summer residents, the swifts, and one dominant winter resident, the Crag Martin.

5.5. A COMPARISON OF THE SWIFT/PALLID SWIFT SYSTEM WITH THE BLACKCAP/SARDINIAN WARBLER SYSTEM.

5.5.1. Taxonomy

The resident Sylvia warblers are virtually confined to Gibraltar compared with the more mobile Apus swifts. Indeed, the swifts are so highly mobile that they forage regularly over Spain. Despite the large numbers of resident Blackcaps and Sardinian Warblers which have been ringed at Gibraltar, none has been recovered outside the peninsula. Genetic isolation is possible for the populations of the two species at

Gibraltar, in particular for the Blackcap population since other breeding populations in the vicinity of Gibraltar appear to be rare. The two warbler species appear to be morphologically different from their continental counterparts and they may be undergoing a process of sub-speciation (Mayr 1963) as a result of adapting to the environment at Gibraltar (reduced number of resident species, use of 'atypical' habitats, etc.).

The process may be the same or similar to that of species colonizing islands. When a species enters an uncolonized island, if it succeeds in colonizing, it may expand its niche boundaries in the absence of mainland competitors (Klopfer 1965, MacArthur & Wilson 1967). In general, the changes which are produced when a species colonizes an island may be divided into short-term and long-term (evolutionary) changes (MacArthur & Wilson 1967). Thus when a new species colonizes an island it is likely to encounter new physical conditions as well as a different species community, or a relative change in abundances, such that it may be caused to shift, expand, or contract its preference. These changes are at first likely to be phenotypic but will be translated into genetic differences by natural selection (MacArthur & Wilson 1967).

5.5.2. General Ecology

The main difference between the two species pairs is that the warblers are year-round residents but

the swifts are summer residents. In Morse's (1971) terminology, the warblers are plastic specialists, that is at any point in time they specialise on particular resources but they can switch from one resource to another as new ones become available. For example, the two warbler species feed on arthropods most of the year but they vary foraging location continuously depending on where most food can be obtained. At certain times of year, when arthropods become scarcer and other foods more plentiful, they switch diet and become herbivores. There is some evidence that major switches in the diet of Sylvia warblers may in part be due to endogenous factors (Berthold 1976). Similarly, Leck (1972) found that in Panama, bird species reduced their visits to fruiting trees when alternate foods became available in the dry season. Many insectivores became frugivores when berries were ripe and abundant. Sick (1968) also found regular movements of birds in response to seasonal changes in food supplies.

The swifts are stereotyped specialists (Morse 1971), but the Pallid Swift is more generalised than the Swift. Both species exploit temporary food sources but cannot switch diet in winter, so they have to leave. Within this specialised situation, the swifts can alter somewhat the types of food they take, especially the Pallid Swift which can, as a result, remain longer than the Swift in the breeding area. The two species (pairs) are therefore specialists as they utilise

TABLE 5.1. Comparison of the breeding bird communities at Jews' Gate Gibraltar and at Terrubia Sardinia.

Foraging Group	Pairs/hectare	
	Sardinia	Gibraltar
Foliage Insectivores		
Subalpine Warbler	1.46	0
Coal Tit	1.44	0
Blackcap	1.16	1.87
Firecrest	0.86	0
Wren	0.72	0.24
Dartford Warbler	0.64	0
Great Tit	0.59	0
Sardinian Warbler	0.52	6.50
Blue Tit	0.35	0.27
Melodious Warbler	0	0.30
Sallying Flycatchers		
Spotted Flycatcher	0.30	0
Ground Foragers		
Robin	2.91	0
Chaffinch	0.72	0
Blackbird	0.44	1.34
Jay	0.20	0
Red-backed Shrike	0.05	0
Barbary Partridge	0.04	(0)
Spotless Starling	0	0,04
Nightingale	0	0.10
Blue Rock Thrush	0	0.07
Seed Eaters		
Goldfinch	0.59	0
Serin	0.30	0
Greenfinch	0.05	0
House Sparrow	0	1.20
Aerial Foragers		
Swift	+	+++
Pallid Swift	0	+++
Alpine Swift	0	+
Total	13.34	11.90
Species	20	13

Note : Terrubia data from Cody & Mooney (1978).

coarse-grained, homogenous parameters (MacArthur & Levins 1964, Levins 1968) but the warblers are more plastic, and hence more opportunistic, than the swifts.

It has been demonstrated in several studies that resident species depend on permanent resources which do not show great seasonal variation (Blondel 1969, Frochot 1971, Karr 1975, 1976 a, Herrera 1978 a). The residents at Gibraltar, especially the two Sylvia warbler species, do not rely on permanent resources as the habitats they occur in and the foods they take are seasonally variable. However they can remain resident by changing the foods they consume, an alternative strategy to the commoner one described by other authors (see above), for residents. This alternative may not be open to mainland residents which inhabit areas with more complex communities.

Non-residents, on the other hand, are expected to concentrate on unpredictable and/or seasonal, and perhaps superabundant foods (Willis 1966, Leck 1972, Thiollay 1970, Karr 1976 b). The two species of swifts exemplify this, as do the migrant warblers in spring, for example the Phylloscopus which foraged extensively on flowering Calicotome villosa. The migrants often capitalised on these supplies to deposit migratory fat (Ferns 1975, Bibby et al. 1976, Rappole & Warner 1976, Smith 1979, Thomas 1979).

As a result of the different levels of permanence of the two species pairs at Gibraltar, their basic ecological events have been modified

accordingly. The two species pairs have one feature in common. Within the range of options open to them, one species in the pair appears to be less specialised than the other. The Sardinian Warbler occupies a wider range of habitats and feeding positions than the Blackcap, and the Pallid Swift takes a wider range of prey items and nest sites than the Swift. It is the more generalised species in each pair which has the longest breeding season. The breeding season of the Pallid Swift extends from April to mid-October at Gibraltar and individuals of this species are present from February to November. The Swift only breeds between April and July and raises just one brood instead of the two raised by most Pallid Swift pairs. The Sardinian Warbler starts breeding at the end of March (Irby 1895 found a nest with eggs at Gibraltar on 12th March) and most pairs probably raise more than one brood. The Blackcap commences a month later and only raises one brood as a rule.

The moult period also reveals interesting contrasts. The adults of the resident warbler species take about three months to moult after breeding. The moult is slow probably because they do not have to migrate and this slow moult may be advantageous as food is scarce during that time. The swifts have a long moult because they cannot afford to replace more than one primary pair at a time as this would seriously affect their capabilities (de Roo 1966). As the two species have to migrate, they must either moult while breeding or undertake at least part of their moult in the

winter quarters. As many Pallid Swifts remain on the breeding grounds into October or November, a complete moult cannot be squeezed in the winter quarters, so they have to commence moulting while still breeding and then suspend it in order to migrate.

5.5.3. Resource Partitioning

The two species pairs studied are probably separated by habitat in more natural environments than at Gibraltar (Voous 1960, Lack 1971). It is difficult to know with certainty what the natural nesting habitats of the swifts are since they nest mainly in buildings at present. Pallid Swifts nest in sea-caves at Gibraltar and their present geographical distribution suggests that they must have nested almost exclusively in caves and cliffs not far from the sea in the past (Voous 1960). Inland observations of Pallid Swifts are rare (Affre & Affre 1967, Konig 1975). Pallid Swifts probably did not nest in holes in trees (but see Laferrere 1972), unlike Swifts which still do so frequently in some areas (Lack 1956 a). Swifts are also known to nest in caves in northern Europe (Lack 1956 a). It seems possible that in the past the two species were separated by habitat, ine nesting in coastal cliffs and caves, the other mainly in trees, but sometimes also in caves although probably inland except where Pallid Swifts were not present. The Blackcap and the Sardinian Warbler are also separated by habitat (Lack 1971) and the situation at Gibraltar is probably recent and must be rare.

Mechanisms which allow these species pairs to partition resources are probably imperfect as the pairs have only come into contact in recent times (Kalinoski 1975). The high overlaps observed in the dimensions studied support this view. In the case of the swifts, in the town they show differences in nesting sites which may reflect their natural modes of nesting. The Swifts occupy holes, the Pallid Swifts cracks and under eaves. The feeding methods are similar which again perhaps suggests that they occupied similar feeding niches in different geographical areas in the past. Their morphologies are practically identical, though minor differences in the feeding apparatuses seem to account for differences in diet. These differences probably arose as a result of the differences in climatic conditions, and hence food supplies, which the two species exploited before coming into contact (the Pallid Swift occupying milder, less continental climates than the Swift).

The warblers also had differences, especially in habitat occupation and these differences could be related to differences found in other parts of their ranges (Lack 1971). In this species pair the problem is more complex because the Sardinian Warbler's choice of habitats overlaps completely with that of the Blackcap. Thus the swifts differ in nest site occupation, and even though they overlap widely, there are some situations which appear to be occupied by only one species. In the case of the warblers, the Sardinian Warbler can

potentially use all the habitats at Gibraltar and within the habitats it is probably capable of using most of the resources which the Blackcap uses (except possibly the largest berries). In classical terminology (Miller 1967), the fundamental niche of the Blackcap is included within that of the Sardinian Warbler. The realized niche of the Blackcap is the same as its fundamental niche but the realized niche of the Sardinian Warbler is smaller than its fundamental niche probably owing to the presence of the Blackcap. The fundamental niches of the Pallid Swift and of the Swift are similar and overlap extensively but they have areas which are exclusive to one or other of the species. It is possible that, as the Pallid Swifts may be expanding into all types of buildings that the Swifts can occupy, in the future the swift pair may resemble the warbler pair in nesting niche, in that in this dimension the niche of the Swift may become engulfed by that of the Pallid Swift.

The two species pairs therefore partition resources imperfectly. They are aggressive towards the other member of the species pair and hold exclusive or partially exclusive areas in space and/or in time (Cody 1974) where they forage, nest, etc. In the warbler pair, the larger species, the Blackcap, is socially dominant over the Sardinian Warbler (Morse 1974). As its niche is included within that of the more generalised Sardinian Warbler, the two species can probably coexist in equilibrium. If the Sardinian

Warbler were dominant over the Blackcap, it is likely that the Blackcap would be pushed out of the matorral, or it might not have colonised it in the first place. The Swift is larger than the Pallid Swift but there is no evidence to show that it is the socially dominant species. In fact, the difference in size, though significant, is smaller than in the warbler pair and individuals of the two species do overlap in size. If there is no such social dominance, then the species with the widest range of tolerance should eliminate the other.

It is possible that interspecific aggression and territoriality is not related to competition. Take a species pair in which 5 resource dimensions are critical in determining the competitive outcome of a pairing. If the two species overlap totally (100%) in 4 dimensions and not at all (0%) in the other, then it is generally assumed that the two species are isolated ecologically (Lack 1971, Cody 1974). If they overlap highly on all dimensions, say 80% in each, then it is generally suspected that they may be competing. However high overlaps may at times be related to lowered competition so that the two species may not require to separate any further than they are (Zaret & Rand 1971, Pianka 1974, Herrera 1978 a). Now, an 80% overlap in a dimension may be considered as a 20% non-overlap which, for 5 dimensions, gives a non-overlap of 100%, as in the earlier example. Aggression may be related to disturbance between individuals and not

with competition for resources (Goss Custard 1970, Green & Davies 1972, Davies & Green 1976). For example, it may benefit an individual Blackcap to defend a territory from a Sardinian Warbler because the latter's proximity may disturb the Blackcap's prey. The Sylvia method of foraging, by jumping between branches must disturb arthropods and the presence of another warbler nearby could reduce considerably the efficiency of capture (Davies & Green 1976). In structurally simple habitats this becomes most likely. Two birds in the same horizontal position in 2 metre high scrub will come into contact more frequently than two in the same horizontal position in 10 metre vegetation. Indeed, it appears that species occupying simplest habitats are most frequently interspecifically territorial (Orians & Willson 1964, Cody 1969). Ground-dwelling passerines, particularly chats, are often interspecifically territorial (Hartley 1949, Stresemann 1950, Simmons 1951, Lack 1970, Cornwallis 1975, Davies 1976, Finlayson in prep.). In most examples fights between dissimilar species are not uncommon. Davies (1976) found that Pied Wagtails chased Meadow Pipits, Skylarks, Robins, House Sparrows and Linnets. The aggression between very different migrants and residents at Gibraltar (3.4.10.) replicates this. These examples further emphasize that interspecific aggression may be related to interference. Murray (1969, 1971) proposed a non-adaptive model where interspecific aggression was due to mistaken identity but this view has been

contradicted by Lyon et al. (1977).

Leck (1972) suggests that the increase in aggression in fruit-eating birds during the dry season in Panama may be due to overcrowding as food was apparently superabundant. The increase in aggression with migrant density at Gibraltar and in other studies (Recher & Recher 1969, Kalinoski 1975) confirms this. Aggression has also been linked directly with competition for food in times of severe shortage (Lockie 1956, Martin 1970, Kalinoski 1975, Woolfenden et al. 1976).

Thus the action of Man in modifying natural situations has resulted in two unusual species pairings. The matorral at Gibraltar has been modified extensively by Man over the years and has produced a balance of two resident Sylvia species which are not usually in contact. The question remains as to why Blackcaps are not resident in the mainland near Gibraltar. It seems most likely that the answer may lie in the habitats which are available on the mainland, especially the absence of Wild Olive scrub. For example in three communities near Gibraltar (Herrera 1977, Cortes 1978 b) the resident species were tits, bark insectivores and ground polyphages. These habitats did not have a winter supply of berries and Blackcaps were only transients. If most of the habitats around Gibraltar are unproductive in terms of berries so that Blackcaps cannot overwinter, then the advantage which they migh have in spring over

migrants may be lost. Other migrants, better able to exploit foliage arthropods would replace the Blackcap. In Herrera's (1977, 1978 a) study, it was the resident tits which were the main breeding foliage insectivores.

In the two cases investigated in this thesis, pronounced resource-partitioning mechanisms do not appear to have evolved and they may not do so as the habitats available are not very stratified (Cody 1969). The results are situations which are probably maintained chiefly through direct behavioural interactions between species.

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APPENDIX 1. Number of birds trapped per day per hectare of low Maquis at Jews' Gate, Gibraltar for each month of the year. Average for all study years. The percentage by numbers of individuals of each species in the community is also given.

Species	Birds/day/ha	% in community
January		
Wryneck	0.05	0.40
Blackcap(N)	4.57	38.87
Blackcap(L)	1.00	8.50
Sardinian Warbler	1.48	12.55
Chiffchaff	0.48	4.05
Blue Rock Thrush	0.10	0.81
Black Redstart	0.57	4.86
Robin	2.33	19.84
Blackbird	0.52	4.45
Song Thrush	0.10	0.81
Blue Tit	0.38	3.24
Chaffinch	0.10	0.81
Serin	0.10	0.81
February		
Hoopoe	0.07	0.39
Blackcap(N)	10.29	56.25
Blackcap(L)	0.89	4.88
Sardinian Warbler	0.96	5.27
Dartford Warbler	0.04	0.20
Chiffchaff	0.79	4.30
Stonechat	0.04	0.20
Black Redstart	0.43	2.34
Robin	2.21	12.11
Blackbird	0.82	4.49
Song Thrush	0.32	1.76
Blue Tit	0.39	2.15
Short-toed Tree Creeper	0.04	0.20
Rock Bunting	0.04	0.20
Chaffinch	0.07	0.39
Serin	0.21	1.17
Greenfinch	0.18	0.98
House Sparrow	0.50	2.73
March		
Scops Owl	0.06	0.47
Hoopoe	0.10	0.78
Wryneck	0.02	0.16
Wren	0.06	0.47
Dunnock	0.02	0.16
Blackcap(N)	6.62	51.32
Blackcap(L)	0.76	5.89
Sardinian Warbler	0.88	6.82
Subalpine Warbler	0.12	0.93
Willow Warbler	0.36	2.79
Chiffchaff	1.22	9.46
Blue Rock Thrush	0.02	0.16
Black Redstart	0.26	2.02

Robin	0.88	6.82
Blackbird	0.32	2.48
Redwing	0.02	0.16
Song Thrush	0.16	1.24
Blue Tit	0.10	0.78
Chaffinch	0.06	0.47
Serin	0.22	1.71
Greenfinch	0.16	1.24
Goldfinch	0.02	0.16
Linnet	0.02	0.16
House Sparrow	0.79	3.41

April

Little Owl	0.02	0.17
Scops Owl	0.10	0.84
Turtle Dove	0.02	0.17
Tree Pipit	0.10	0.84
Woodchat Shrike	0.02	0.17
Wren	0.02	0.17
Melodious Warbler	0.06	0.50
Orphean Warbler	0.16	1.34
Garden Warbler	0.27	2.35
Blackcap(N)	1.69	14.43
Blackcap(L)	0.80	6.88
Whitethroat	0.37	3.19
Sardinian Warbler	1.18	10.07
Subalpine Warbler	0.41	3.52
Spectacled Warbler	0.04	0.34
Willow Warbler	1.24	10.57
Chiffchaff	0.57	4.87
Bonelli's Warbler	0.37	3.19
Pied Flycatcher	0.22	1.85
Spotted Flycatcher	0.02	0.17
Whinchat	0.04	0.34
Wheatear	0.02	0.17
Black-eared Wheatear	0.04	0.34
Blue Rock Thrush	0.04	0.34
Redstart	0.33	2.85
Robin	0.31	2.68
Nightingale	1.22	10.40
Blackbird	0.53	4.53
Song Thrush	0.04	0.34
Blue Tit	0.14	1.17
Ortolan Bunting	0.08	0.67
Chaffinch	0.04	0.34
Serin	0.08	0.67
Greenfinch	0.14	1.17
Goldfinch	0.24	2.01
Linnet	0.24	2.01
House Sparrow	0.50	4.19
Golden Oriole	0.02	0.17

May

Little Owl	0.04	0.42
Turtle Dove	0.02	0.21
Red-necked Nightjar	0.04	0.42
Wryneck	0.04	0.42
Tree Pipit	0.02	0.21
Woodchat Shrike	0.06	0.63
Wren	0.15	1.47
Reed Warbler	0.21	2.10
Melodious Warbler	1.09	10.71

Olivaceous Warbler	0.06	0.63
Orphean Warbler	0.26	2.52
Garden Warbler	0.98	9.66
Blackcap(N)	0.23	2.31
Blackcap(L)	0.81	7.98
Whitethroat	0.09	0.84
Sardinian Warbler	1.45	14.29
Subalpine Warbler	0.09	0.84
Spectacled Warbler	0.02	0.21
Willow Warbler	0.62	6.09
Bonelli's Warbler	0.28	2.73
Pied Flycatcher	0.34	3.36
Spotted Flycatcher	0.45	4.41
Redstart	0.15	1.47
Nightingale	0.21	2.10
Blackbird	0.55	5.46
Blue Tit	0.30	2.94
Ortolan Bunting	0.09	0.84
Serin	0.04	0.42
Greenfinch	0.04	0.42
Goldfinch	0.02	0.21
House Sparrow	1.24	13.24
Spotless Starling	0.04	0.42

<u>June</u>

Tree Pipit	0.04	0.38
Wren	0.21	1.92
Melodious Warbler	0.21	1.92
Orphean Warbler	0.04	0.38
Blackcap(L)	1.17	10.77
Sardinian Warbler	4.38	40.38
Blue Rock Thrush	0.08	0.77
Nightingale	0.13	1.15
Blackbird	1.29	11.92
Blue Tit	0.46	4.23
Serin	0.04	0.38
Greenfinch	0.13	1.15
House Sparrow	2.58	23.85
Spotless Starling	0.08	0.77

<u>July</u>

Wren	0.47	1.96
Melodious Warbler	0.60	2.52
Blackcap(L)	3.73	15.69
Sardinian Warbler	13.0	54.62
Blue Rock Thrush	0.13	0.56
Nightingale	0.20	0.84
Blackbird	2.67	11.20
Blue Tit	0.53	2.24
House Sparrow	2.40	10.08
Spotless Starling	0.07	0.28

August

Woodchat Shrike	0.08	0.66
Wren	0.21	1.64
Reed Warbler	0.13	0.98
Melodious Warbler	0.42	3.28
Orphean Warbler	0.04	0.33
Garden Warbler	0.04	0.33
Blackcap(L)	1.79	14.10
Whitethroat	0.04	0.33
Sardinian Warbler	5.08	40.00
Willow Warbler	0.13	0.98
Chiffchaff	0.08	0.66
Bonelli's Warbler	0.04	0.33
Pied Flycatcher	0.04	0.33
Spotted Flycatcher	0.04	0.33
Blue Rock Thrush	0.04	0.33
Nightingale	0.04	0.33
Blackbird	1.79	14.10
Blue Tit	0.13	0.98
Greenfinch	0.08	0.66
House Sparrow	2.46	19.34

September

Turtle Dove	0.02	0.28
Red-necked Nightjar	0.02	0.28
Wren	0.12	1.67
Reed Warbler	0.02	0.28
Melodious Warbler	0.08	1.11
Garden Warbler	0.23	3.33
Blackcap(N)	0.02	0.28
Blackcap(L)	1.77	25.56
Whitethroat	0.04	0.56
Sardinian Warbler	1.90	27.50
Spectacled Warbler	0.04	0.56
Willow Warbler	0.25	3.61
Bonelli's Warbler	0.02	0.28
Pied Flycatcher	0.12	1.67
Stonechat	0.02	0.28
Rufous Bush Chat	0.02	0.28
Blue Rock Thrush	0.08	1.11
Redstart	0.02	0.28
Robin	0.08	1.11
Nightingale	0.21	3.06
Blackbird	1.31	18.89
Blue Tit	0.27	3.89
Ortolan Bunting	0.04	0.56
Greenfinch	0.02	0.28
House Sparrow	0.23	3.33

October

Wryneck	0.02	0.18
Wren	0.08	0.92
Dunnock	0.06	0.73
Reed Warbler	0.02	0.18
Garden Warbler	0.06	0.73
Blackcap(N)	2.06	23.49

Blackcap(L)	1.19	8.07
Sardinian Warbler	1.00	11.38
Spectacled Warbler	0.02	0.18
Willow Warbler	0.11	1.28
Chiffchaff	0.29	3.30
Firecrest	0.04	0.37
Pied Flycatcher	0.10	1.10
Spotted Flycatcher	0.02	0.18
Stonechat	0.05	0.55
Blue Rock Thrush	0.02	0.18
Black Redstart	0.18	2.02
Redstart	0.11	1.28
Robin	1.71	19.45
Nightingale	0.02	0.18
Blackbird	0.77	8.81
Song Thrush	0.16	1.83
Blue Tit	0.34	3.85
Short-toed Tree Creeper	0.02	0.18
Chaff9nch	0.03	0.37
Serin	0.21	2.39
Greenfinch	0.21	2.39
Goldfinch	0.03	0.37
Linnet	0.02	0.18
House Sparrow	0.34	3.85

November

Nightjar	0.03	0.16
Wren	0.03	0.16
Dunnock	0.41	2.43
Blackcap(N)	4.46	26.74
Blackcap(L)	0.68	4.05
Sardinian Warbler	1.68	10.05
Chiffchaff	1.19	7.13
Firecrest	0.22	1.30
Black Redstart	0.59	3.57
Robin	4.49	26.90
Blackbird	1.03	6.16
Song Thrush	0.22	1.30
Blue Tit	0.19	1.13
Rock Bunting	0.08	0.49
Chaffinch	0.27	1.62
Serin	0.11	0.65
Greenfinch	0.51	3.08
Goldfinch	0.08	0.49
House Sparrow	0.43	2.59

December

Alpine Accentor	0.03	0.19
Dunnock	0.05	0.38
Blackcap(N)	4.95	36.35
Blackcap(L)	0.87	6.40
Sardinian Warbler	1.46	10.73
Dartford Warbler	0.03	0.19
Chiffchaff	0.72	5.27
Firecrest	0.15	1.13
Stonechat	0.03	0.19
Blue Rock Thrush	0.08	0.56
Black Redstart	0.85	6.21
Robin	3.15	23.16
Blackbird	0.36	2.64
Song Thrush	0.13	0.94

Blue Tit	0.23	1.69
Chaffinch	0.05	0.38
Serin	0.08	0.56
Goldfinch	0.05	0.38
House Sparrow	0.36	2.64

APPENDIX 2. Main foraging strata and foods of Passeriformes in low Maquis and Garigue at Gibraltar.

Species	Stratum/Food
Short-toed Lark	GI
Crested Lark	GP
Sky Lark	GP
Sand Martin	AI
Crag Martin	AI
Swallow	AI
Red-rumped Swallow	AI
House Martin	AI
Tawny Pipit	GI
Tree Pipit	GI
Meadow Pipit	GI
Yellow Wagtail	GI
Grey Wagtail	GI
White Wagtail	GI
Woodchat Shrike	GI
Great Grey Shrike	GI
Wren	GI
Alpine Accentor	GP
Dunnock	GP
Reed Warbler	FI
Melodious Warbler	FI
Olivaceous Warbler	FI
Orphean Warbler	FI
Garden Warbler	FI/P
Blackcap	FI/P
Whitethroat	FI
Sardinian Warbler	FI/P
Subalpine Warbler	FI
Spectacled Warbler	FI
Dartford Warbler	FI
Willow Warbler	FI
Chiffchaff	FI
Bonelli's Warbler	FI
Firecrest	FI
Fan-tailed Warbler	FI
Pied Flycatcher	A/FI
Spotted Flycatcher	A/FI
Whinchat	GI
Stonechat	GI
Wheatear	GI
Black-eared Wheatear	GI
Rufous Bush Chat	GP
Blue Rock Thrush	GP
Black Redstart	GI
Redstart	GI
Robin	GP
Nightingale	GP
Bluethroat	GP
Ring Ouzel	GP
Blackbird	GP
Song Thrush	GP
Blue Tit	FI
Great Tit	FI
Short-toed Tree Creeper	FI +
Corn Bunting	GP
Rock Bunting	GP

Ortolan Bunting	GP
Cirl Bunting	GP
Chaffinch	GG
Serin	GG
Greenfinch	FG
Goldfinch	FG
Linnet	GG
House Sparrow	GP
Spotless Starling	GP

Strata: First letter, G = Ground, F = Foliage, A = Aerial

Foods: Second letter, I = Insectivore, G = Granivore,
P = Polyphage

+ Strictly a bark insectivore but lumped here for convenience.

APPENDIX 3. Amount of foliage arthropod and fruit food in different seasons at Jews' Gate, Gibraltar.

(a) Arthropods

Season	$\bar{x}$	Max.	Min.	N	s.d.
Autumn	5.93	26.31	0.06	6	10.09
Winter	11.75	45.10	0	6	17.48
Spring	13.33	60.13	0.06	7	21.08
Summer	3.15	11.27	4.8^{-3}	7	3.79

Data calculated from mean for different bush species in Table 3.20. Ground arthropod data in Table 3.22.

(b) Berries

Plant Species	Ripe Berries Present			
	Autumn	Winter	Spring	Summer
Wild Olive	+	+		
Buckthorn			+	+
Osyris	+	+		
Lentisc	+	+		
Rubia	+			
Asparagus		+		
NO Species	4	4	1	1

A10

APPENDIX 4. Built-up areas in Gibraltar.

Early 19th century ⊡ 1979 ⊠

