The ecology of three species of warblers, Sylviidae, in scrubland in south east Scotland.

by

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Declaration

I declare that this thesis has been composed by myself and that the results it contains have not been submitted in whole or in part for any other degree.

S.R.D. da Prato.

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Absract

Willow Warblers, Phylloscopus trochilus, Whitethroats, Sylvia communis, and Sedge Warblers, Acrocephalus schoenobaenus, were studied from 1979-1982 in scrub in Midlothian, Scotland. Some breeding birds were present in the site between April and August but most birds arrived in May and left in July. Males usually arrived before females with Willow Warblers the earliest and Sedge Warblers the latest species. Arrival timing showed some links with weather. One year old birds were no later than older birds. Most birds were single brooded though some Willow Warblers and Whitethroats reared second broods with different mates. Females varied considerably in the time spent between arrival and egg laying. Late broods tended to be lighter, or smaller in number, than earlier broods. Mammal predation was the main cause of egg and chick loss; very few chicks starved. Some Willow Warblers started moult before their young fledged. Some Willow Warblers and all Whitethroats left before moult was complete. Adult moult in Willow Warblers took 38-45 days. Chicks from late broods, and in some cases their parents, tended to spend less time on the site after fledging than birds from earlier nests. Juveniles of all species left the site before completion of post juvenile moult, probably to undertake local dispersal. Estimates of the duration of post juvenile moult were 36-40 days for Willow Warblers, 31-37 days for Whitethroats and around 30 days for Sedge Warblers. No birds achieved pre migratory weight gains.

There were links between the birds' breeding cycles and available prey. Invertebrate biomass peaked earlier in trees and shrubs than in herbs and this was reflected in the birds' feeding stations, though there were interspecific differences in prey choice, feeding methods and use of the vegetation for feeding and nesting. Willow Warblers made more use of trees and tall shrubs than the other species, which made more use of herbaceous vegetation, and this was reflected in the composition of the birds' territories. Birds collected different proportions of prey for their young than they ate themselves.

The return rates of adult Willow Warblers were 48% for males and 42% for females but only 5% for juveniles. The return rates of Whitethroats were 33% for adult males, 24% for adult females and 2.7% for juveniles. The return rates of adult Sedge Warblers were 22% for males, 25% for females and 3.9% for juveniles. These data imply that one year old warblers are markedly less site faithful than older birds and that Whitethroat and Sedge Warbler populations may be in decline.

In 1982 all warbler species were censused over 16.22 km^2 of predominantly agricultural land. Numbers were much higher in woods and former industrial land than farmland since most farm hedges held few or no warblers.

It is argued that the relatively short time that these three species of warblers spent in south east Scotland is a response both to the available food supply on their breeding grounds and to conditions on their migration routes to and from tropical Africa.

Contents

Chapter 1 Introduction

1:1 General introduction

The warblers, Sylviidae, constitute one of the most important families of passerine birds in Europe with some 26 breeding species (Voous 1960). There are considerable differences in the number of warbler species breeding in different regions with a tendency for Mediterranean and central Europe to support the greatest variety and a marked decline in the number of breeding species to the north west; Voous (1960) shows 19 species breeding in Austria, 18 in Portugal but only 12 in the British Isles although 15 species of warbler breed as far north as Finland. Within the British Isles fewer species breed in Scotland than in England and the densities of several species in Scotland are probably lower (Sharrock 1976) although quantitative evidence of the latter point is rather scarce except for some woodlands, mainly in western Scotland, (eg. Williamson 1969, 1972, 1974a, 1974b, 1976 and Moss 1978).

Lack (1971) suggested that the reduction in the diversity of breeding warblers in north west Europe was due to a relatively impoverished invertebrate food supply, which meant that fewer bird species occupied wider ecological niches than in regions where food was more abundant. Most work on warbler ecology has concentrated on possible competition between congeneric species (eg.Cody 1978) although as Cody has pointed out European warblers show considerable habitat overlap between disgeneric species.

In Britain relevant information on aspects of warbler biology has been gathered at bird observatories (Davis 1967, Riddiford & Findley 1981) through the British Trust for Ornithology's (BTO) nest record scheme (Cramp 1955, Mason 1976, Bibby 1978), ringing scheme (Spencer & Hudson 1982, da Prato & da Prato 1983) and moult enquiry (Ginn & Melville 1983).

Although these methods have produced large amounts of data their usefulness is limited by a number of biases in the effort and distribution of observers and ringers (Mead 1974) in seasonal variation which can affect nest recording (Newton 1964) and in the effects of weather, which is the major influence on the numbers of birds seen at coastal observatories (Lack 1963). Also the way in which breeding, moult and migration interact requires more detailed study, ideally of individually recognizable birds.

Relatively few such studies have been carried out. Apart from work on the small and sedentary populations of Dartford Warblers, Sylvia undata, (Bibby 1979) and Cetti's Warblers, Cettia cetti, (Bibby 1982) in southern England effort has recently been concentrated on comparisons of the breeding (eg. Catchpole 1972, 1973) and migration systems (Bibby,Green,Pepler&Pepler 1976,Bibby&Green 1981) of Reed Warblers, Acrocephalus scirpaceus, and Sedge Warblers, Acrocephalus schoenobaenus, though some work has also been done on the relationships between Willow Warblers, Phylloscopus trochilus, and Wood Warblers, Phylloscopus sibilatrix, (Edington & Edington 1972). The best accounts of the breeding biology of several British species are still those

of Howard (1907-14) and, for the Willow Warbler, that of May (1949) ; neither of these workers marked their birds which meant that observations away from the nest were limited.

In Scotland the best account of breeding warblers is still Brock's (1910) work on Willow Warblers in Midlothian though MacDonald (1979) has recently published observations on a small number of Whitethroats, Sylvia communis, in northern Scotland ; again these studies were carried out on unmarked birds. No comprehensive account of the breeding biology of other species of warblers in Scotland has been published though McMillan (1978) has published some data on Sedge Warblers in reed beds on the Tay estuary.

Preliminary work by the author in Midlothian between 1973 and 1978 using mist netting and Common Bird Census (CBC) techniques had indicated that in south east Scotland breeding warblers had a shorter season than that quoted in standard reference works (eg. Baxter & Rintoul 1953, Witherby,Jourdain,Tucker&Ticehurst 1938-41)and raised questions over the birds' ability to rear more than one brood, complete moult and acquire energy reserves before starting autumn migration. Examination of the sites where warblers were caught in nets suggested that there might be differences in feeding stations during the season and a trial programme of invertebrate sampling indicated that this was linked to changes in food availability,which might help explain the timing of arrival and departure (da Prato & da Prato 1977).

1:2 Aims of the study

The aim of the study was to compare the ecology of the three most common warbler species breeding in Scotland, the Willow Warbler, the Whitethroat and the Sedge Warbler. In particular the following aspects were examined in detail :

The dates of arrival and departure of breeding birds.

The timing and number of breeding attempts.

The timing of departure by the young.

Breeding success in the three species.

The timing of moult in adults and juveniles.

Weight changes throughout the season and especially before departure.

Site tenacity and recruitment to the breeding population.

Habitat preference.

The birds' choice of feeding sites and prey for themselves and their young.

The relative abundance of potential invertebrate prey throughout the time the warblers were present.

1:3 The study area

The main study site was a 10.4 hectare area of scrub in a shallow valley 110-140 metres above sea level in Midlothian (55°55'N 2°59'W , Figure 1). The valley consists of two approximately equal parts . The western end has been regenerating naturally from horticultural land since at least 1945. It holds large areas of hawthorn, Crataegus monogyna, and appreciable amounts of birch, Betula sp., willow, Salix caprea, elder, Sambucus nigra, wild rose, Rosa canina, broom, Cytisus scoparius, gorse, Ulex europaeus, and bramble, Rubus sp. Among the scrub are areas of grass and taller herbaceous plants, notably perennial nettle, Urtica dioica, sometimes mixed with bishop weed, Aegopodium podagraria, and stands of rosebay willowherb, Epilobium angustifolium. There are also a few deciduous trees, mainly on or near the boundaries, including wych elm, Ulmus procera, ash, Fraxinus excelsior, and one or two each of beech Fagus sylvatica, and sycamore, Acer pseudoplatanus. A major factor in the development of this varied habitat has been the exclusion of livestock and occasional cutting of the trees and larger bushes for firewood.

By contrast the eastern end was used by cattle in the four years when the study was carried out. Several large areas of hawthorn with smaller amounts of gorse, rose, bramble and willow exist in the grazed end in the form of thickets and two large boundary hedges. Herbs and creepers are scarce and only exist inside thickets where they are protected from grazing animals. An overgrown orchard occupied

FIGURE 1 THE MAIN STUDY SITE AND ITS VEGETATION

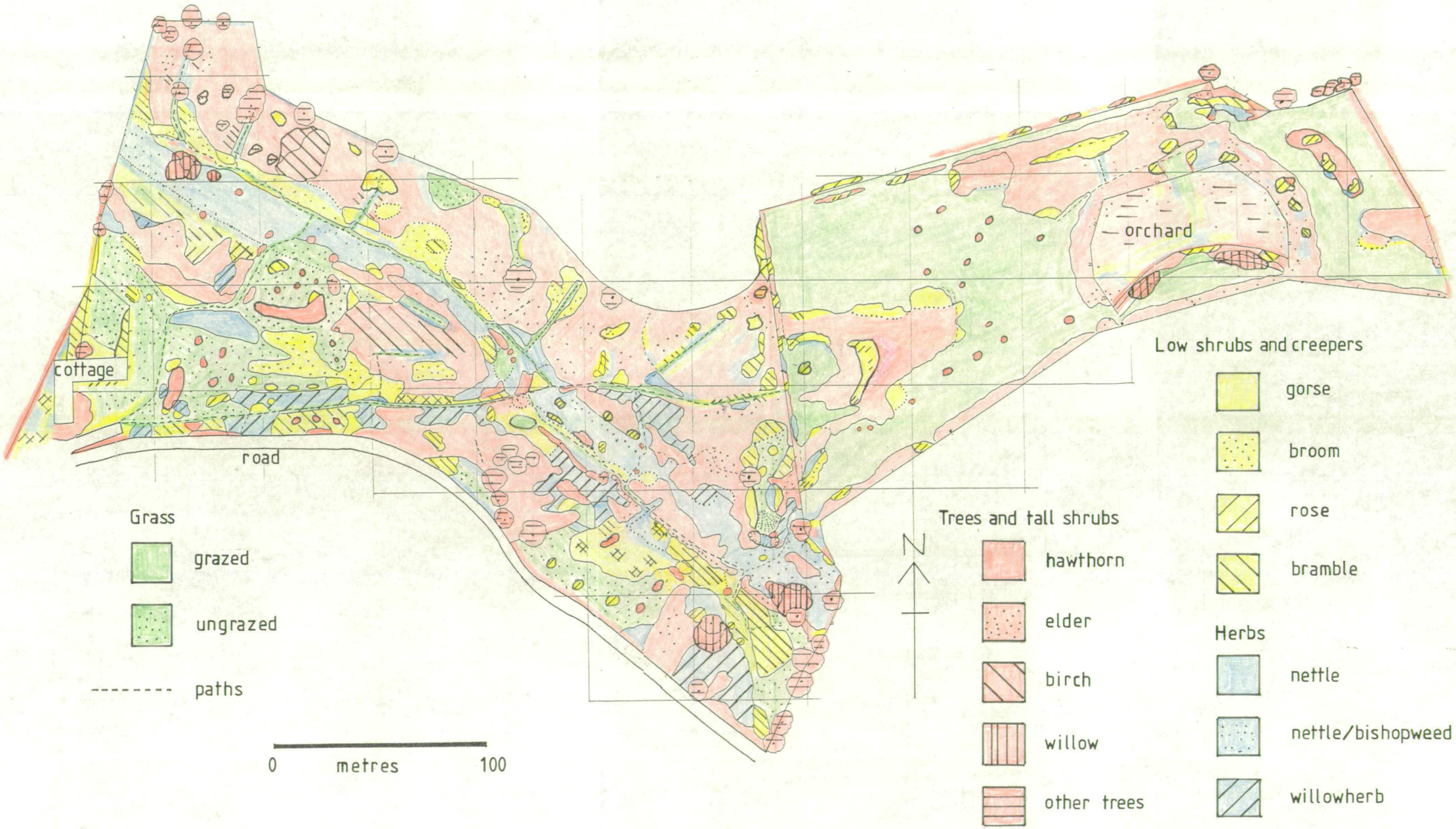
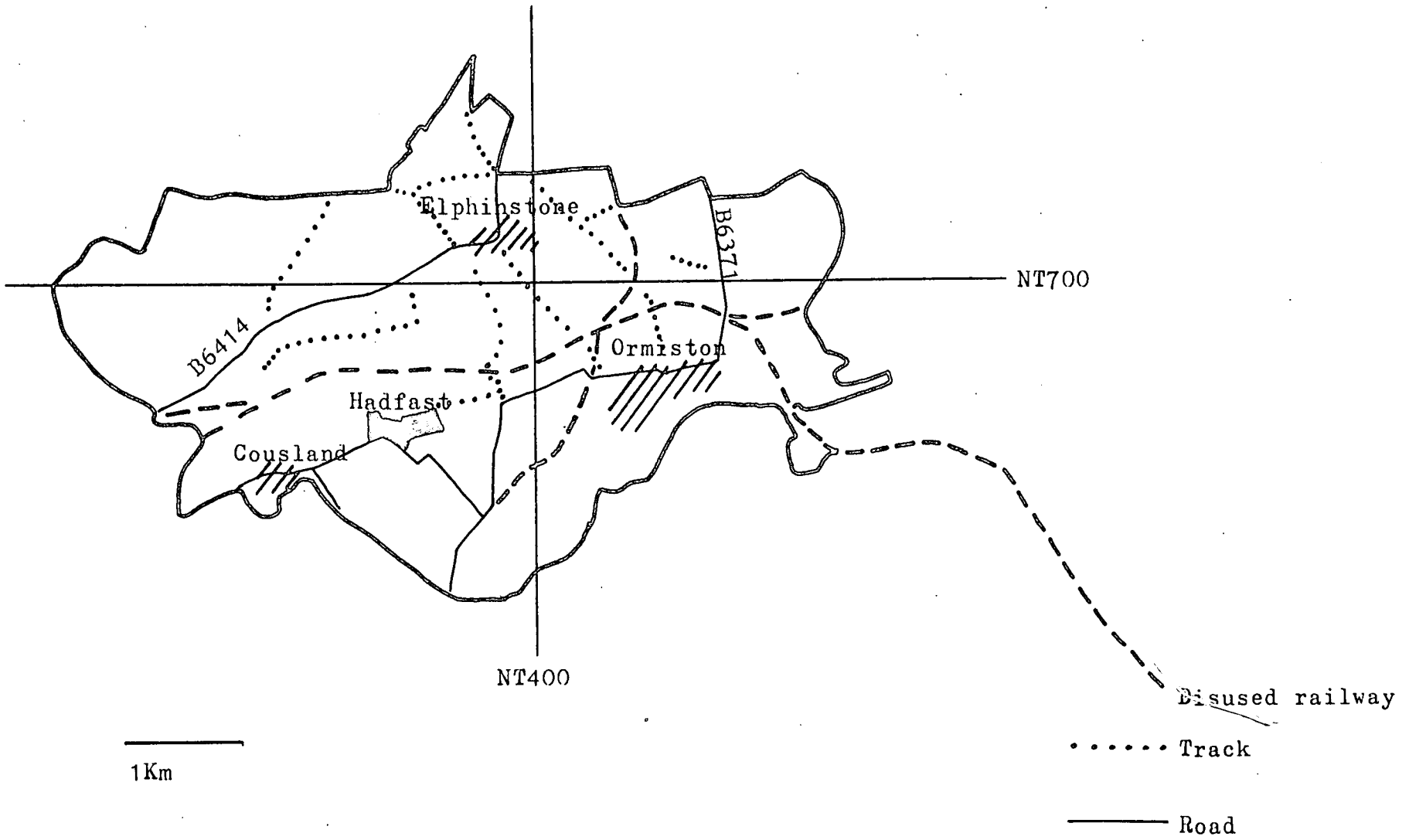


Figure 2 The location of the main study site at Hadfast Valley and the larger area in which warblers were censused in 1982.



3303 m^2 of the grazed end and, since livestock were excluded, the ground flora was more developed in the orchard than outside it.

Warblers were also studied, less intensively, in the surrounding countryside. A progressively larger area was involved each year until 1982 when 16.22 km^2 was covered (Fig. 2). This area was mainly high grade agricultural land devoted to arable farming. There were much smaller areas of permanent grazing and a variety of hedges, tree lines, ditches and shelterbelts. Besides the farms the area included three villages. Another important feature was the number of disused railway lines, which formerly served the coal mining industry, itself also defunct, although many colliery bings (spoil tips) and sidings remain to a greater or lesser extent now covered by vegetation. The larger study area also contained several small woods and plantations made up of a variety of native and exotic tree species.

The main study site was used for studies of breeding biology, moult, the timing of arrival and departure and feeding ecology. The larger study area was used to provide information on warbler numbers in different habitats and movements in and out of the main study site. More detailed accounts of how these studies were carried out can be found adjacent to the appropriate results.

Chapter 2 The timing of breeding, migration and moult.

2:1 Methods

A 50 metre square grid was superimposed on the 10.4 ha main study site using a sighting compass, ranging rods and a tape measure. Plastic markers tied to bushes proved satisfactory grid points except in a few open areas where piles of stones or stakes were used. A system of paths and mist net rides already in existence was extended in the 1978-79 winter and cleared out in February - March each year when the position of markers was also checked.

The site was visited daily between the end of March and late September in the three years 1979-1981. A route was walked around and through the site each day, usually just after dawn, but frequently in the evening as well, especially in the periods when birds were likely to be arriving or leaving the site.

The first birds to arrive in spring were invariably males. They were easily detected as they were mobile and vocal and most of the vegetation had not leafed out. As more males arrived they became even more territorial and therefore relatively easy to locate within a defined area. Although females did not sing, their arrival caused obvious behavioural changes in the males, which indicated those areas where females could be looked for.

Birds were caught in mist nets (see Spencer 1972 for details of the licensing procedures involved). Up to 26 nets totalling 415 metres in length were used each weekend. Nets were normally set around 1500 hours B.S.T. each Friday and netting continued until midday on Saturday, the nets being furled overnight, since early morning and evening proved by far the best times to catch birds. When unringed birds were found in the course of daily checks nets were erected in the appropriate area (there were net sites available

in all the warbler territories). If necessary a portable tape recorder was used to catch unringed birds by playing a continuous tape loop of the species' song near to the net. All adult warblers were given a unique combination of up to three plastic colour rings on one leg and a B.T.O. numbered metal ring on the other. Males were ringed with the metal ring on the right leg and the colours on the left. Females were given colour rings on the right leg and the B.T.O. ring on the left leg. All three species could be sexed on the presence or absence of brood patches (females) and cloacal protuberances (male)(Svensson 1975). In addition virtually all adult Willow Warblers could be sexed on wing length (males $>$ 66mm, females $<$ 66mm) and Whitethroats on the plumage characteristics described by Svensson (1975). Decisions made on all these criteria were checked by observation of the birds' behaviour in the field. Feather wear allowed some Willow Warblers and Whitethroats to be aged as one year old birds in spring. The absence of tongue spots gave an indication if Sedge Warblers were older than one year. Since ringing had taken place in the area since 1973 a number of birds were of known age (i.e. ringed as nestlings or juveniles) and others could be given a minimum age (e.g. 3 years or more in 1979 if ringed as an adult in 1977.) In the course of daily checks the position of colour ringed birds was noted on base maps incorporating the 50 metre grid, net sites and paths and other land marks. Notes were made of the birds' behaviour since this was often a good guide to the stage of the breeding cycle: for example adult behaviour changed markedly when their eggs started to hatch. Nests were found largely by watching the adults (see also Ch.3) and nestlings were colour ringed around six to eight days old. Departure dates were taken as the last day a bird was recorded in the study site in a particular

year. In a few cases birds disappeared for several days in the late summer, and reappeared, before finally departing. Accurate data on the timing of departure were harder to obtain than with arrivals, although intensive daily observation on a small site, backed up by the use of mist nets and tape recordings, made it unlikely that a bird could escape detection for long.

Moult was studied in the juveniles of all three species since they undergo a partial (post juvenile) moult before flying to Africa, and also in adult Willow Warblers and Whitethroats, but not Sedge Warblers which moult south of the Sahara (Svensson 1975, Ginn & Melville 1983). In adults moult was recorded using the scoring method outlined by Snow (1967) which involves giving a number from 0-5 to each primary feather in one wing, since for practical purposes wing moult encompasses the duration of moult in all other feather tracts. This method is open to criticism basically on the grounds that primary feathers are of unequal length and therefore the true rate of moult must be non-linear (see Summers, Swann & Nicholl 1983 for discussion). In practice the problem seems to be much less acute in small passerines than larger birds (Newton 1966) and can be avoided if the same bird can be trapped several times during moult since daily increments can then be calculated. No agreed method exists for scoring the body and small wing feathers of a bird. This is relatively unimportant with adults, but must be dealt with if post juvenile moult is to be quantified, since these birds only moult body feathers and a variable proportion of their wing coverts. Post juvenile moult was recorded in 1980 and 1981 in the following way. Three areas were scored. They were underparts, upperparts and head. These areas were chosen as they were the feather tracts consistently

found to be moulted by all three species. Each area was scored from 0-5 giving a maximum score of 15 when post juvenile moult was complete. The same scoring system was used for adults and juveniles but maximum scores differed as the ten primaries of an adult's wing gave a score of 50 when moult was complete. The scoring system was as follows:

old feather	0
feather dropped - new feather in pin	1
pin burst - 1/3 grown	2
1/3 - 2/3 grown	3
2/3 - full grown with sheaths	4
new feather complete without wax sheaths	5

2:2 The timing of arrivals

The arrival and departure dates of all individually colour ringed Willow Warblers, Whitethroats and Sedge Warblers which held territory in the main study site for the three years 1979-1981 are shown in Tables 1-3. The most striking point to emerge from these data is the relatively short time most birds were present in the study site. The only group with arrivals before the end of April in all three years were male Willow Warblers. Apart from two unusually early male Whitethroats in 1980 all other males arrived in May. No females arrived before May apart from two early Willow Warblers in 1980. Few birds remained on the study site after mid August, with most departing in July, and a few individuals disappearing by the end of June.

There were interesting differences between sexes, species and years. In general males arrived earlier than females (Tables 1-3). This was most marked with Willow Warblers where males arrived significantly earlier than females (1979/80/81 male means 2nd May/ 1st May/23rd April: 1979/80/81 females 14th May/10th May/10th May) in all three years. Male Sedge Warblers were also earlier than females in all three years but only significantly so in 1979 and 1980 (1979/80/81 male means 20th/19th/19th May; 1979/80/81 females 26th/23rd/22nd May). With Whitethroats males arrived significantly earlier than females in only two out of the three years (1979/80 males 17th/13th May; 1979/80 females 25th/24th May; 1981 male 13th May female 14th May).

In view of these differences between the sexes annual comparisons for each species were examined for males and females separately and are also shown in Tables 1-3. There was no significant difference in the mean arrival dates of Willow Warbler males between 1979 and 1980 but arrival dates in 1981 were

Table 1 Arrival and departure dates of Willow Warblers that held territory in the main study site 1979-81.

Arrivals	MALES	DIFFERENCES BETWEEN SEXES	FEMALES	DIFFERENCES BETWEEN YEARS
1979 mean	2nd May		14th May	
S.D.	4.2		3.1	
range	28th Apr.-10th May		10th-19th May	
n	15*	(t=7.64, p<0.001)	13	
MALE				t=0.86, NS
FEMALE				t=1.50, NS
1980 mean	1st May		10th May	
S.D.	6.5		7.1	
range	16th Apr.-12th May		26th Apr.-25th May	
n	14	(t=3.70, p<0.001)	15	
MALE				t=2.65, p<0.02
FEMALE				NO DIFFERENCE
1981 mean	23rd April		10th May	
S.D.	9.4		3.4	
range	11th Apr.-10th May		4th -17th May	
n	19**	(t=7.22, p<0.001)	19	
MALE				t=3.34, p<0.01
FEMALE				t=2.71, p<0.02
1979 mean	2nd May		14th May	
Departures				
1979 mean	29th July		15th July	
S.D.	14.0		18.1	
range	30th June-12th Aug.		17th June-11th Aug.	
n	14***	(t=2.04, NS)	13	
MALE				t=0.80, NS
FEMALE				t=0.13, NS
1980 mean	24th July		14th July	
S.D.	12.8		20.2	
range	30th June-12th Aug.		12th June-5th Aug.	
n	14	(t=1.53, NS)	15	
MALE				t=1.69, NS
FEMALE				t=2.03, NS
1981 mean	15th July		2nd July	
S.D.	15.9		15.5	
range	18th June-8th Aug.		9th June-28th July	
n	18	(t=2.55, p<0.02)	20****	
MALE				t=2.39, p<0.05
FEMALE				t=2.23, p<0.05
1979 mean	29th July		15th July	

* includes one male killed after securing a territory and one unmated male.
**includes one male killed after securing a territory.

*** includes an unmated male.
**** the third female of the polygamous male was included in departures only.

Table 2 Arrival and departure dates of Whitethroats that held territory in the main study site 1979-81.

Arrivals	MALES	DIFFERENCES BETWEEN SEXES	FEMALES	DIFFERENCES BETWEEN YEARS
1979 mean	17th May		25th May	
S.D.	6.6		6.7	
range	12th-31st May		15th May-2nd June	
n	10*	(t=2.50, p<0.05)	9**	
MALE				t=1.03, NS
FEMALE				t=0.24, NS
1980 mean	13th May		24th May	
S.D.	10.4		7.9	
range	26th Apr.-28th May		11th May-1st June	
n	9	(t=2.40, p<0.05)	9***	
MALE				NO DIFFERENCE
FEMALE				t=3.09, p<0.01
1981 mean	13th May		14th May	
S.D.	6.6		4.8	
range	8th-25th May		9th-24th May	
n	8	(t=0.08, NS)	8	
MALE				t=1.17, NS
FEMALE				t=3.78, p<0.01
1979 mean	17th May		25th May	
Departures				
1979 mean	24th July		28th July	
S.D.	15.6		22.7	
range	18th June-11th Aug.		18th June- 23rd Aug	
n	10****	(t=0.41, NS)	9	
MALE				t=1.46, NS
FEMALE				t=0.37, NS
1980 mean	15th July		25th July	
S.D.	10.0		10.4	
range	30th June-30th July		12th July-15th Aug.	
n	9	(t=2.03, NS)	10	
MALE				t=0.68, NS
FEMALE				t=1.67, NS
1981 mean	20th July		16th July	
S.D.	16.7		11.6	
range	30th June-15th Aug.		28th June- 28th July	
n	8	(t=0.51, NS)	8	
MALE				t=0.57, NS
FEMALE				t=1.30, NS
1979 mean	24th July		28th July	

*includes an unmated male
** two late females were not included) second mates of
*** one late female was not included) double brooded males
**** includes an unmated male

Table 3 Arrival and departure dates of Sedge Warblers that held territory in the main study site 1979-81.

Arrivals	MALES	DIFFERENCES BETWEEN SEXES	FEMALES	DIFFERENCES BETWEEN YEARS
1979 mean	20th May		26th May	
S.D.	5.3		4.6	
range	15th-31st May		18th May-1st June	
n	12	(t=2.55, p<0.02)	12	
MALE				t=0.73, NS
FEMALE				t=1.45, NS
1980 mean	19th May		23rd May	
S.D.	2.6		4.1	
range	17th-26th May		18th-28th May	
n	10	(t=2.41, p<0.05)	10	
MALE				t=0.11, NS
FEMALE				t=0.26, NS
1981 mean	19th May		22nd May	
S.D.	5.0		5.5	
range	8th-25th May		17th May-2nd June	
n	11*	(t=1.44, NS)	10	
MALE				t=0.71, NS
FEMALE				t=1.54, NS
1979 mean	20th May		26th May	
Departures				
1979 mean	4th August		2nd August	
S.D.	8.3		9.8	
range	20th July-15th Aug.		14th July-19th Aug.	
n	12	(t=0.51, NS)	12	
MALE				t=0.88, NS
FEMALE				t=0.10, NS
1980 mean	31st July		1st August	
S.D.	7.8		7.0	
range	15th July-11th Aug.		20th July-14th Aug.	
n	10	(t=0.23, NS)	10	
MALE				t=0.75, NS
FEMALE				t=0.63, NS
1981 mean	3rd August		4th August	
S.D.	8.3		9.7	
range	21st July-19th Aug.		18th July- 19th Aug.	
n	11*	(t=0.12, NS)	10	
MALE				t=0.11, NS
FEMALE				t=0.48, NS
1979 mean	4th August		2nd August	

* include one unmated male

significantly earlier than in the two previous years. Female Willow Warblers showed a different year to year pattern since the mean arrival date in 1979 was significantly later than in 1981 but there was no significant difference in mean arrival dates between 1979 and 1980 or 1980 and 1981.

Whitethroat males showed no significant differencesin the timing of arrivals between years. Whitethroat females showed no significant difference in arrival timing between 1979 and 1980 but in 1981 they were significantly earlier than in the two previous years.

Male and female Sedge Warblers showed no significant differences in arrival dates between years.

Comparisons of the timing of arrivals between species were made separately for each sex and season and are shown in Table 4. Male Willow Warblers arrived significantly earlier than both male Whitethroats and male Sedge Warblers in all three years. Differences between Whitethroat and Sedge Warbler males were much less clear cut. In all three years mean arrival dates of male Whitethroats were earlier than male Sedge Warblers but not significantly so.

Female Willow Warblers arrived significantly earlier than female Whitethroats in 1979 and 1980 but in 1981 the difference was not statistically significant. Female Willow Warblers also arrived significantly earlier than female Sedge Warblers in all three seasons. There was no significant difference in mean arrival dates between female Whitethroats and Sedge Warblers in 1979 and 1980 but female Whitethroats were significantly earlier in 1981 than female Sedge Warblers.

Table 4 Comparisons of the timing of arrivals between Willow Warblers, Whitethroats and Sedge Warblers 1979,1980 and 1981.

		Willow Warbler	Whitethroat	Sedge Warbler	Willow Warbler
1979 MALES	n	15	10	12	15
	mean	2/5	17/5	20/5	2/5
	range	28/4-10/5	12/5-31/5	15/5-31/5	28/4-10/5
			t=6.66 p<0.001	t=1.13 NS	t=9.49 p<0.001
FEMALES	n	13	9	12	13
	mean	14/5	25/5	26/5	14/5
	range	10/5-19/5	15/5-2/6	18/5-1/6	10/5-19/5
			t=5.25 p<0.001	t=0.19 NS	t=7.48 p<0.001
1980 MALES	n	14	9	10	14
	mean	1/5	13/5	19/5	1/5
	range	16/4-12/5	26/4-28/5	17/5-26/5	16/4-12/5
			t=3.39 p<0.01	t=1.64 NS	t=8.13 p<0.001
FEMALES	n	15	9	10	15
	mean	10/5	24/5	23/5	10/5
	range	26/4-25/5	11/5-1/6	18/5-28/5	26/4-25/5
			t=4.32 p<0.001	t=0.50 NS	t=4.87 p<0.001
1981 MALES	n	19	8	11	19
	mean	23/4	13/5	19/5	23/4
	range	11/4-10/5	8/5-25/5	8/5-25/5	11/4-10/5
			t=5.27 p<0.001	t=1.88 NS	t=8.22 p<0.001
FEMALES	n	19	8	10	19
	mean	10/5	14/5	22/5	10/5
	range	4/5-17/5	9/5-24/5	17/5-2/6	4/5-17/5
			t=2.02 NS	t=3.24 p<0.01	t=6.97 p<0.001

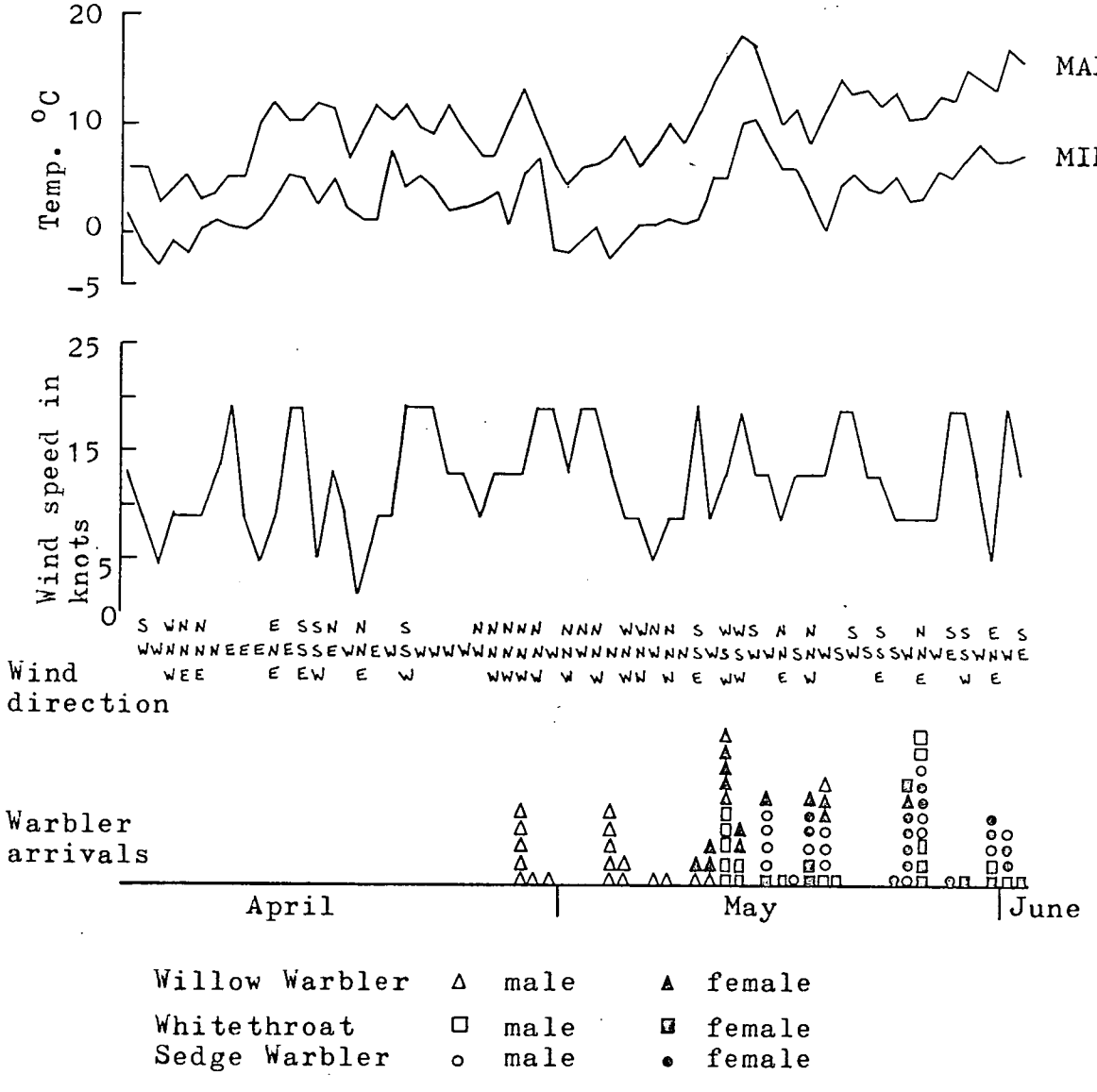
Only birds that stayed to breed or attempted to breed are included.

2:3 Arrivals in relation to weather

The data indicated consistent differences in the timing of arrivals between the sexes and, to some extent, between the species but with some seasonal variation (with 1979 the latest season for most groups and 1981 the earliest). Figures 3-5, which include all birds which arrived in the study site whether they secured a territory or not, show that several birds often arrived on the same day whereas none at all arrived on other days. Since weather conditions were likely to affect warblers moving north through Britain, data on temperature and wind speed and direction from the nearest comparable site are also shown in Figs. 3-5 although it is stressed that local weather conditions by themselves are inadequate to explain when individual migrants arrive at a breeding site. The dates when groups of birds arrived in the study site sometimes lagged slightly behind peaks in temperature which could be the result of the time needed for a bird to fly to its breeding site from a point further south where the change in local weather conditions did not occur at the same time as in S.E.Scotland.

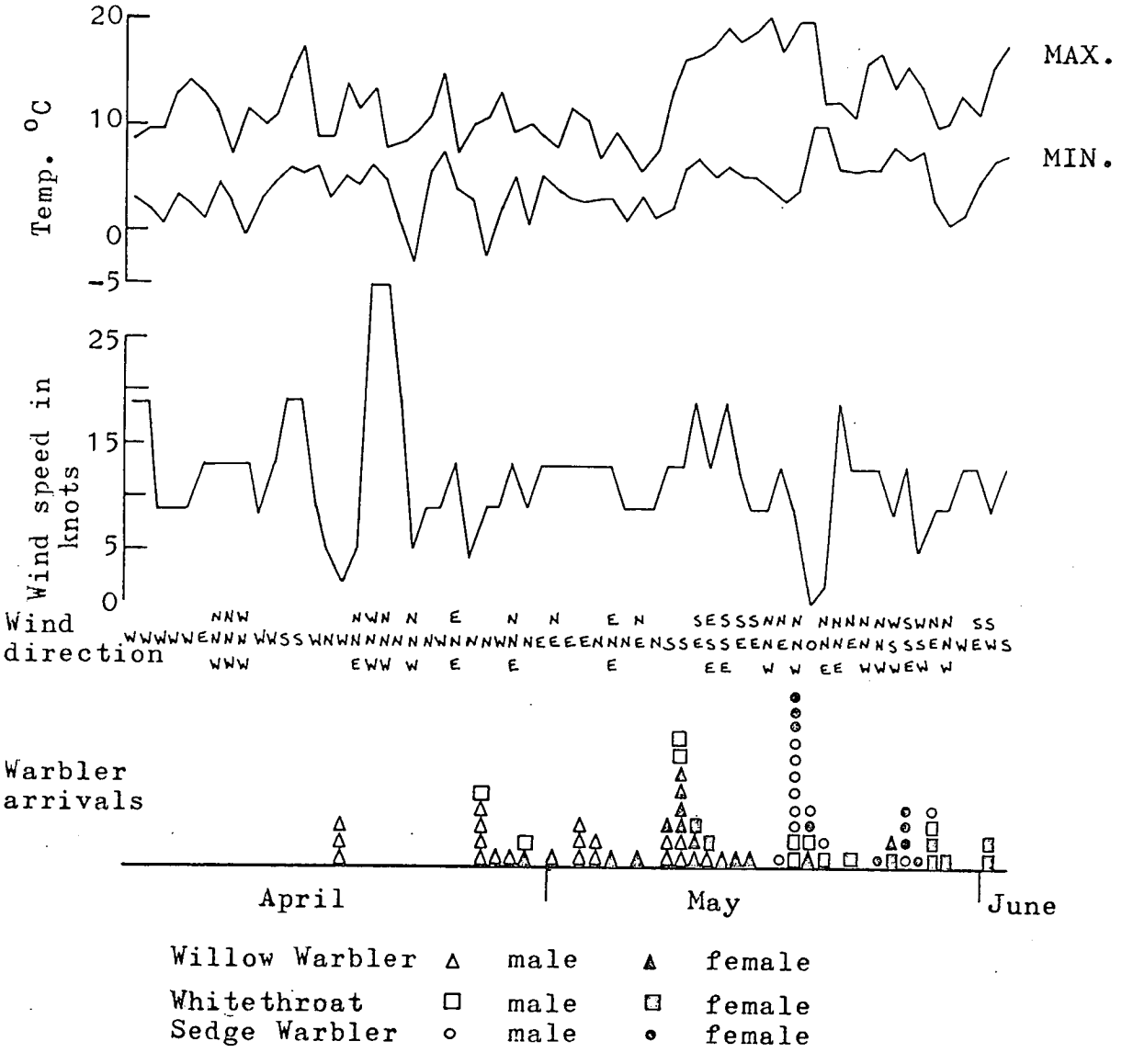
The effects of weather were most marked with the earliest arrivals. For example, in 1981 seven Willow Warblers arrived between 11th-13th April following an anticyclonic period, which produced light winds and maximum temperatures around 17°C locally and around 20°C in southern England (Meteorological Office Reports), although the temperature was falling locally as the birds arrived. No Willow Warblers arrived between 14th-15th April when unsettled thundery weather affected southern England but another eight birds did so between 16th and 18th April as the weather cleared to the south and local temperatures increased. Temperatures

Figure 3 The arrival of warblers in relation to weather in 1979.



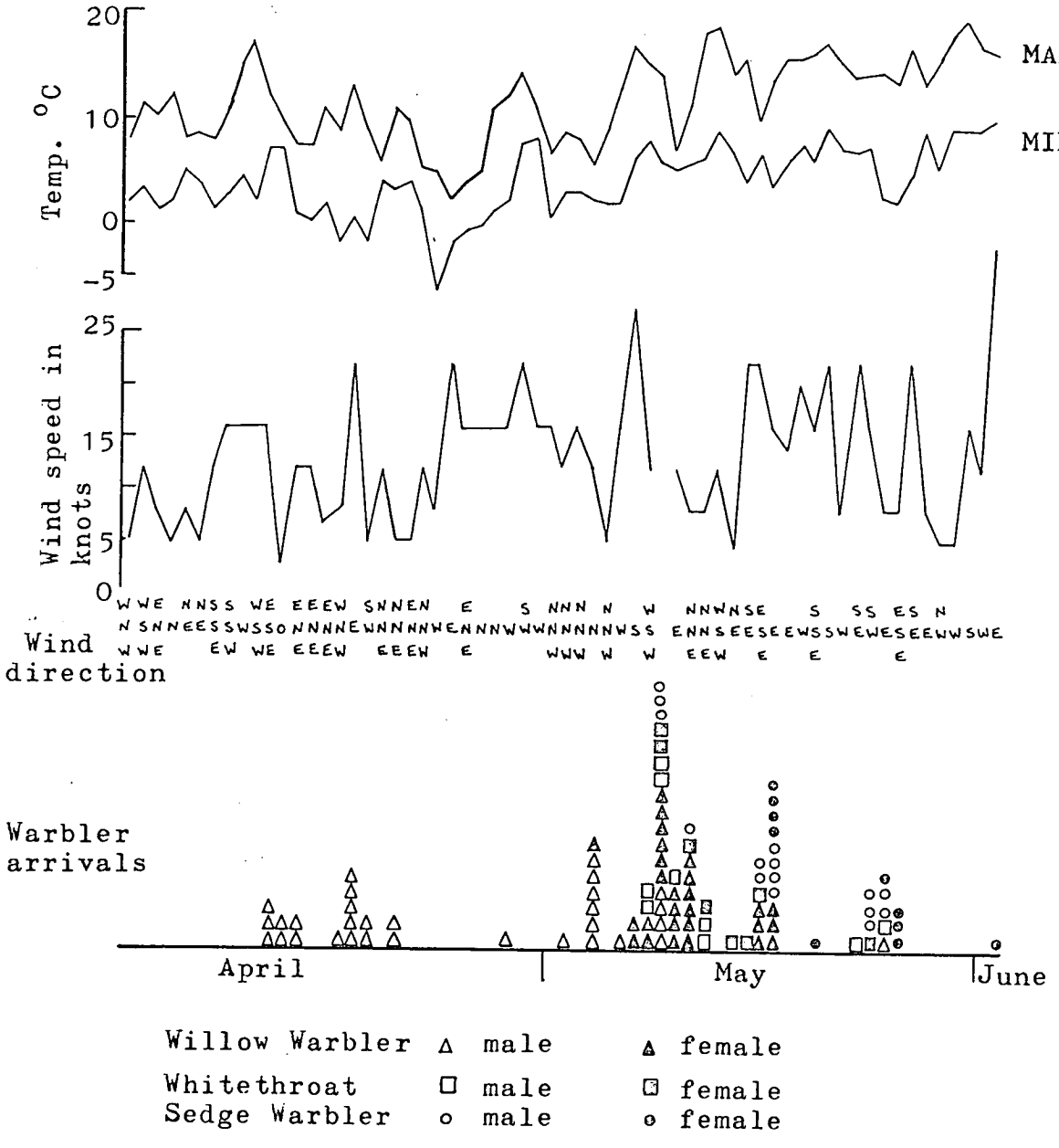
Weather data from a station at the same latitude but 70 metres higher a.s.l. than the main study site. Warbler arrivals include birds that secured territories and birds that moved elsewhere.

Figure 4 The arrival of warblers in relation to weather in 1980.



Weather data from a station at the same latitude but 70 metres higher a.s.l. than the main study site. Warbler arrivals include birds that secured territories and birds that moved elsewhere.

Figure 5 The arrival of warblers in relation to weather in 1981.



Weather data from a station at the same latitude but 70 metres higher a.s.l. than the main study site. Warbler arrivals include birds that secured territories and birds that moved elsewhere.

fell again around 18th April as the wind moved northerly, rose briefly in the next two days and then fell rapidly behind a cold front; only two Willow Warblers arrived in this period, both on the 20th April during the brief increase in temperature which coincided with a drop in wind speed. An even colder spell ensued with daily maxima rarely above 5°C and minima below freezing, strong winds with a northerly component and heavy snowfalls. No birds at all arrived until the 18th April when the wind had changed to the south west and temperatures were increasing.

In 1980 three early Willow Warblers (only one of which stayed to breed) arrived on the 16th April during a spell of light winds and above average temperatures caused by an area of high pressure extending from Britain to Portugal. No further birds appeared until April 26th as a cold northerly airstream became established by April 19th. Seven more Willow Warblers, and the only two Whitethroats to reach the site before May, arrived between 26th-29th April following several days of increased temperature.

In 1979 no warblers arrived until 28th April when temperatures increased towards the end of a month when temperatures were below average, both locally and throughout England, and frontal systems crossed Britain from the north west (Met.Office Reports). Temperatures fell again on 1st May due to a depression in the North Sea and its associated N.W. winds. Five Willow Warblers arrived on 4th May when temperatures were still below average - though increasing - and the wind speed dropped. In 1980 and 1981 some Willow Warblers also arrived in May when maximum temperatures did not reach 10°C, although none had arrived in such conditions in April, suggesting that cold weather became less inhibiting

as the spring progressed.

This pattern was less obvious in Whitethroats and Sedge Warblers which tended to arrive later than Willow Warblers and were less likely to encounter cold weather. However, the gap in Whitethroat arrivals in 1980 between the two early males at the end of April and the next Whitethroats on 10th May shows a similar pattern to Willow Warbler males in April, but occurred later in the spring: note that 11 Willow Warblers arrived during the gap between Whitethroat arrivals (Fig.4).

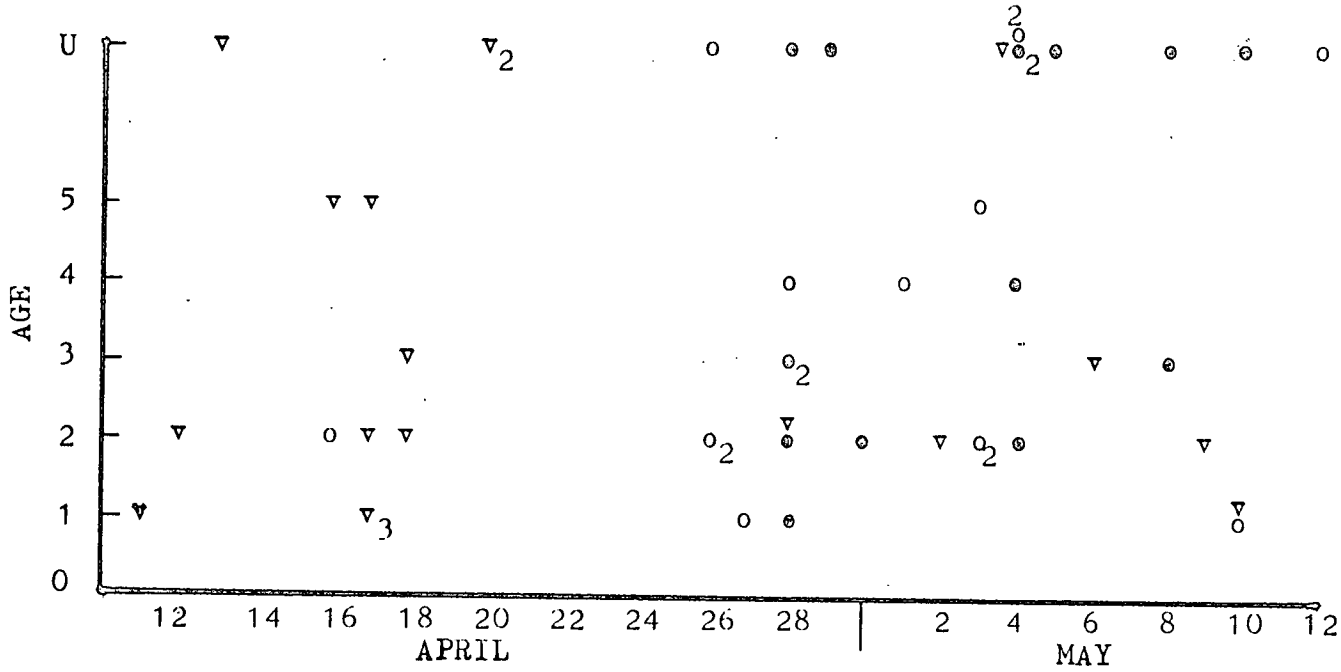
2:4 Arrival dates in relation to age

A high percentage of Willow Warblers was ringed (both in the main study site during and prior to this study and in the surrounging countryside) making it possible to look at arrival dates in relation to age (Figures 6-7). No significant differences were found between one year old and older birds (Mann-Whitney U-test) as one year old males and older birds were spread throughout the arrival period. For example, in 1979 the first five males arrived on 28th April - one was one year old, one at least two years old, two at least three years old and one of unknown age. Over three years there was a suggestion that one year old males (6 out of 8) were more likely to arrive earlier than the mean arrival dates. Females showed no significant difference in arrival dates between first year and older birds (Mann-Whitney U-test).

Sample sizes of known age birds were smaller with Whitethroats and Sedge Warblers, but the data available showed no correlation between age and arrival dates, although it seems worth mentioning that the two early male Whitethroats in 1980 were both aged (on plumage wear - see Svensson, 1975), as one year old birds.

One case suggests that an older bird could secure a territory despite arriving later than some one year olds. In 1979 a one year old male Willow Warbler returned to the main study site on 4th May, but left on 10th May, after losing his territory to a male of unknown age. He then held territory in a nearby shelterbelt. This bird successfully held territory in the main study site in 1980 and 1981. In 1981 he arrived on 18th April to find his 1980 territory occupied by a male that had been ringed in a nest less than 100 metres away in 1980. He was soon able to take over his former territory, although the

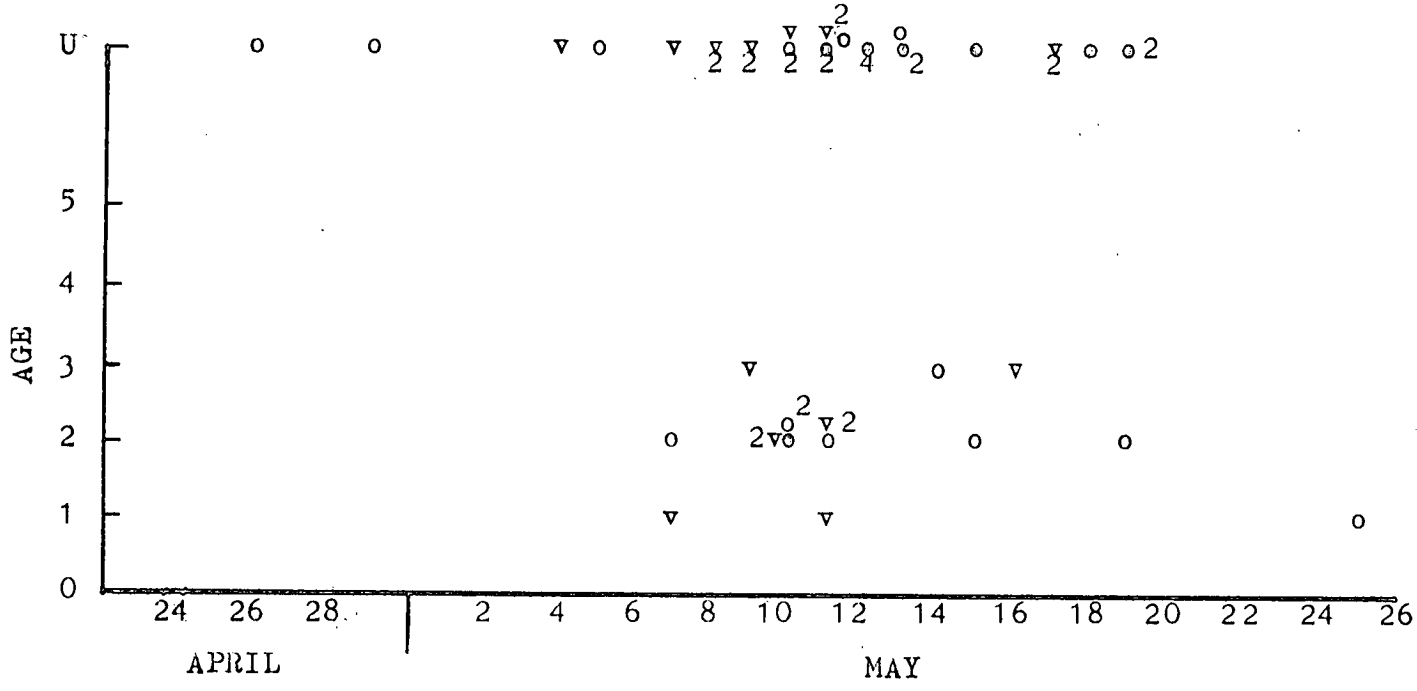
Figure 6 The timing of arrivals of male Willow Warblers in relation to their age.



o 1979
o 1980
▽ 1981

U = unknown age ie. could be one year old or older.
All birds aged one are one year old.
Ages 2-5 in some cases are minimum ages.
Numbers alongside symbols show where more than one individual arrived on the same day.

Figure 7 The timing of arrivals of female Willow Warblers in relation to their age.



o 1979
o 1980
v 1981

U = unknown age ie. could be one year old or older.
All birds aged one are one year old.
Ages 2-5 in some cases are minimum ages.

Numbers alongside symbols show where more than one individual arrived on the same day.

one year old male did succeed in holding another territory nearby.

Every year a number of Willow Warblers which arrived in the site did not secure territories and moved elsewhere, usually within a day or two (see also Ch. 3.3). Over the three years 22 males did not secure territories; seven were definitely one year old, 14 were of unknown age and only one was an older bird that had bred in the study area before. By contrast, on the 48 occasions when male Willow Warblers secured territories, 26 were older than one year, 14 were of unknown age and eight were definitely one year old.

With Whitethroats and Sedge Warblers all the males that failed to secure territories were unringed on arrival. The eight male Whitethroats and seven male Sedge Warblers that returned after breeding in a previous year all secured territories.

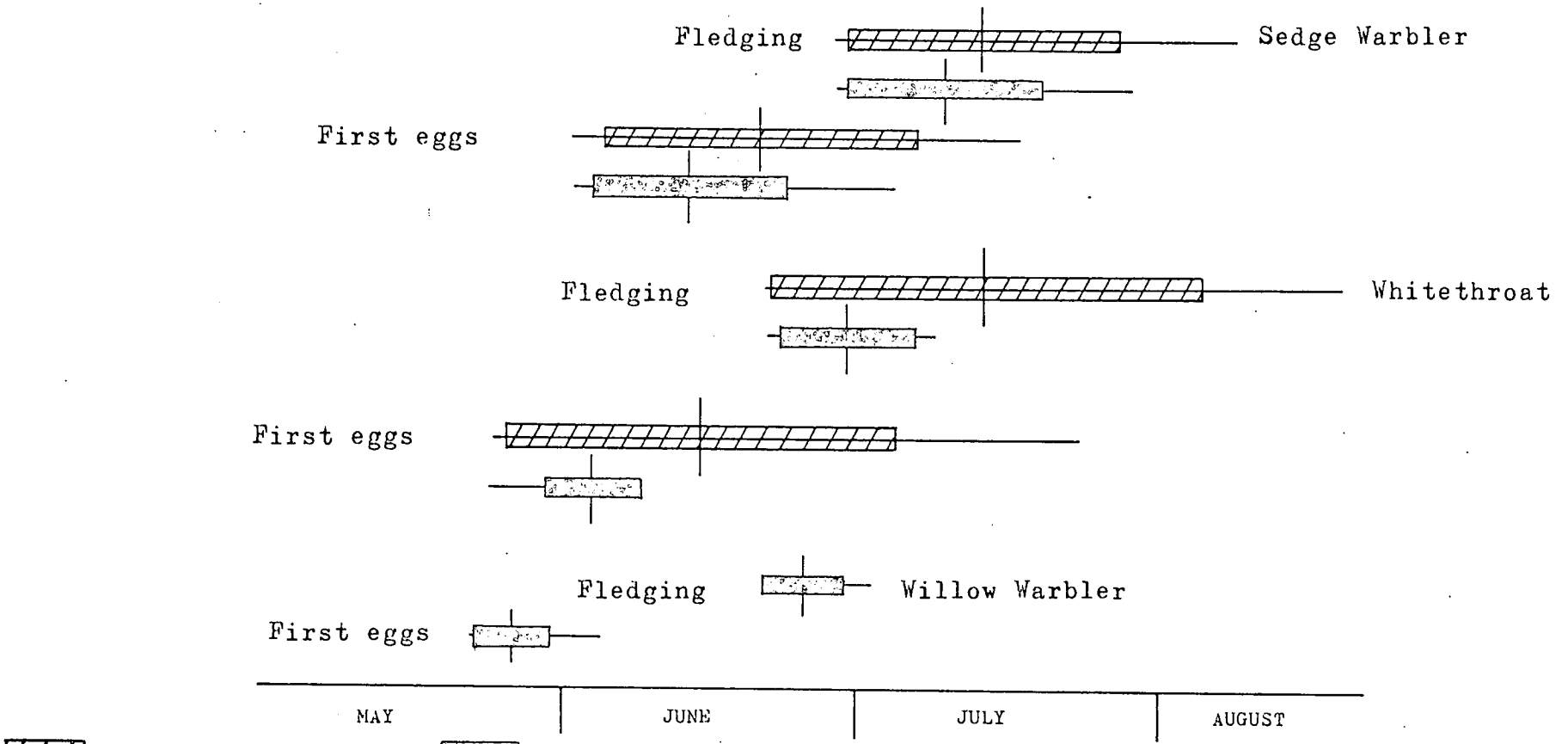
When breeding birds returned in a later year they did not always occupy their former territory although it must be stressed that territory boundaries varied from year to year. There were ten instances of male Willow Warblers returning to the same territory (defined as 75% overlap between years) and 12 instances when males returned to different territories. There were five instances of female Willow Warblers returning to the same territory and 11 of females returning to a different territory. One male Whitethroat returned to his former territory and seven male Whitethroats returned to different territories. The seven female Whitethroats that returned did so to different territories. There were three instances of male Sedge Warblers returning to the same territory and four instances of males returning to different territories. There were five instances of female Sedge Warblers returning to the same territory and three instances of females returning to different territories.

2:5 The timing of breeding

Figures 8-10 show the dates when the first egg of each clutch was laid and also show the dates when broods that survived to fledging left the nest. The situation was complicated by the fact that in some years a few individuals of some species were involved in polygamy, changes of mate or replacing first nests or clutches after disturbance or predation. Figs. 8-10 therefore show mean first egg and fledging dates with such individuals included and excluded.

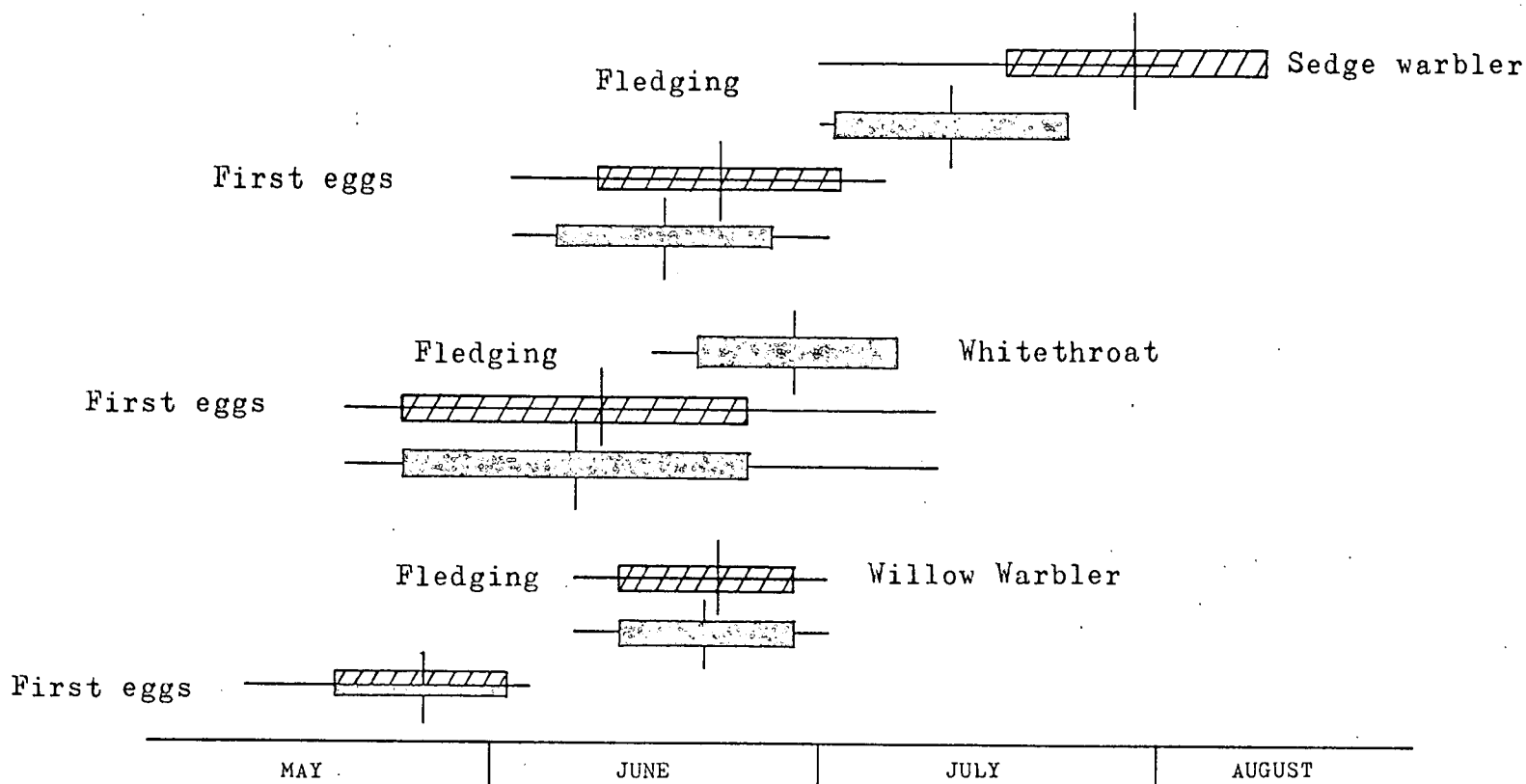
Willow Warblers seemed to be more closely synchronized than the other two species. The range of first egg dates for Willow Warbler in 1979 was only 13 days but longer in 1980 (26 days) and 1981 (34 days). However in 1981 the timing was affected by the behaviour of a polygamous male while there was good evidence that the other three late females in 1981 were delayed by disturbance (from cattle in two cases and a predator in the third case) since they were seen changing sites and rebuilding their nests. Two of these three birds nested in an area open to livestock which was not used by other species. If these birds are excluded the range is reduced to 14 days. Whitethroat first egg dates were also fairly well synchronized in 1979 (15) and 1981(17) but ranged over 54 days in 1980 (32 days if one female whose clutch failed to hatch is excluded). Eight Whitethroats were involved in second broods which all involved mate changes; including these lengthens the ranges of first egg dates to 60, 54 and 40 days. Sedge Warblers were never involved in double brooding or polygamy but three hens moved nest sites and nine others relaid after predation or disturbance. Excluding these 12 birds gives ranges of 33 days in 1979, and 29 days in both 1980 and 1981; including

Figure 8 The first egg and fledging dates of warblers in 1979.



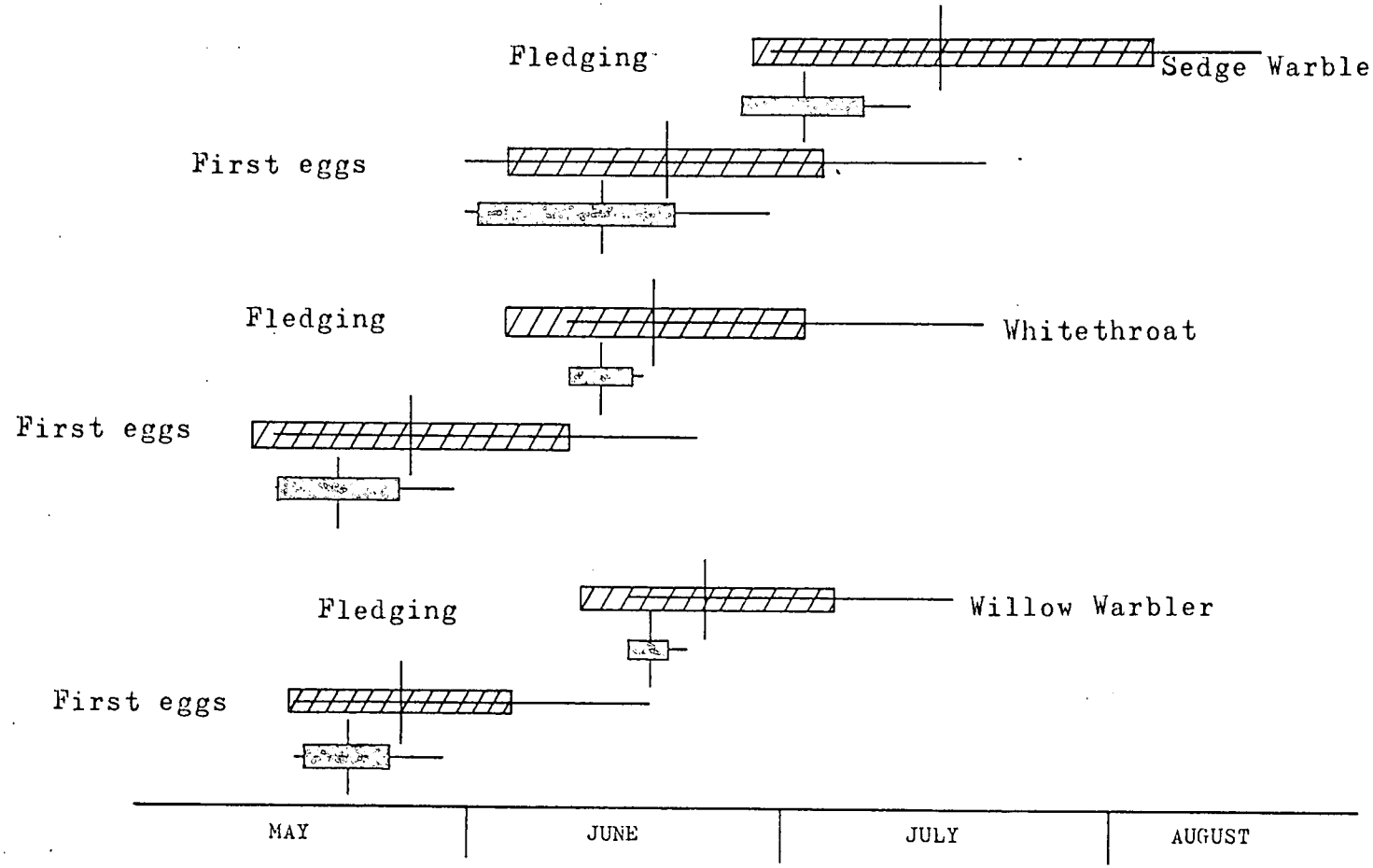
all clutches S.D. excludes replacement and second clutches/broods S.D.
Means (|) and ranges (——) are shown.

Figure 9 The first egg and fledging dates of warblers in 1980.



all clutches S.D. excludes replacement, second and polygamous clutches/broods S.D. Means (|) and ranges (——) are shown.

Figure 10 The first egg and fledging dates of warblers in 1981.



all clutches S.D. excludes replacement, second and polygamous clutches/broods S.D.
Means (|) and ranges (——) are shown.

them gives ranges of 46 days in 1979, 34 days in 1980 and 49 days in 1981.

Mean first egg dates differed between species (Table 5). Willow Warblers were significantly earlier than both Whitethroats and Sedge Warblers in 1979 and 1980, and significantly earlier than Sedge Warblers in 1981, but not Whitethroats, whether "late" clutches were included in the calculations or not. Whitethroats' mean first egg dates were earlier than Sedge Warblers in all three seasons but only significantly earlier in 1981. When second broods and relays are excluded, Whitethroats were also significantly earlier than Sedge Warblers in 1979. In 1980 there was no significant difference between the mean first egg dates of Whitethroats and Sedge Warblers.

The spread of first egg dates meant that there was a considerable amount of overlap between Willow Warblers and Whitethroats in all three seasons, and between Whitethroats and Sedge Warblers in 1979 and 1980, whereas Willow Warblers and Sedge Warblers showed little overlap. These differences broadly reflect differences in arrival dates.

There was some intraspecific year to year variation in mean first egg dates. Willow Warblers were significantly earlier in 1981 than in 1979 when the three late hens and the second and third hens of the polygamous male are excluded (1979/81 $t = 3.9$, $p < 0.001$). If these late females are included there was no significant difference between years. Whitethroat first broods were also significantly earlier in 1981 than in the previous two years (1979-81 $t=5.1$, $p < 0.001$, 1980-81 $t=3.1$, $p < 0.01$). With Sedge Warblers there was no significant difference between years in the mean first egg dates.

There was considerable variation in the time spent by individual

Table 5 Comparisons of first egg dates of warblers 1979-81.

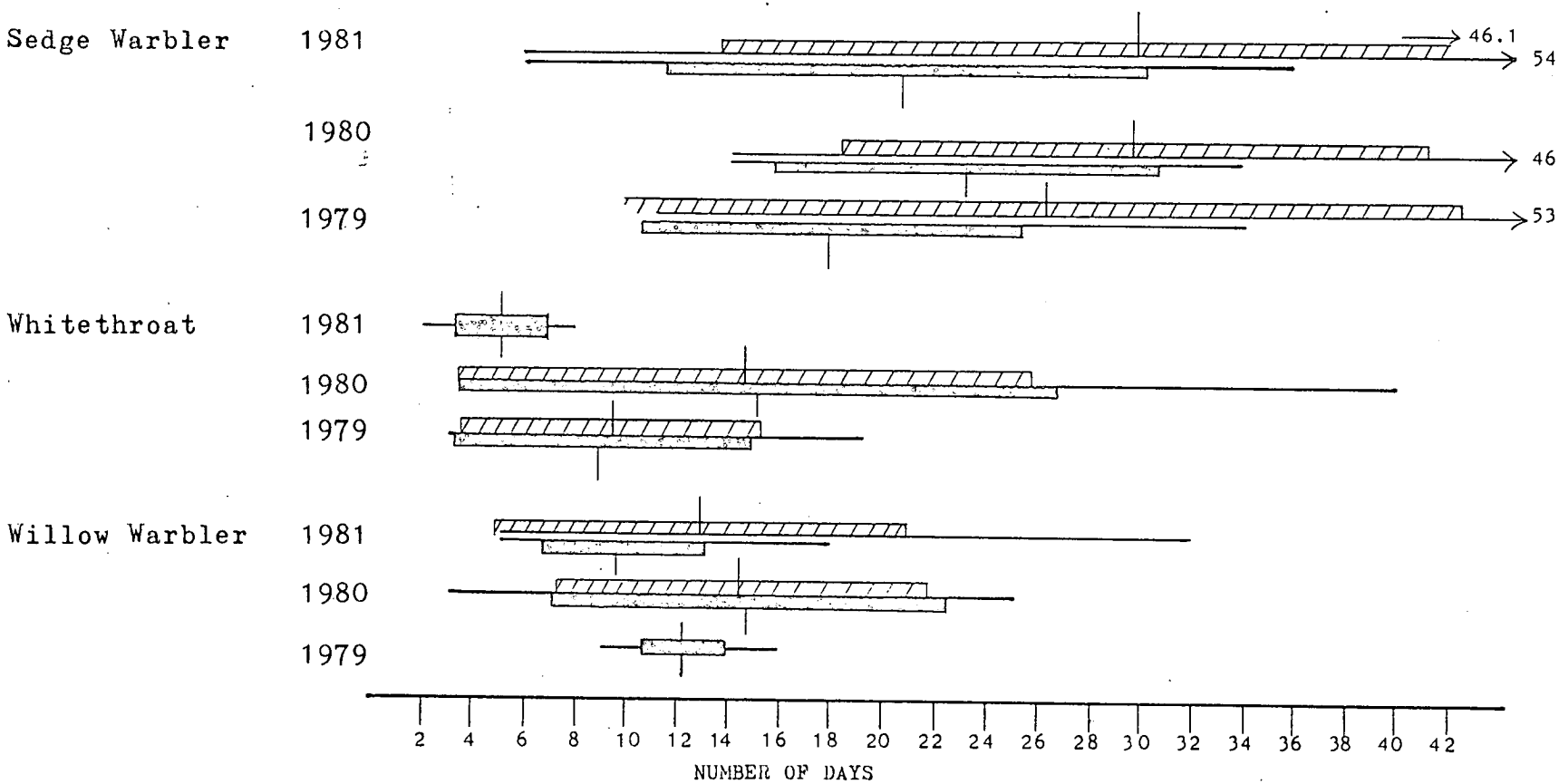
Excluding replacement, second and polygamous clutches.

		Willow Warbler		Whitethroat		Sedge Warbler		Willow Warbler
1979	mean	26/5		3/6		13/6		26/5
	range	22/5-4/6		24/5-8/6		1/6-4/7		22/5-4/6
			t=3.74		t=2.40		t=5.62	
			p<0.01		p<0.05		p<0.001	
1980	mean	25/5		8/6		16/6		25/5
	range	9/5-4/6		18/5-11/7		2/6-1/7		9/5-4/6
			t=2.58		t=1.12		t=5.12	
			p<0.02		NS		p<0.001	
1981	mean	20/5		19/5		13/6		20/5
	range	15/5-29/5		13/5-30/5		31/5-29/6		15/5-29/5
			t=0.48		t=5.16		t=6.98	
			NS		p<0.001		p<0.001	
All clutches								
1979	mean	26/5		14/6		20/6		26/5
	range	22/5-4/6		24/5-23/7		1/6-17/7		22/5-4/6
			t=3.19		t=0.82		t=5.16	
			p<0.01		NS		p<0.001	
1980	mean	25/5		10/6		21/6		25/5
	range	9/5-4/6		18/5-11/7		2/6-6/7		9/5-4/6
			t=3.10		t=1.77		t=6.84	
			p<0.01		NS		p<0.001	
1981	mean	25/5		26/5		19/6		25/5
	range	15/5-18/6		13/5-22/6		31/5-19/7		15/5-18/6
			t=0.20		t=3.68		t=5.51	
			NS		p<0.01		p<0.001	

females between arrival in the study site and the laying of their first eggs (Fig.11). Sedge Warblers (annual means 18, 23, 21 days) tended to spend more time between arrival on the site and laying than Whitethroats (annual means 9, 15, 5) or Willow Warblers (annual means 12, 15, 10) but all species showed considerable variation.

Comparison of first year and older female Willow Warblers showed no significant difference in the time that elapsed between arrival on the breeding site and the commencement of egg laying (Mann-Whitney U-test). This test could not be carried out for Whitethroats and Sedge Warblers as there were too few females of known age. Comparison of the actual dates of laying did not show that older birds laid earlier than one year old birds, although the sample size for one year old hens was very small.

Figure 11 The number of days between the arrival of females and their first egg dates.



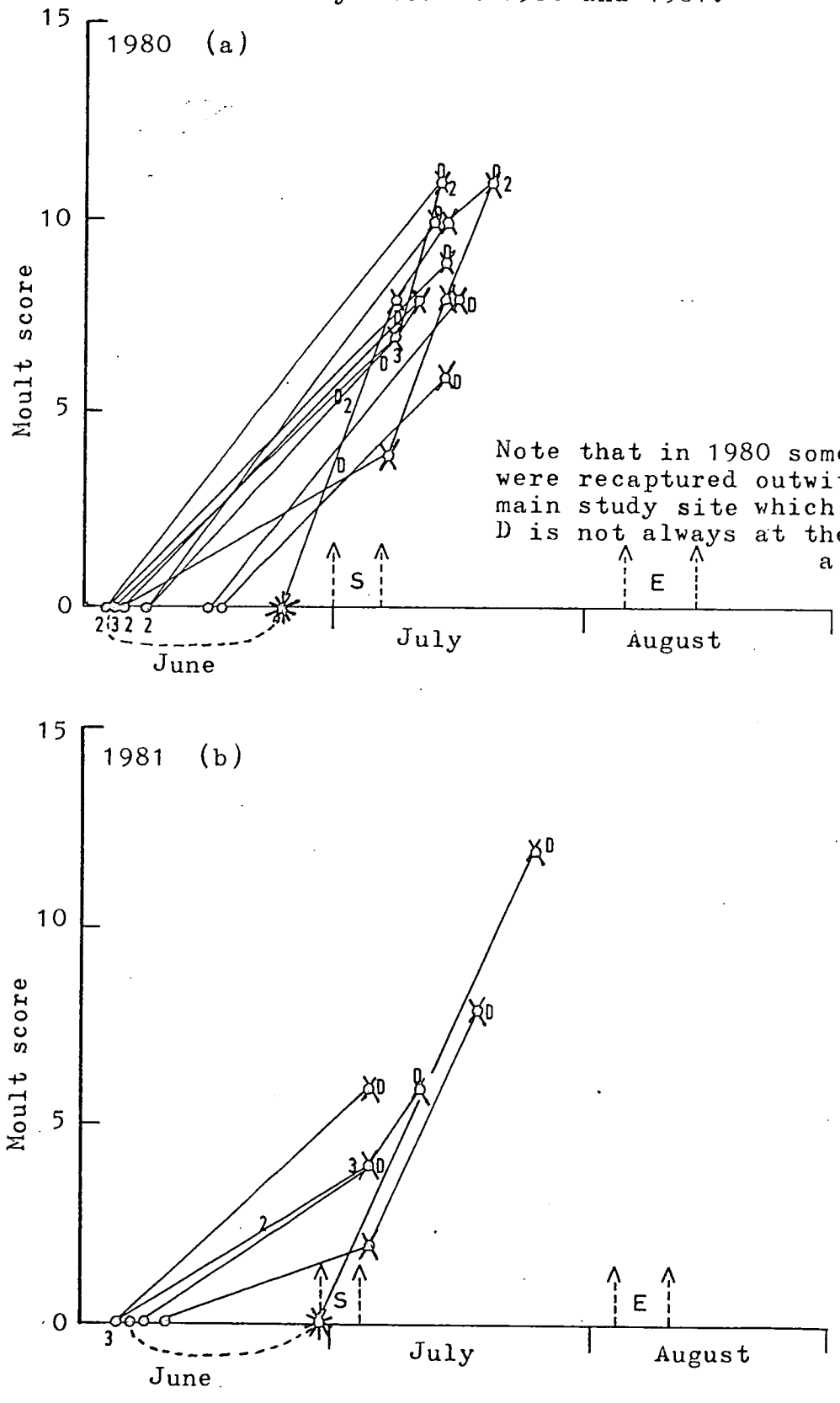
all clutches S.D. excludes replacement, second and polygamous clutches/broods S.D.
Means (|) and ranges (———) are shown.

2:6 Post juvenile moult

The post juvenile moult of Willow Warblers bred in the main study site in 1980 and 1981 is shown in Figure 12.

The 59 Willow Warblers successfully reared in the study site in 1980 left it between 21 and 45 days old. Of the 13 young recaptured after fledging eight were caught at sites in the surrounding area. In 1981, when young left the main study site between 16 and 52 days old, no catching was done elsewhere so Fig.12b shows fewer recaptures than Fig.12a. In both years a number (15 in 1980, 13 in 1981) of wandering juveniles (birds definitely not hatched in the main study site, see also Ch.4) were also captured on more than one occasion. Data from these birds were used to calculate daily incremental values (Table 6). These figures suggest that feather growth is rapid up to score 3 and then slows down. When these incremental values were applied to young of known age they gave estimates of the duration of post juvenile moult of between 36 and 40 days, starting when the birds were between 20 and 28 days old. Since the young Willow Warblers that were retrapped hatched between 2nd and 16th June 1980 and 3rd-9th June 1981, this means that they would finish post juvenile moult between 5th and 14th August in 1980 and 3rd to 10th August in 1981. Later broods were less likely to be trapped after fledging; presuming they moulted at the same rate as the others they would have finished by 26th August 1980 and by 11th September 1981, with most birds finishing between early and mid August. In fact no juveniles reared in the main study site were seen there after 19th July in 1980 and 26th July in 1981 which suggests that they may have left on migration around these dates as post juvenile moult approached completion.

Figure 12 The post juvenile moult of Willow Warblers as shown by recaptures of nestlings bred in the study site in 1980 and 1981.



D departure from the main study site.
hatching dates are shown by closed circles on the X axis.
-----✳ recapture of nestling before start of post juvenile moult.
✳ recapture of nestlings; solid lines connect individuals.
S estimated start of post juvenile moult.
E estimated end of post juvenile moult.

Table 6 Incremental values for different stages of post juvenile moult in Willow Warblers calculated from birds recaptured during 1980 and 1981.

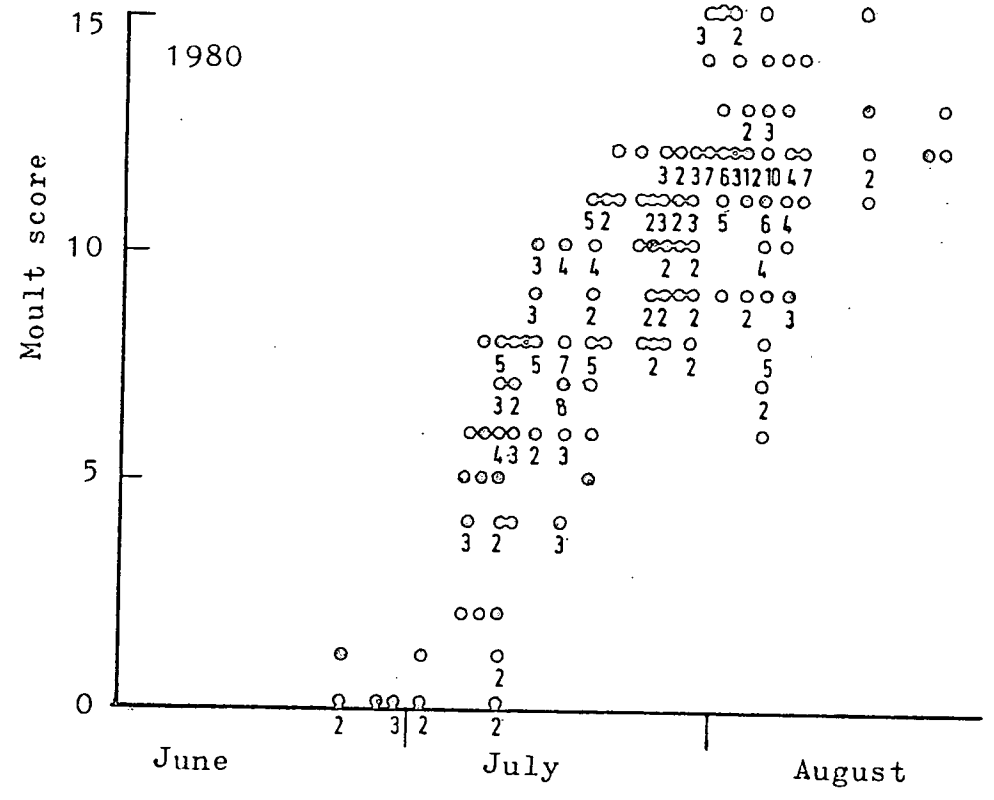
Moult score	Number of birds	Change in moult score per day ± S.E.
3-6	7	0.866 ± 0.049
7-9	11	0.647 ± 0.010
10-12	14	0.436 ± 0.008
13-15	13	0.208 ± 0.018

The data from the much larger number of birds that were trapped only once during this period (Fig.13) also indicate post juvenile moult starting in late June or early July and finishing between late July and mid August.

The scattergrams for Whitethroats (Fig.14) suggest that for most birds post juvenile moult started around late June or early July and finished around the middle of August. The change in moult score per day, calculated from six birds, ranged from 0.833-0.285 units per day, with feather growth slower towards the end of moult, and indicate that post juvenile moult in this species takes between 31 and 37 days.

The scattergrams (Fig.15) for Sedge Warblers suggest a more rapid post juvenile moult than in Willow Warblers or Whitethroats. As with Whitethroats there is also quite a wide scatter, which reflects the considerable variation in fledging dates in both species. Only three individual Sedge Warblers were retrapped twice during post juvenile moult, giving a mean change in moult score per day of 0.760 units per day. This suggests post juvenile moult takes around 20 days. However this estimate is probably too short since these incremental values were obtained from a small sample of birds caught during what is probably the most rapid stage of post juvenile moult. Regression analysis was used to give another estimate of the duration of post juvenile moult in Sedge Warblers. Since this method tends to estimate the duration of moult of the population as a whole, rather than that of individual birds when individuals start to moult at different times (Ginn & Melville 1975, Pimm 1976), only 1980 data was used, since in that year the moult scores available (with the exception of two obviously late birds which were excluded from the analysis)

Figure 13 The post juvenile moult scores of Willow Warblers caught once during moult. Numbers indicate more than one individual.



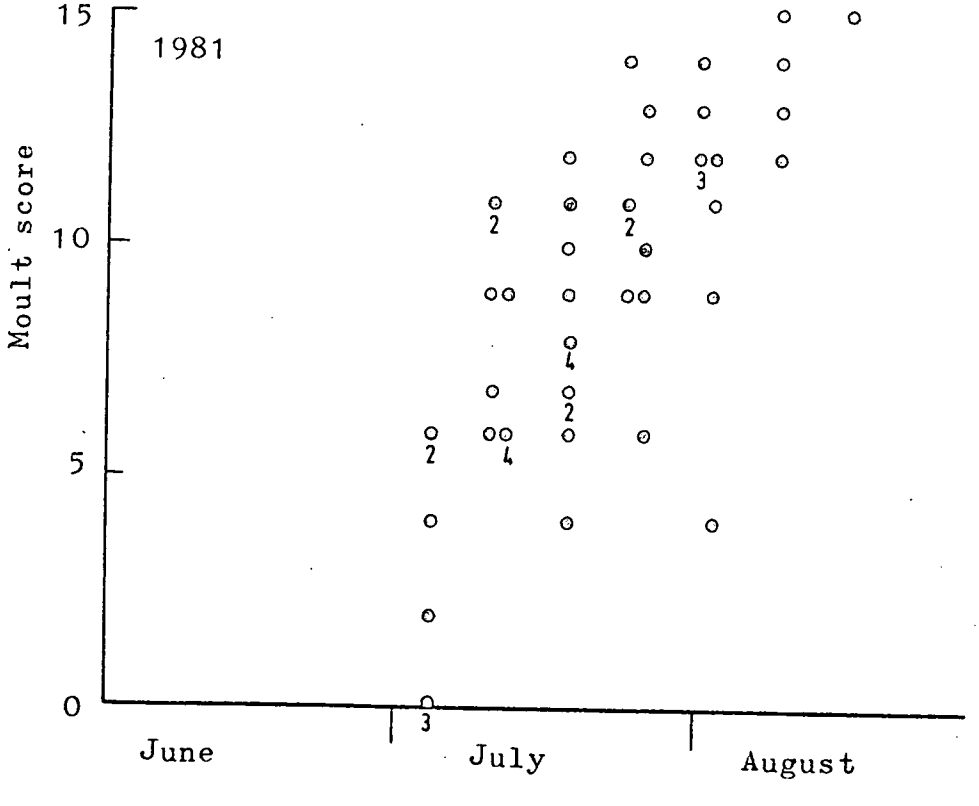


Figure14 The post juvenile moult scores of Whitethroats.

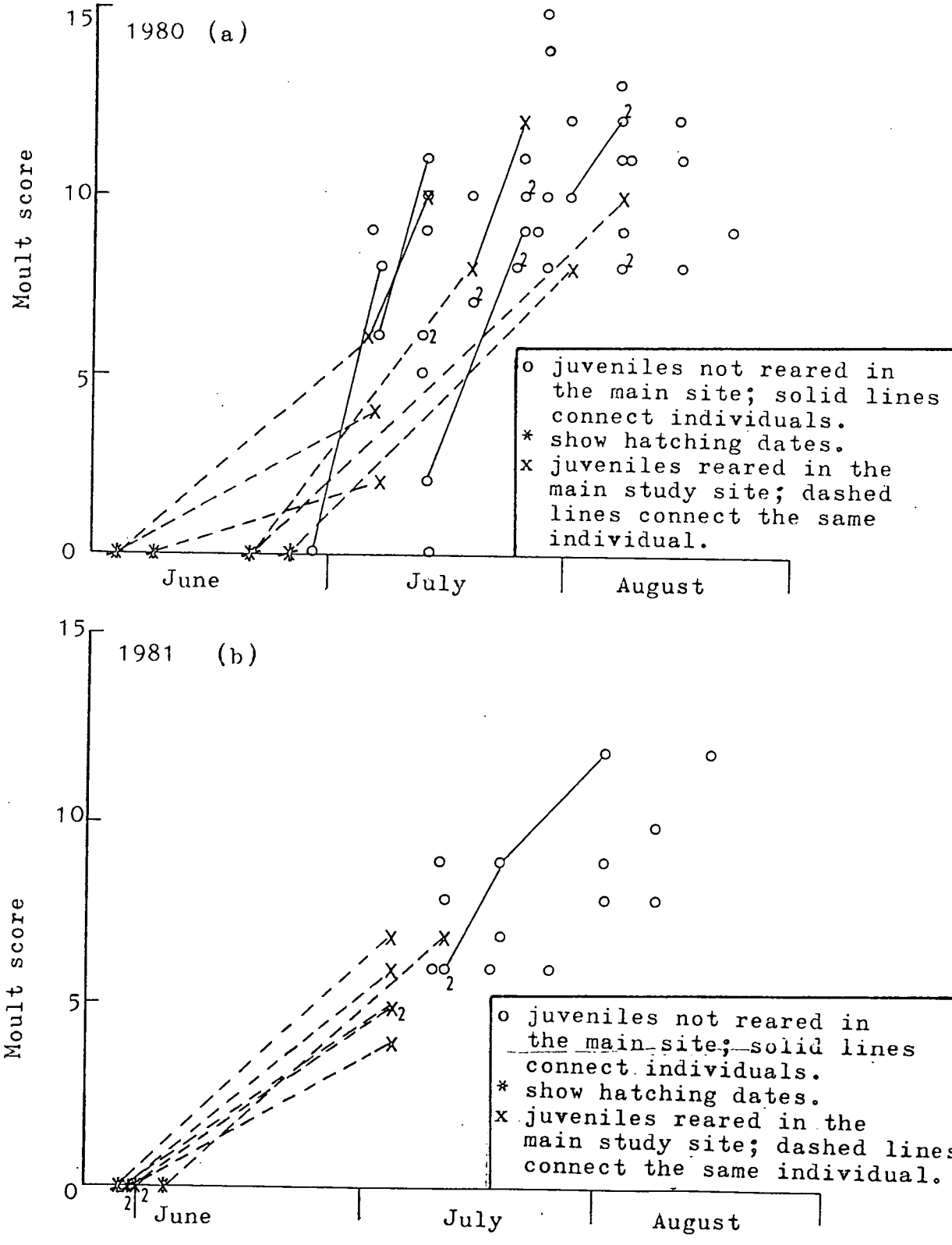
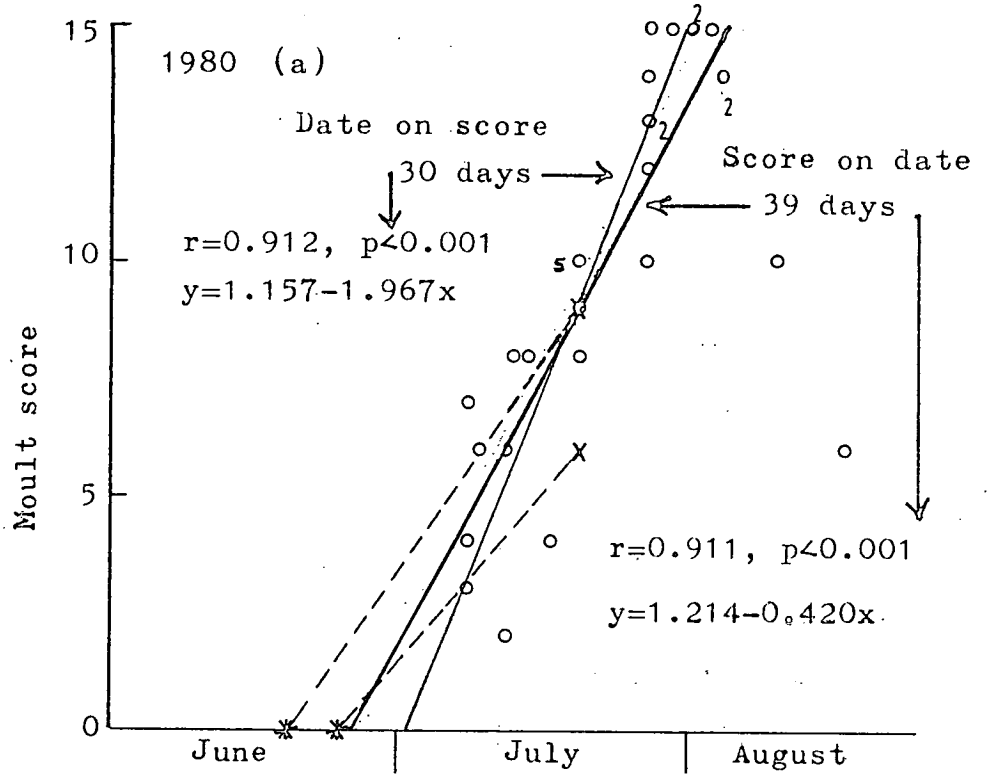
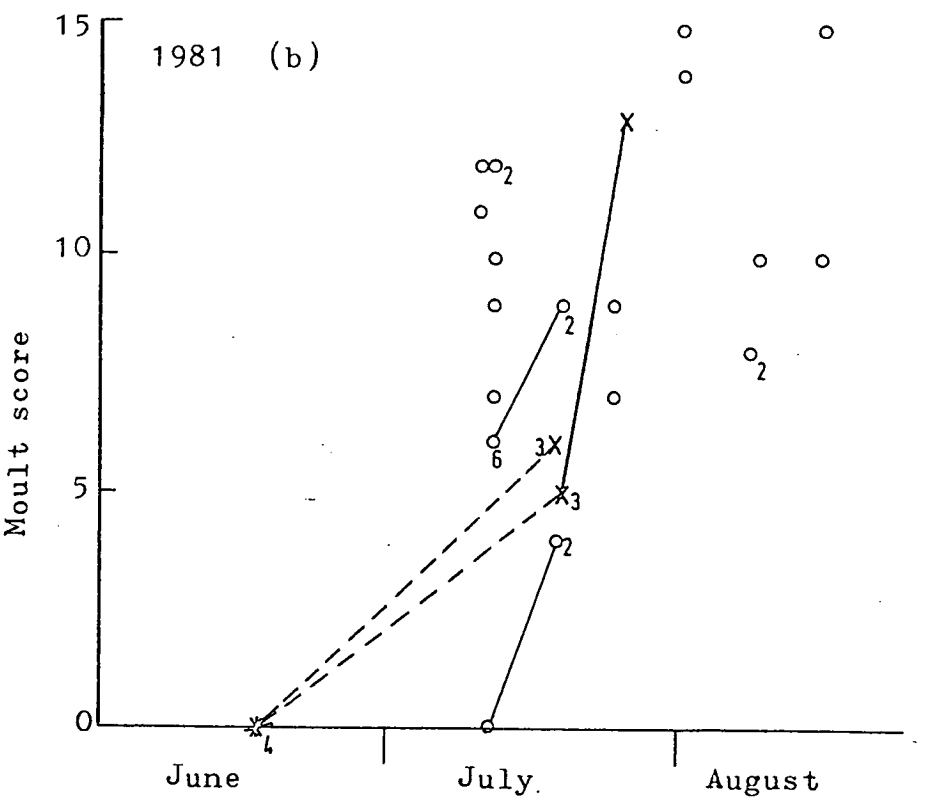


Figure15 The post juvenile moult scores of Sedge Warblers.





* show hatching dates and dashed lines connect the same individual reared in the main site.

o juveniles not reared in the site. Solid lines connect individuals.

x juveniles reared in the main study site.

indicated that they were from birds that had started to moult around the same time (Fig.15).

Conventionally moult score is treated as the dependent variable and therefore regressed on date (Ginn & Melville 1983) although some workers have recently suggested that a more accurate estimate of the duration of moult in an individual is obtained by regressing date against score, since the alternative method gives too high an estimate as it measures the duration of moult in the sample population rather than in individuals (see Summers, Swann & Nicholl 1983 for a fuller discussion).

Both methods were applied to the 1980 data from juvenile Sedge Warblers. Regression of moult score against date gave an estimate of the duration of post juvenile moult of 39 days whereas the alternative method gave an estimate of 30 days. The longer estimate implies that nestlings retrapped on 19th July (Fig.15a) had started their post juvenile moult around 1-4 days before fledging. Even the shorter estimate of 30 days implies that post juvenile moult had started within 1-2 days of fledging. It therefore seems likely that post juvenile moult in Sedge Warblers is particularly rapid; unfortunately no young Sedge Warblers were trapped in the early stages of moult to check this.

2:7 Moult in adults

In 1980 a special effort was made to retrap breeding adults at weekly intervals to study weight changes and, when appropriate, moult, although the sample sizes later in the summer were reduced since some adults left the site after nest failure or in company with their young. Individual Willow Warblers were trapped up to five times during the 1980 moult season and only five birds out of the 22 birds for which moult was recorded had fewer than three moult scores recorded. Examination of the data on primary moult from these birds indicated changes in the rate of moult around scores of 10 and 37 therefore the primary moult scores were divided into three categories (Table 7) and these categories further subdivided into males and females. Daily incremental values were calculated and showed variation in the rate of primary moult with both male and females moulting more rapidly in the middle of the moult period than towards the start or finish (Table 7). These data were used to calculate the duration of the moult period for males and females for each of the three years (Table 8). These was very little variation between years but males (40-45 days) took slightly longer to moult than females (38-42 days) (Mann-Whitney U-test $d = 6.477$, $p < 0.001$) and in two out of three years male Willow Warblers started moulting significantly earlier than females (1979 $t = 2.85$, $p < 0.02$, 1980 $t = 1.71$, NS, 1981 $t = 2.92$, $p < 0.01$). A further point about Willow Warbler moult is that in all three years a small proportion of adults started to moult before their young had fledged, with males (17.7%) as likely to do so as females (8.3%) ($x^2 = 1.099$, NS) (Table 9). Normally overlap with breeding was relatively slight. In 1979 two males started six days before

Table 7 Daily incremental values for the primary moult of male and female Willow Warblers calculated from retrapped birds.

	Primary moult score					
	0-10		10-37		37-50	
	male	female	male	female	male	female
mean	1.01	0.927	1.49	1.44	0.855	1.26
S.E.	0.084	0.092	0.071	0.072	0.145	0.021
n	5	4	7	6	2	3

Table 8 Estimated duration of primary moult and moulting period for male and female Willow Warblers 1979-81. The mean start of moult for each year is also shown.

1979		
Duration in days	40-45	38-42
mean start date	29th June	10th July
S.D.	6.7	8.8
range of dates	19th June-25th Aug.	30th June-8th Sept.
n	10	9
1980		
Duration in days	40-45	38-42
mean start date	25th June	28th June
S.D.	3.8	3.7
range of dates	17th June-12th Aug.	23rd June-13th Aug.
n	13	9
1981		
Duration in days	40-44	38-42
mean start date	27th June	1st July
S.D.	2.3	5.0
range of dates	23rd June-13th Aug.	24th June-17th Aug.
n	14	9

Table 9 The moult of adult Willow Warblers in relation to their breeding cycle, 1979-81.

	Males	Females
Numbers left before starting moult	7(15.5)	20(41.6)
Numbers starting to moult before young fledged	8(17.7)	4(8.3)
Numbers starting to moult after young fledged	21(46.6)	20(41.6)
Numbers started after nest predation	9(20.0)	4(8.3)
Total	45	48

Figures in parentheses show percentages

their young had fledged; no females started moulting before the young fledged. In 1980 four males started moulting two to six days prior to their young fledging and two females started three and four days prior to young fledging. However in 1981 two males started 17 and 18 days before the young had fledged which means that they were beginning moult during the incubation period. Their respective mates started seven and 12 days prior to their young fledging. The considerable overlap shown by these two pairs in 1981 was due to their breeding attempts being much later than normal. In one case the female built several nests before laying, due to disturbance, and the other case involved a polygamous male and his third mate.

The final point about the moult of breeding Willow Warblers is that only a minority of the adult birds completed moult on their breeding grounds; Table 10 shows that only five birds in 1979, two in 1980 and none in 1981 did so. Although some left early due to nest failure (22%) and others left with their young and, presumably, moulted elsewhere, the largest group of birds (44.6%) left the breeding site while in the later stages of primary moult.

Much less data on moulting Whitethroats were obtained than for Willow Warblers simply because so few birds stayed to moult in the main study site. Table 11 shows that the majority of breeding Whitethroats left before even starting moult, while of the remainder none was ever found with a primary score of more than 24 (Fig.16) and at least one hen definitely arrested moult just before departure. Five adult Whitethroats that visited the site in July or early August were in moult but none of these had scores higher than 10. The only Whitethroat with a moult

Table 10 The stage of moult of adult Willow Warblers on their departure from their breeding site in relation to breeding success over three years.

	1979				1980				1981			
	male		female		male		female		male		female	
Stages of moult	F	S	F	S	F	S	F	S	F	S	F	S
Numbers leaving before moult started	2	0	3	0	1	0	3	3	4	0	8	3
Numbers leaving between start of moult and at least one week before completion	0	5	1*	8*	2	4	1	2	4	6	2	6
Numbers leaving shortly before completion of moult	0	3	0	0	1	4	0	6	1	3	0	1
Numbers leaving when moult complete	2	2	0	1	0	2	0	0	0	0	0	0

*includes one bird thought to be arresting moult.

F failed breeders

S successful breeders

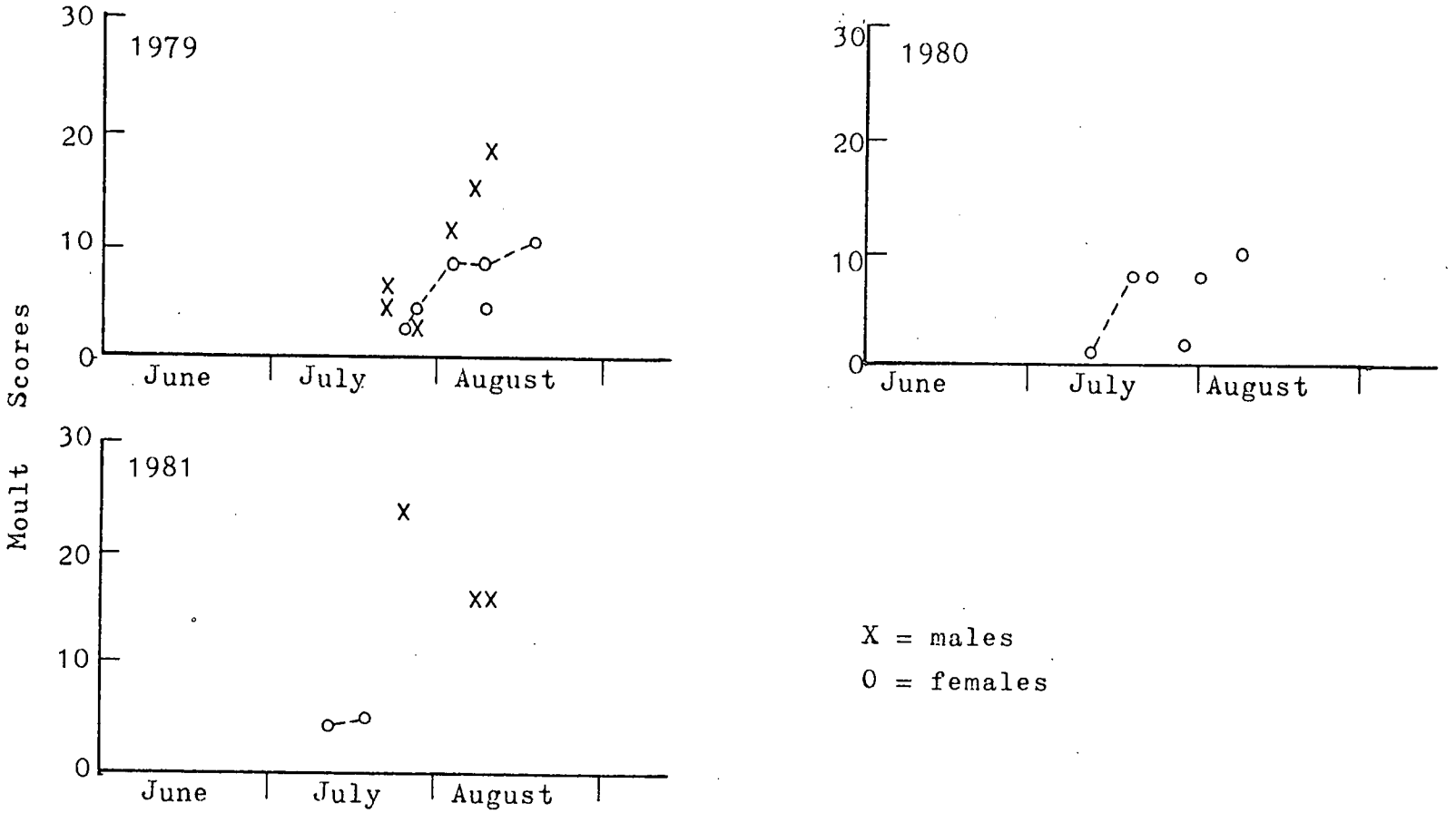
Table 11 The stage of moult of adult Whitethroats on their departure from their breeding site over three years.

	1979				1980				1981			
	male		female		male		female		male		female	
Stage of moult	F	S	F	S	F	S	F	S	F	S	F	S
Numbers leaving before moult started	2	2	1	6	3	6	4	3	2	3	3	4
Numbers leaving during moult	1	5	0	2	0	0	0	3	0	3	0	1
Numbers leaving near to or at completion of moult	0	0	0	0	0	0	0	0	0	0	0	0

F failed breeders

S successful breeders

Figure16 The primary moult scores of adult Whitethroats in the main study site 1979-81。



score anywhere near completion was a bird of unknown origin which was trapped on August 26th 1979 with a score of 35, three days later than the latest date for any breeding adult to be still present on the site over the three years when daily checks were made.

2:8 The timing of departures

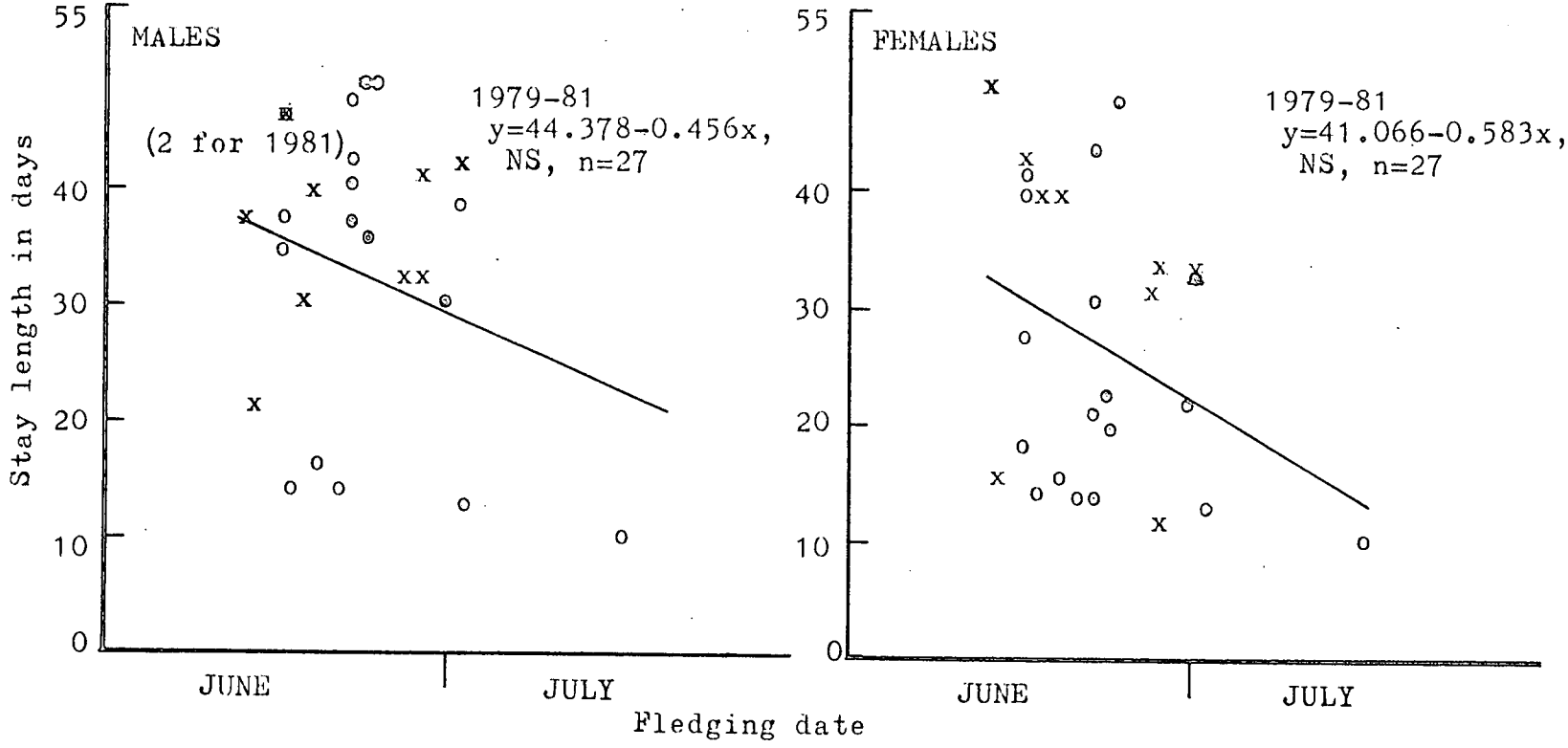
Departure dates from the main study site showed considerably more variation than arrivals (Tables 1-3) and were linked to breeding success. Over three years failed male Willow Warblers (mean 13th July, S.D. 17.2 days, range 18th June - 12th August) departed significantly earlier than successful males (mean 26th July, S.D. 12.2 days, range 1st July - 12th August; $t = 2.99$, $p < 0.01$, $n = 43$). Failed females (mean 23rd June, S.D. 11.8 days, range 9th June - 22nd July) departed significantly earlier than successful females (mean 21st July, S.D. 12.1 days, range 30th June - 11th August; $t = 7.24$, $p < 0.001$, $n = 43$). There were also differences between the sexes and years. Male Willow Warblers left significantly later than females in all three years (male range of mean departure dates 15th - 29th July, female range 2nd - 15th July, Table 1). Comparing years, males and females left earlier in 1981 than in 1979 but not in 1980 (Table 1). Early female departure was linked to nest failure. Eighteen females left the site after nest failure. Three left between two and 15 days after failure at the egg stage and 15 left up to five days after nestling failure. In all these cases the females were seen after nest failure so clearly had survived predation which was the commonest cause of failure (Tables 15 and 16). In six cases when females left before mid June (18th June was the latest 1st egg date for any female that successfully reared a brood) they could conceivably have bred again elsewhere. This seems to have happened in one case where a female with an inactive brood patch (i.e. unfeathered but no longer vascularized and indicative of an earlier breeding attempt) appeared in the main study site on 11th June 1981 and successfully bred with a male

that had already fathered two broods (both of which were taken by predators, one on the day the third female laid her first egg). Failed males were significantly more likely to remain than failed females (1979-81 $t = 3.73$, $p < 0.001$ $n = 32$). Successful females left the study site before successful males though the difference was not significant. Males were more likely to remain behind, and sometimes resumed singing, which tends to suggest a willingness to breed again. However only one male had more than one hen (though in two out of three seasons), no genuine second broods were recorded as opposed to polygamy and song production ended with the onset of moult.

The parents of late broods tended to spend less time in the study site once the young fledged than the parents of earlier broods, though only with males in 1979 was there a statistically significant relationship between adult stay length and the fledging dates of their young (Fig.17).

Young Willow Warblers reared in the main study site left it from 5 - 39 days after fledging. Although initially often accompanied by an adult, they gradually became independent, and were often seen in wandering groups, sometimes with several other species (Ch.4). There were instances of juveniles reappearing in the study site up to 11 days after leaving it, indicating that the day a bird left the site was not necessarily the day it commenced long distance migration. However, in all three years there was a significant tendency for the young from later broods to spend less time on the site than birds which had hatched earlier. (Fig.18). Over three years the last dates when Willow Warblers reared in the site were seen there ranged from 19th - 28th July.

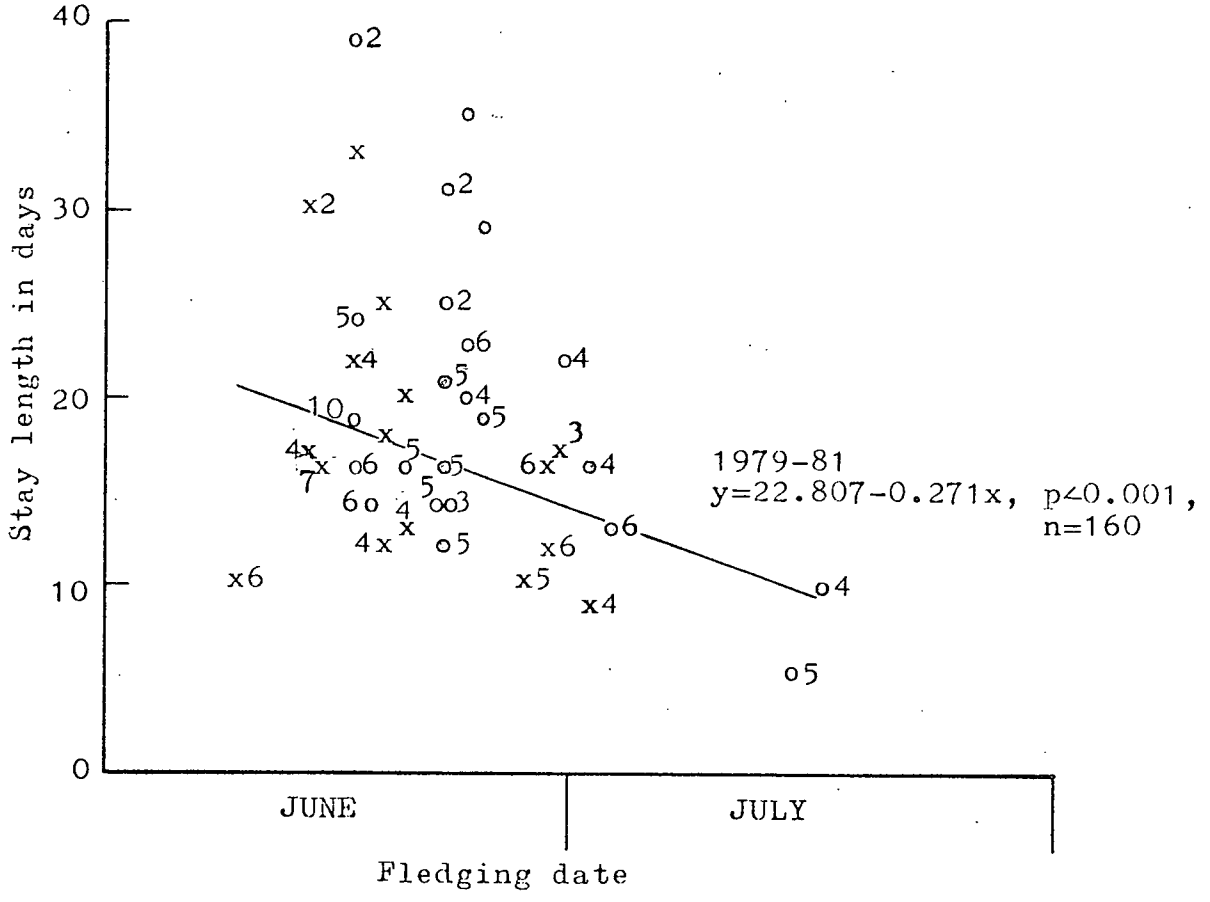
Figure 17 The number of days adult Willow Warblers remained on their breeding site after their young had fledged in relation to the fledging dates of their young.



o 1979 y=82.178-1.771x, p<0.05, n=9
x 1980 y=29.933+0.266x, NS, n=9
o 1981 y=46.392-0.812x, NS, n=9

o 1979 y=52.386-0.945x, NS, n=9
x 1980 y=47.131-0.640x, NS, n=9
o 1981 y=35.091-0.629x, NS, n=9

Figure 18 The number of days juvenile Willow Warblers remained on the main study site in relation to their fledging dates, 1979-81.



o 1979 y=29.722-0.425x, p<0.05, n=48

x 1980 y=18.858-0.188x, p<0.05, n=59

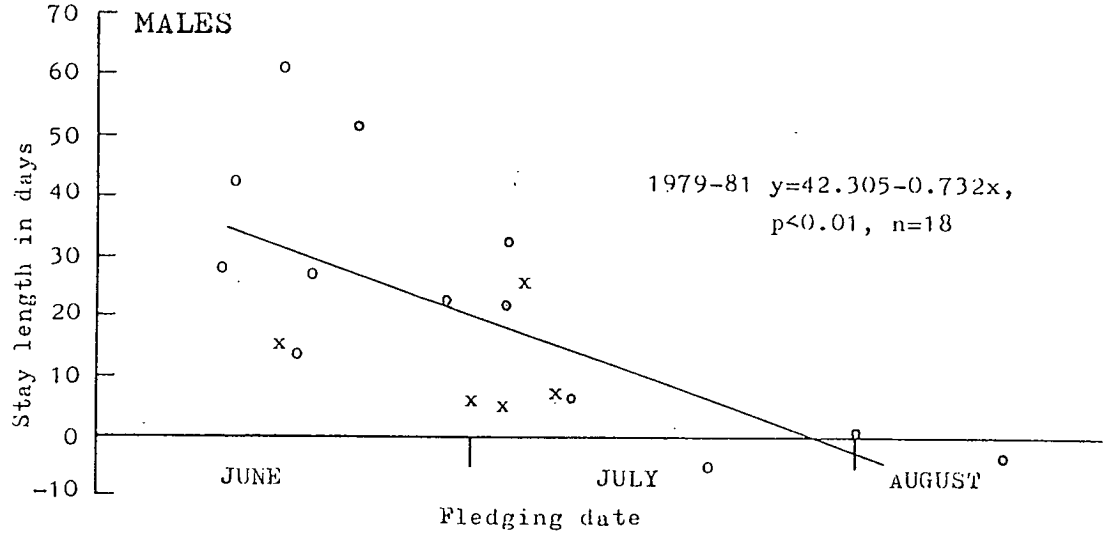
o 1981 y=25.923-0.421x, p<0.001, n=53

Whitethroats also showed considerable variation in departure dates (Table 2). There were no significant differences between males and females or between years. Over the three seasons successful females (mean 25th July, S.D. 15.7 days, range 28th June - 23rd August) stayed significantly later than females that failed to fledge young (mean 13th July, S.D, 12.9 days range 18th June - 27th July; $t = 2.06$, $p < 0.05$, $n = 27$).

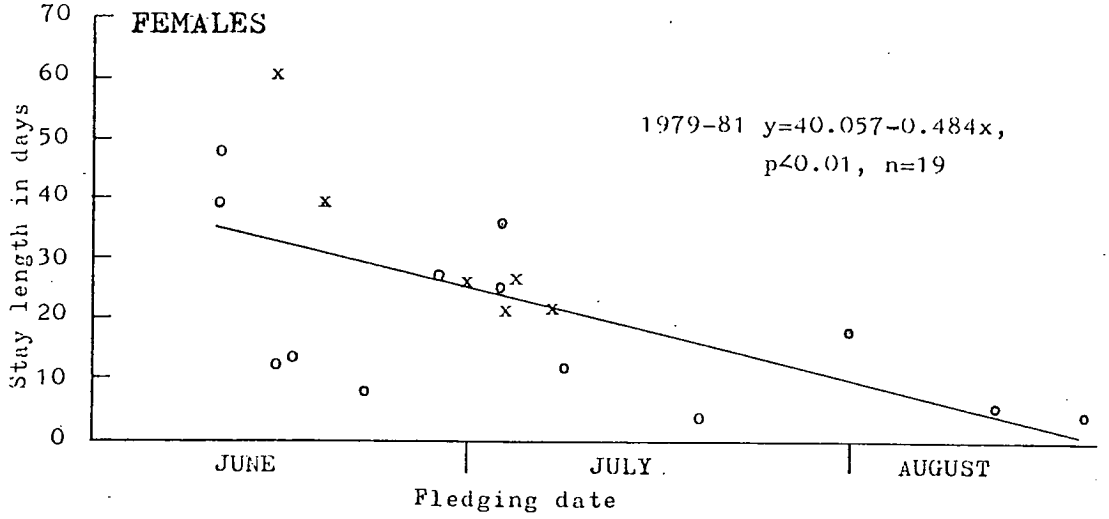
Failed female Whitethroats did not leave earlier than failed males (mean 11th July, S.D. 15.4 days, range 18th June - 29th July) and successful females did not stay significantly later than successful males (mean 22nd July, S.D. 14.5 days, range 30th June - 15th August). Over three years there was a significant tendency for both males and females with late broods to spend less time in the study site after their young had fledged than occurred with the parents of earlier broods (Fig.19). The young from later broods also spent significantly less time in the site before disappearing than the young from earlier broods (Fig.20). Young birds left the main study site up to 33 days after fledging.As with Willow Warblers some disappeared and reappeared,suggesting local movements. The last dates Whitethroats reared in the study site were seen ranged from 23rd July to 23rd August over three years,though most left in July.

Sedge Warblers showed no significant differences in departure dates between males and females or between years (Table 3). Successful adults did, however, stay longer than failed breeders but not significantly so (males: successful mean 4th August, S.D. 7.0 days, range 22nd July - 19th August, failed mean 1st August, S.D. 9.9 days range 15th July - 12th August,

Figure 19 The number of days adult Whitethroats remained on their breeding site after their young had fledged in relation to the fledging dates of their young.

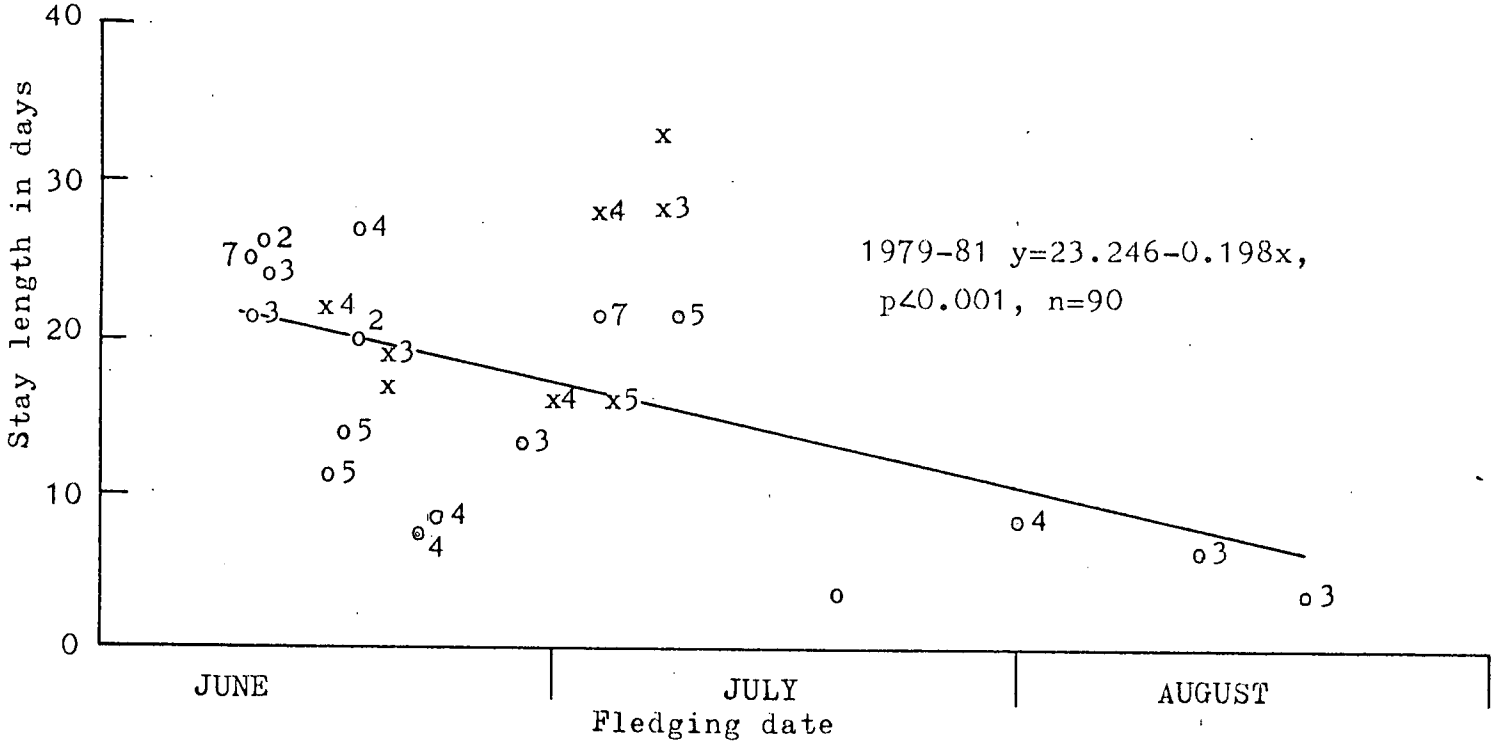


o 1979 y=53.681-0.856x, p<0.02, n=7
x 1980 y=16.308-0.151x, NS n=5
o 1981 y=49.666-1.110x, NS n=6



o 1979 y=30.836-0.298x, NS n=8
x 1980 y=77.803-1.606x, p<0.01, n=6
o 1981 y=40.159-0.818x, NS n=5

Figure 20 The number of days juvenile Whitethroats remained on the main study site in relation to their fledging dates, 1979-81.



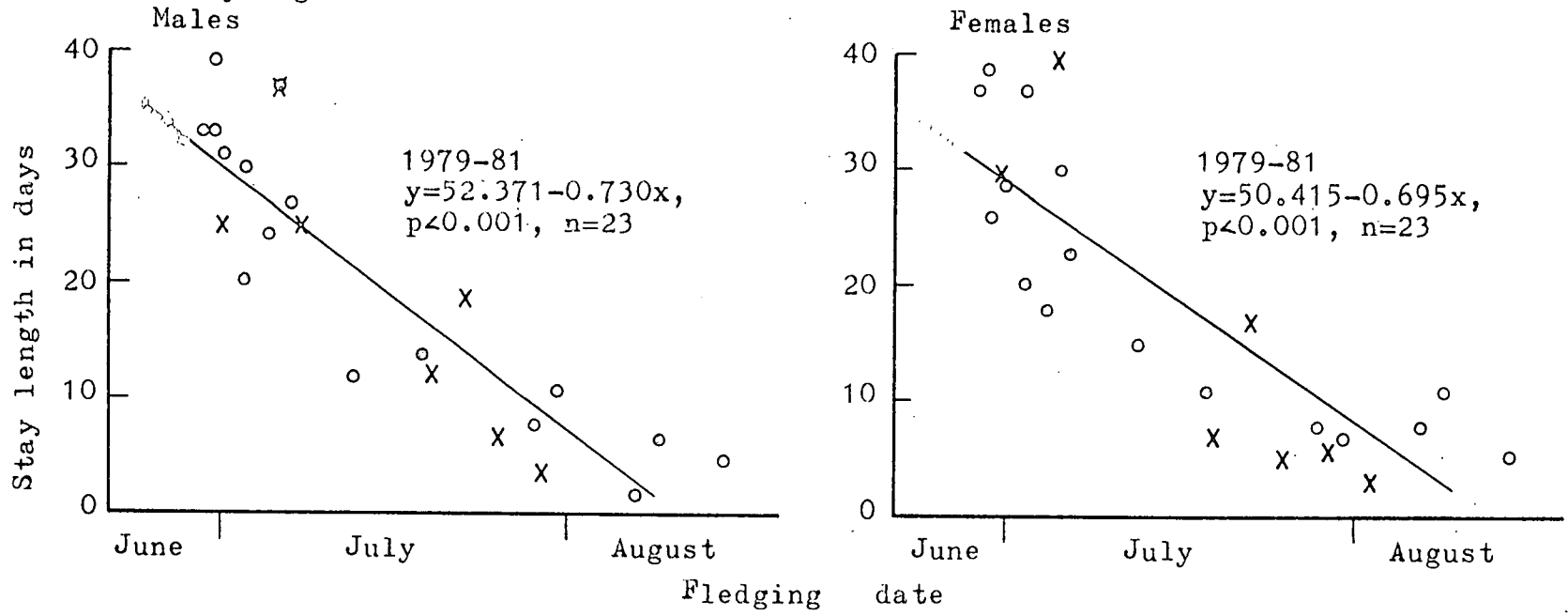
o 1979 y=18.256-0.137x, p<0.02, n=33

x 1980 y=16.469-0.175x, NS, n=25

o 1981 y=27.677-0.535x, p<0.001, n=32

females: successful mean 3rd August, S.D. 8.1 days, range 22nd July - 19th August, failed, mean 30th July, S.D. 10.3 days, range 14th July - 10th August). There were significant correlations between the fleding dates of their young and the time spent by the adults in the main study site once their young had fledged (Fig.21). There were also significant correlations between the time spent by juvenile Sedge Warblers reared in the site and their fledging dates (Fig.22). Young Sedge Warblers left the site 3-33 days after fledging. Unlike young Willow Warblers and Whitethroats, none were seen at nearby sites, nor were any recorded back in the main study site after a short term absence in late summer. Over three years the last dates when young Sedge Warblers reared in the site were seen there ranged from 14th - 25th August, with the majority leaving around the end of July.

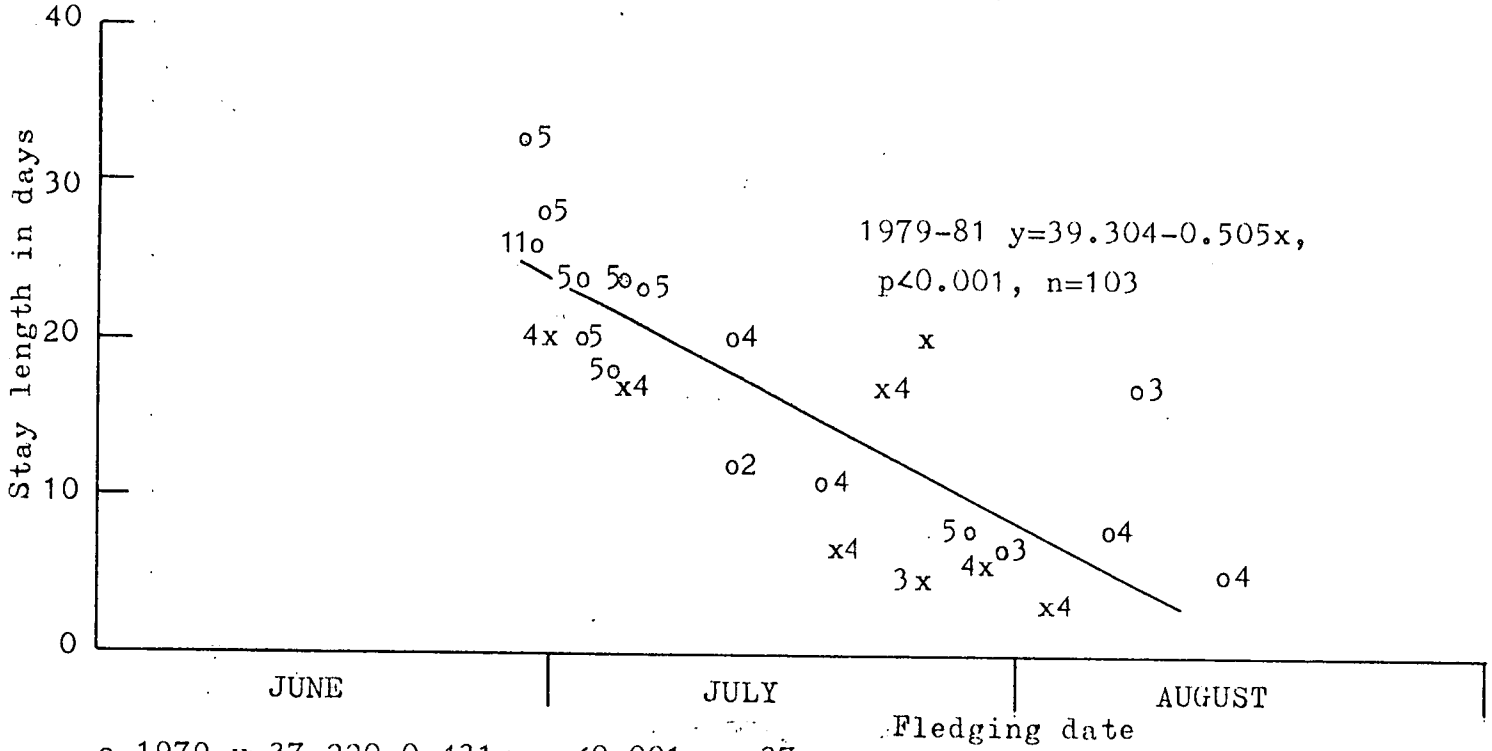
Figure 21. The number of days adult Sedge Warblers remained on their breeding site after the young had fledged in relation to the fledging dates of their young.



o 1979 y=49.090-0.655x, p<0.01, n=8
x 1980 y=59.593-0.904x, p<0.01, n=7
o 1981 y=52.227-0.700x, p<0.001, n=8

o 1979 y=42.916-0.545x, p<0.05, n=8
x 1980 y=67.102-1.055x, p<0.01, n=7
o 1981 y=50.572-0.655x, p<0.01, n=8

Figure 22 The number of days juvenile Sedge Warblers remained on the study site in relation to their fledging dates, 1979-81.



o 1979 y=37.220-0.431x, p<0.001, n=37

x 1980 y=33.758-0.459x, p<0.001, n=28

o 1981 y=40.644-0.501x, p<0.001, n=38

2:9 Summary

Most birds arrived in May though some male Willow Warblers arrived in late April. Males arrived significantly earlier than females except for Whitethroats and Sedge Warblers in 1981. Willow Warblers usually arrived before the other species. Whitethroats sometimes arrived earlier than Sedge Warblers. Arrivals were clumped, rather than being spread uniformly over the arrival period, and warblers were unlikely to arrive in certain weather conditions. There was some variation between years in mean arrival timing with 1979 the latest and 1981 the earliest years. No significant differences in arrival dates were found between one year old and older birds. More birds visited the site in spring than secured territories there. Birds returning to the site did not always return to their previous years' territory. Mean first egg dates differed between species with Willow Warblers significantly earlier than Sedge Warblers in three years and Whitethroats in two years. Whitethroats were significantly earlier than Sedge Warblers in two years. There was no evidence that older females laid earlier than one year olds. Females varied considerably in the time spent between arrival in the site and starting their clutches. Young Willow Warblers fledged between 8th June and 16th July, young Whitethroats between 10th June and 19th August and young Sedge Warblers between 28th June and 14th August. Post juvenile moult was estimated as taking 36-40 days in Willow Warblers, 31-37 days in Whitethroats and around 30 days in Sedge Warblers. No nestlings of any species completed this moult in the main study site. Most young Willow Warblers probably finished post juvenile moult in early to mid August, most Whitethroats by mid August and most Sedge Warblers by mid August. All the young Willow Warblers reared in the study

site left by the end of July though some other juveniles were present in August. Most Whitethroats and Sedge Warblers reared in the study site had left by the end of July, though some Whitethroats were present until 23rd August and some Sedge Warblers were present until 25th August. In all species young from later broods spent less time in the main study site between fledging and departure than young from earlier broods. This was also true of adult Sedge Warblers and Whitethroats over all three years and male Willow Warblers in one year. Moult in adult Willow Warblers was estimated as taking 40-45 days in males and 38-42 days in females, with the latter starting later. Some birds started moult before their young fledged; most did not complete moult before leaving the site. Very few Whitethroats moulted on the site and all left before moult was complete. Some birds that had not bred in the site moulted there. Most of the breeding Willow Warblers and Whitethroats left the main study site in July; most Sedge Warblers left around the end of July. The latest date in any year for a bird from the breeding population to be present in the site was 23rd August.

Chapter 3 Breeding biology and weight changes

3:1 Methods

In the three years, 1979-81, a principal aim of the daily visits to the main study site was to find all the warbler nests as early in the breeding cycle as possible. Once found, nests were checked daily until either they failed or the young fledged. During these daily checks data were obtained on clutch size, hatching success, fledging success and growth rates of chicks.

The advantage of intensive study on a relatively small site was that most nests were found early in the breeding cycle (44 at building, 27 during laying, 52 during incubation and only 9 after the young had hatched). Nest finding was helped considerably by intensive observation of the colour ringed adults' behaviour. Even when nest building was not seen a change in the behaviour of a female to a more secretive pattern indicated the start of nesting and the need to search in a particular territory. Nests were found at the egg stage by a combination of searching whenever a bird was flushed and by watching feeding females back to their nests. Once young had hatched it became relatively easy to watch the parents take food to the nestlings. Even when the actual nest site was not discovered immediately it was possible to infer what stage the birds were at in their breeding cycle by their behaviour. A further advantage of having all the breeding adults colour ringed is that it is possible to provide accurate figures on the output per pair (or individual since there were several cases of mate changing).

Weights of warblers caught in mist nets were routinely recorded using a 50 gm Pesola balance and recording to 0.1 of a gram, with an extra effort in 1980, by a programme of regular trapping throughout the season at approximately weekly intervals.

Since the birds were individually recognizable in the field these weights can be linked to specific stages of the birds' stay on their breeding grounds. Most weights were obtained within four hours of sunrise since the need to feed and defend territories made birds mobile, and easy to catch, and the low angle of the sun meant that nets were less visible. It is known that the body weights of small passerines are subject to considerable changes within a 24 hour period (Newton 1972, Perrins 1979). Weights obtained in the evening were therefore converted by subtracting a constant derived from individual birds that had been weighed in the evening and the subsequent morning. These values were 7.1% (n = 10) for Willow Warblers, 6.2% (n = 6) for Sedge Warblers and 5.4% (n = 7) for Whitethroats. The difference between species reflects differences in the size of the birds, with the smallest losing most weight, since small birds need relatively more energy than larger ones to maintain their body temperatures (Calder & King, 1974). Mist netting was relatively unproductive between mid morning and late afternoon and the few weights obtained then have not been used.

Nestlings were weighed daily (with few exceptions) using a 50 gm. Pesola balance recording to 0.1 gm. Very young chicks were marked with an alcohol based felt tipped pen to allow individual recognition of birds which were too small to carry numbered rings. Nestlings were weighed in the course of the daily visits.

3:2 Nest sites and nest building

Chapter 2 described differences between the species in arrival dates and the timing of breeding. To some extent this was related to choice of nest sites. Willow Warblers, which tended to breed ahead of the other species, nested on the ground in grassy areas, often near the base of a shrub and often on banks. Only two nests were recorded 45-60 cms. off the ground in small gorse bushes. Whitethroat nest sites (10-75 cms.) were generally higher than Willow Warblers but not as high as Sedge Warblers which also varied more in height (24-300 cms.) Both Whitethroats and Sedge Warblers used the herb layer for nest sites though Whitethroats, by building lower down, could start earlier than Sedge Warblers. For example both species often used nettle and willow-herb stands; Whitethroat nest sites in nettles (mean 20.5 cms, range 15-25 cms) were lower than Sedge Warblers (mean 39.5 cms, range 33-50 cms.) and in willow-herb Whitethroats(mean 20.7 cms, range 17-30 cms) were again lower than Sedge Warblers(mean 53.4 cms, range 38-75 cms.) Both species also made use of shrubs such as broom, hawthorn and bramble, especially where grass and herbs grew up through the bushes. Overall the differences in mean height between the species was significant: Whitethroat mean 29.8 cms, range 10-75 cms, n = 32, Sedge Warbler mean = 63.6 cms, range 24-300 cms. n = 46, ($t=4.26$, $p < 0.001$).

In all species the nests were built by the hen alone in between one and two days, though occasionally finishing touches such as linings were put in just before the first egg was laid up to four days after completion of the basic nest. Two female Whitethroats took a little longer than this; one took three days to build and laid the first egg another three days later, she appeared sickly

and took nine days to complete her clutch of five eggs which were not brooded properly. The other was a bird that took five days to build her nest after much chivying from her mate who was seen to put dried grass stems into her bill. Thereafter egg laying and brooding proceeded normally. Whitethroat males often built cocks' nests even prior to pairing. Two males built up to four of these in one season but none were ever used by a female; there function may be a form of male display (Campbell & Ferguson-Lees, 1972). Males of all three species were seen on occasion to hold grass stems in their bills but none were ever seen adding to the nest. Eggs were laid at daily intervals and incubation commenced either on the day the second last or the last egg was laid. All clutches that hatched did so within a 24 hour period.

3:3 Breeding behaviour and success

Willow Warblers were single brooded and monogamous except for one male which had two mates in 1980, another three in 1981 (all different birds as were three further mates in 1982) and one female (the third mate of the polygamous male in 1981) which on the evidence of a defunct (see page 54) brood patch appeared to have tried to breed outwith the main study site in 1981 before breeding in the site. No evidence was found for birds holding more than one territory either in the main study site or elsewhere. One male Willow Warbler that held a territory in 1979 failed to secure a mate and 22 males that failed to secure territories left the site between late April and early May 1979-81. All the female Willow Warblers that stayed throughout the breeding season secured mates but over the three years ten that were colour ringed soon after arrival did not stay to breed in the site.

Eight Whitethroats (five males and three females) were also involved in more than one brood although none attempted to rear a second brood with its original mate. The three females both reared their first broods but their mates took over the feeding of the brood after fledging and left the site with them. Two of the females paired with males that had already attempted to breed in the main study site. The other female's second mate was not identified as no male was seen to accompany her after her first brood fledged, and she was alone during the incubation and rearing of her second brood. The other male Whitethroats all paired with females which arrived later in the study site. A small number (5 birds over 3 years) of male Whitethroats did not secure territories and left the study site each spring. Only one female Whitethroat definitely left the site in spring without pairing.

In 1979 one male stayed on the site without securing a mate. This bird wandered over a large part of the study site apparently trying to avoid territory holders. All other male Whitethroats and all the females secured mates.

No Sedge Warblers were involved in polygamy or double brooding. Seven males and two females that were colour ringed in spring did not stay to breed. One male Sedge Warbler which held a territory in 1981 failed to secure a mate. The other male and female Sedge Warblers that stayed in the study site all secured mates.

The breeding statistics of the three species are shown in Tables 12-14. There were no statistically significant differences in mean clutch size over the three years in any species. There was a significant correlation between clutch size and laying date in all three species when three years data were combined (Figs. 23-25). When each year was examined separately the relationship did not always reach statistical significance. Willow Warblers' clutch sizes showed a significant reduction with laying date in 1980 and 1981 but not in 1979 (Fig.23). Figure 24 shows Whitethroat first egg dates in relation to clutch size. Late clutches were smaller but the relationship between clutch size and laying date only reached statistical significance when the three years were combined. Sedge Warblers (Fig.25) showed a significant reduction in clutch size the later the clutch was started in 1981, but there was no significant correlation in 1979 and 1980.

Egg loss was higher for all three years in Sedge Warblers (22-33%) than Willow Warblers (1-16%) but only significantly higher in 1979 and 1981 (1979 $X^2 = 23.69$, $p < 0.001$, 1980 $X^2 = 1.42$, N.S, 1981 $X^2 = 6.99$, $p < 0.01$). Although percentage egg loss was higher in all three years for Sedge Warblers than Whitethroats (4-21%) the

Table 12 Willow Warbler breeding statistics.

	1979	1980	1981
Mean clutch size	5.69	5.73	5.75
S.D.	0.86	1.16	0.85
range	4-7	3-7	4-7
Number of clutches	13	15	20
Mean brood size	5.61	5.54	5.63
S.D.	0.87	1.13	0.90
range	4-7	3-7	4-7
Number of broods	13	13	19
Mean number fledged/male	3.7	4.2	2.9
Number of males	13	14	18
Mean number fledged/female	3.7	3.9	2.7
Number of females	13	15	20

Table 13 Whitethroat breeding statistics.

	1979	1980	1981
Mean clutch size	4.00	4.40	4.80
S.D.	0.89	0.52	0.79
range	3-6	4-5	3-6
Number of clutches	11	10	10
Mean brood size	4.00	4.20	4.75
S.D.	1.00	0.42	1.17
range	3-6	4-5	2-6
Number of broods	9	10	8
Mean number fledged/male	3.7	2.8	4.0
Number of males	9	9	8
Mean number fledged/female	3.0	2.5	4.0
Number of females	11	10	8

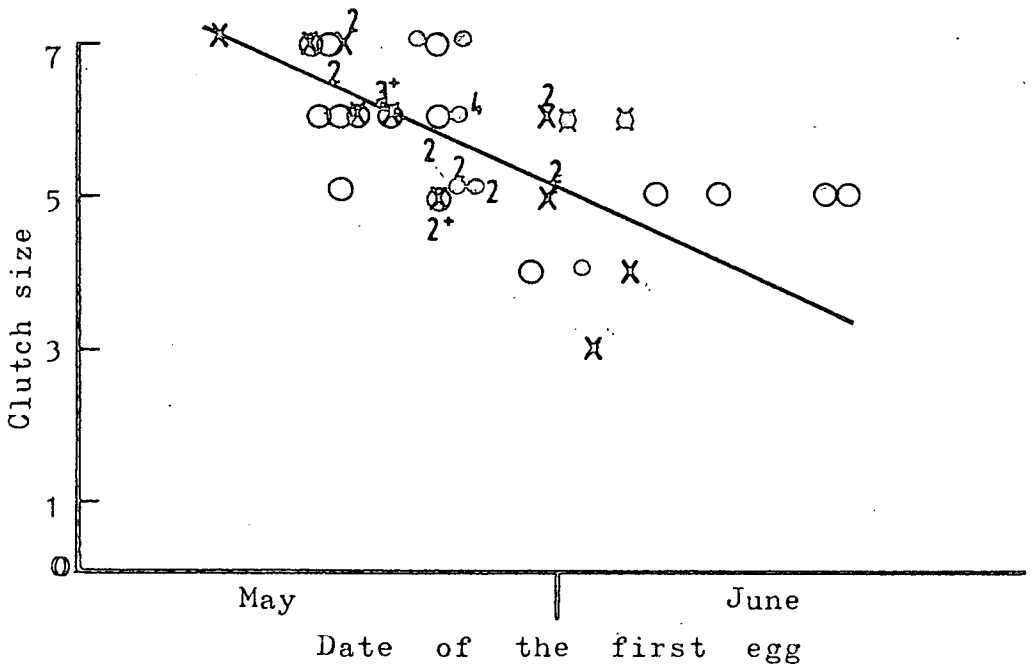
Table 14 Sedge Warbler breeding statistics.

	1979	1980	1981
Mean clutch size	4.56	4.42	4.75
S.D.	0.51	0.90	0.75
range	4-5	3-6	4-6
Number of clutches	16	12	12*
Mean brood size	4.45	4.00	4.60
S.D.	0.69	0.47	0.97
range	3-5	3-5	3-6
Number of broods	11	10	10
Mean number fledged/male	3.1	2.8	3.8
Number of males	12	10	10
Mean number fledged/female	3.1	2.8	3.8
Number of females	12	10	10

* does not include one clutch deserted during egg laying.

Figure 23

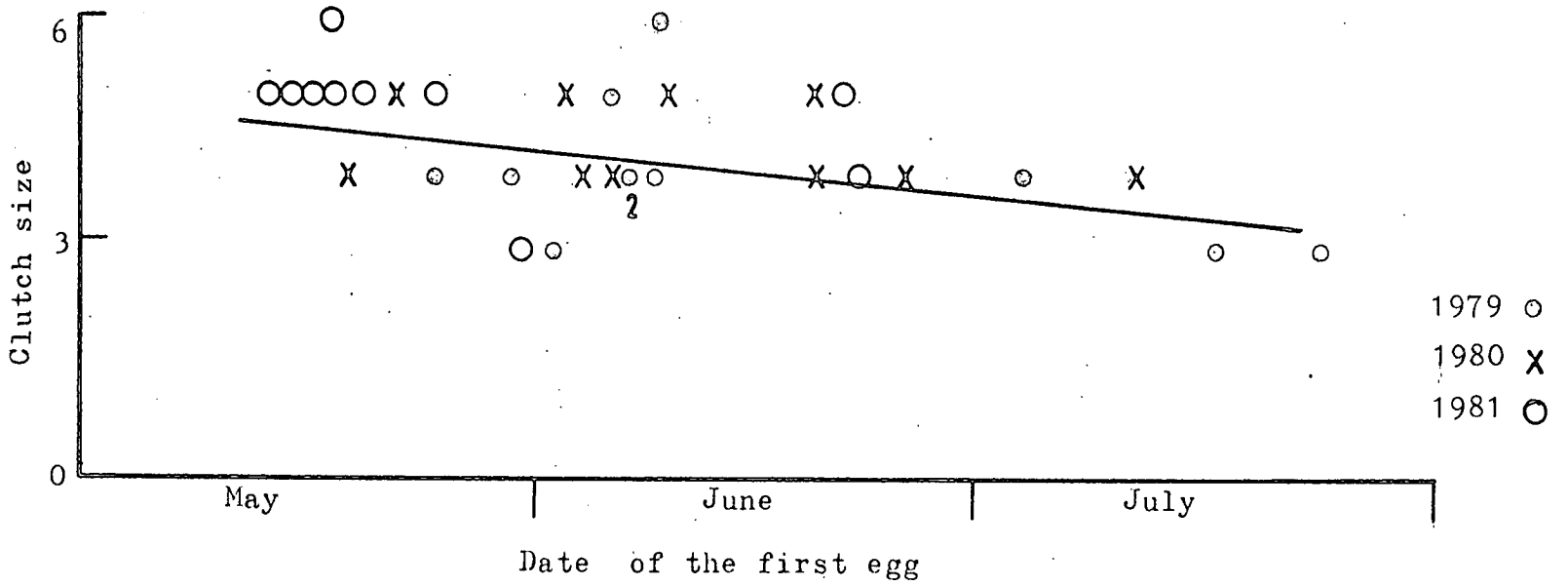
The clutch size of Willow Warblers in relation to the date of laying the first egg.



1979 ⊙	y=7.200-0.058x,	NS,	n=13
1980 X	y=8.178-0.098x,	p<0.01,	n=15
1981 + O	y=6.936-0.048x,	p<0.01,	n=20
1979-81	y=7.317-0.063x,	p<0.001,	n=48

Figure 24

The clutch size of Whitethroats in relation to the date of laying the first egg.



1979 y=4.882-0.020x, NS, n=11

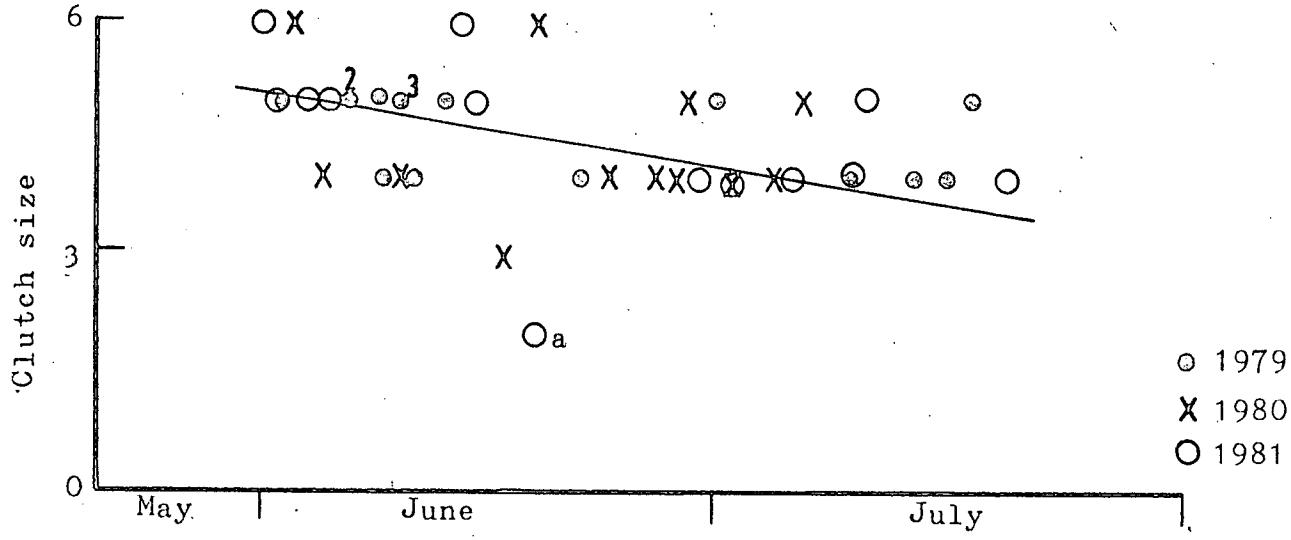
1980 y=4.736-0.008x, NS, n=10

1981 y=5.361-0.022x, NS, n=10

1979-81 y=5.178-0.021x, p<0.01, n=31

Figure 25

The clutch size of Sedge Warblers in relation to the date of laying the first egg.



1979 y=5.292-0.014x, NS, n=16

1980 y=5.065-0.012x, NS, n=12

1981 y=6.382-0.031x, p<0.01, n=12

1979-81 y=5.619-0.020x, p<0.01, n=40

a this figure was excluded from calculations as the clutch was deserted before completion.

difference was not statistically significant. Whitethroats lost a significantly greater percentage of eggs in 1979 and 1981 than Willow Warblers (1979 $X^2 = 8.83$, $p < 0.01$, 1981 $X^2 = 5.3$, $p < 0.05$) but there was no significant difference in 1980. The greatest proportion of all egg loss was due to loss of complete clutches though in most years there was a small number of eggs (from 3-8) that represented partial clutch failure. Complete clutches failed due to predation (12), desertion (2), the female being predated (1), a cow standing on the nest (1) and in one case the eggs did not hatch properly (Table 15). The most likely predators were weasels, Mustela nivalis, which were the major cause of chick loss (Table 16), since the nests from which eggs disappeared were undamaged, although direct evidence was lacking.

There were no significant differences in the number of eggs hatching per nest between years for any species.

Details of losses of nestlings are shown in Table 16. Over the three years, 1979-81, chick loss (Willow Warblers 36.5%, Whitethroats 22.4%) was higher than egg loss (Willow Warblers 8.4%, Whitethroats 14.7%) though only in Willow Warblers was this significant ($X^2 = 61.06$, $p < 0.001$). With Sedge Warblers egg loss (27%) was higher than chick loss (23.7%); the difference is not significant. Over the three years of the study significantly more chicks (150; 29.8%) were lost than eggs (93; 15.6%) when data for the three species are combined ($X^2 = 32.02$, $p < 0.001$).

Fledging success in Willow Warblers was not significantly different between years nor was there any significant difference between normally timed and late (broods delayed by disturbance or the second and third broods of a polygamous male) broods in 1981. There were no significant differences in fledging success in Whitethroats or Sedge Warblers between years.

Table 15 Details of losses at the egg stage over three years 1979-81.

	Number of clutches	Number of eggs laid	Number of eggs hatched	Number of eggs lost	Number of clutches lost	Percentage egg loss	Known cause of loss
Willow Warbler							
1979	13	74	73	1	0	1.35	Not hatched
1980	15	86	72	14	2	16.27	5 eggs from 4 clutches not hatched, 1 clutch not hatched, one clutch killed by a cow.
1981	20	115	107	8	1	6.95	4 eggs from 4 clutches not hatched, 1 clutch predated.
Whitethroat							
1979	11	44	36	8	2	18.18	1 clutch predated, 1 clutch-female killed.
1980	10	44	42	2	0	4.54	2 eggs from 2 clutches not hatched.
1981	10	48	38	10	2	20.80	2 eggs from one clutch not hatched, 1 clutch predated, 1 clutch deserted.
Sedge Warbler							
1979	16	73	49	24	5	32.8	2 eggs from 2 clutches not hatched, 5 clutches predated.
1980	12	53	40	13	2	24.5	1 egg from 1 clutch not hatched, 2 clutches predated.
1981	13*	59	46	13	3	22.3	2 eggs from 2 clutches not hatched, 2 clutches predated, 1 clutch

*includes one partial clutch of two.

Table 16 Details of losses at the nestling stage over three years 1979-81.

	Number of eggs hatched	Number of young fledged	Number of young lost	Percentage young lost	Known cause of loss
Willow Warbler					
1979	73	48	25(4)	34.2	2 chicks fell out nests, 1 brood killed by cow, 3broods pred.
1980	72	59	13(2)	18.0	Predation
1981	107	53	54(9)	50.4	2 chicks fell out of nests the rest were predated.
Whitethroat					
1979	36	33	3(0)	9.09	1 chick dead in nest 2 chicks fell out nests
1980	42	25	17(4)	40.4	Predation
1981	38	32	6(1)	15.7	Predation
Sedge Warbler					
1979	49	37	12(3)	24.4	Predation
1980	40	28	12(3)	30.0	1 chick dead in nest otherwise predation
1981	46	38	8(2)	17.3	Predation

The number of complete broods lost are shown in parentheses.

There was some evidence that variation in fledging success was due to predation rather than starvation. Only two chicks died of starvation whilst in the nest. One was a Sedge Warbler in 1980 and the other a Whitethroat in 1979, (Table 16). The Whitethroat was 3-4 days old when it died but the Sedge Warbler was ready to fledge, but stayed in the nest after its siblings had left, and died two days later. Three Willow Warblers and two Whitethroat pulli died after falling out of the nest. Their parents then ignored them.

On five separate occasions Weasels were disturbed attacking a nest and the young were found bloody, with bite marks in several places. Some of the young were carried off to be eaten elsewhere. On 19 occasions Weasels were suspected as the cause of predation (little damage to the nest accompanied by pieces of chicks lying by the nest.) Fox, Vulpes vulpes, predation ($n = 5$) was also suspected with two Sedge Warbler and two Whitethroat broods (when the nest was pulled down and tilted) and one Willow Warbler nest which was uprooted and torn. All these nests were near to regularly used fox paths. Rats, Rattus norvegicus, were strongly suspected of predating three nests (one from each species) which were in the close vicinity of disused sheds. In all three cases the nest had been pulled down from one side with no sign of the young left.

The most important breeding statistic is the number of young successfully reared. Since there were instances of polygamy and mate changing Tables 12-14 show fledging success separately for males and females rather than per pair. With Sedge Warblers these factors do not apply and output per pair ranged from 2.8 in 1980 to 3.8 in 1981. In 1979 Willow Warblers produced 3.7 fledged young per pair. In 1980 and 1981 one male was polygamous which resulted in the number of young fledged per male (4.2 and 2.9 respectively) being

slightly higher than the number fledged per female (3.9 and 2.7) though the differences were not statistically significant. With Whitethroats a few individuals changed mates and were involved in second broods each year. In 1981 output per male and female was the same at four successful fledgings per breeding adult. In both 1979 and 1980 the number of nestlings that fledged per male (3.7 and 2.8) was slightly greater than with females (3.0 and 2.5) though these differences were not statistically significant.

Since clutch size seemed to decline during the breeding season the fledging success of late clutches was also examined (late clutches were defined as those where the first egg was laid later than one standard deviation after the mean first egg date for each species in a particular year, see Figs. 8-10.) In all cases late clutches produced fewer fledglings per breeding adult than average. Over three years ten late Willow Warbler clutches produced 2.7 fledglings per nest compared to ranges of 2.7 to 3.9 fledglings per breeding female and 2.9 to 4.2 fledglings per breeding male when all nesting attempts were included. Over the three years five late Whitethroat clutches produced 2.2 fledglings per nest compared to ranges of 2.5 to 4 fledglings per breeding female and 2.8 to 4 fledglings per breeding male. From 1979-81 ten late Sedge Warbler clutches produced 2.2 fledglings per nest compared to a range of 2.8 to 3.8 fledglings per nest.

3:4 Weight changes through the season

The weights of breeding Willow Warblers are shown in Table 17 in relation to different stages of their time in the main study site. On arrival in the study site males were significantly heavier than females ($t = 2.98$, $p < 0.01$) which is to be expected since they are very significantly larger (male mean wing length : 69.2 mm range 67-72, female mean wing length : 63.7 mm range 62-66 mm, $t = 18.9$, $p < 0.001$). After a week in the site males were still heavier but females weights had increased proportionately more than males; the weight increase for all males over this period was 2.2% whereas for females it was 6.0%. Between one week after arrival and egg laying, female weights showed very big increases of around 20% over their arrival weights, and by this time they were significantly heavier than males over the same period ($t = 3.60$, $p < 0.01$) despite being smaller birds. Males also gained weight between arrival and the onset of egg laying by their mates. They did not seem to lose weight during the incubation period which was carried out in all cases by the hens alone. Female weights obtained during the incubation period dropped to values similar to those on arrival. Males were not seen to feed females during incubation. Once the chicks hatched the males became involved in the feeding of their young and their weights dropped significantly ($t = 2.48$, $p < 0.05$). Males which were classed as unhelpful to their hens (i.e. gave little help in the feeding of nestlings) had lower mean weights than those of helpful males at one week after arrival and at laying, but they proved to be difficult to catch, and none was caught at all during the important periods of feeding nestlings or fledged young to make further comparisons with more helpful males. Females continued to lose weight after the young hatched being

Table17 The weights of adult Willow Warblers in relation to migration, breeding and moult in 1980.

	Arrival	One week after arrival to egg laying	Egg laying	Incubation	Nestling feeding	After young fledged	During moult moult scores 0-10	10-37	37-50	Departure
Females										
mean	8.3	8.8	10.0	8,3	7.9	8.1	8.2	8.3	8.6	8.4
S.D.	0.52	0.46	0.62	0.22	0.29	0.17	0.35	0.13	0.26	0.27
sample size	9	9	8	11	9	9	7	7	5	10
Males										
mean	8.9	9.1	9.1	9.0	8.7	8.8	8.8	9.1	9.3	9.2
S.D.	0.38	0.38	0.37	0.44	0.37	0.38	0.38	0.41	0.43	0.28
sample size	8	9	10	10	8	8	10	10	7	9

Arrival : weights measured up to one week after arrival

Departure : weights measured no more than four days before departure

significantly lighter when feeding nestlings than when incubating ($t = 3.30$, $p < 0.01$). Their weight loss was proportionately greater even than that of helpful males which reflects the fact that females fed the young more often than their mates (see also Chapter 5 on food and feeding).

Both male and female weights were at their lightest during the nestling period. Once the young fledged female weights increased. Males also did so but only slightly. Weights of both males and females increased during moult. On departure males were not significantly heavier than when they arrived in the study site or when they had spent a week in the site. Female weights on departure showed no significant difference compared to their weights on arrival and they were significantly lighter on departure than after one week in the site ($t = 2.20$, $p < 0.05$).

Whitethroat weights in relation to their breeding cycle are shown in Table 18. There was no significant difference between the weights of males and females on arrival in the site (using wing length as a measure of body size males (mean wing length 71.1 mm, range 68-75 mm) were not significantly larger than females (mean wing length 70.3 mm, range 68-72 mm)). After a week in the site females' weights were not significantly heavier than those of males but during egg laying their weights were significantly heavier. ($t = 5.41$, $p < 0.001$). Male weights showed a slight drop after a week on the site . Their weights stayed fairly constant when the females were laying and then rose during incubation. Females' weights increased significantly between one week after arrival and egg laying ($t = 3.14$, $p < 0.01$). Female weights dropped significantly when they were feeding nestlings ($t = 2.57$, $p < 0.05$). Male weights also dropped but not significantly. Female weights

Table 18 The weights of adult Whitethroats in relation to migration and breeding in 1980.

	Arrival	One week after arrival to egg laying	Egg laying	Incubation	Nestling feeding	After young fledged	Departure
Females							
mean	13.8	14.2	15.9	14.0	13.2	13.7	13.5
S.D.	0.87	1.12	0.66	0.61	0.49	0.70	0.38
sample size	7	4	9	10	6	6	4
Males							
mean	14.1	13.7	13.8	14.1	13.5	13.4	13.6
S.D.	0.62	0.93	0.63	0.54	0.64	0.21	0.45
sample size	6	8	5	8	7	2	6

Arrival : weights measured up to one week after arrival

Departure : weights measured no more than four days before departure

showed a slight increase after fledging but males did not, though the sample size for males was small. After fledging there was no significant difference between male and female weights nor was there any significant difference between weights of either sex obtained prior to departure compared to weights taken soon after arrival on the site.

The weights of breeding Sedge Warblers are shown in Table 19. Females were slightly heavier than males on arrival on the site although on average they were smaller birds (male mean wing length : 67.1 mm, range 64-71 mm, female mean wing length : 64.1 mm, range 62-66 mm; $t = 7.18$, $p < 0.001$). Female weights increased after a week on the site and they were significantly heavier than males before and during egg laying ($t = 2.45$, $p < 0.05$, $t = 8.91$, $p < 0.001$). Males gained weight after arrival, were at their heaviest when the females were incubating and dropped significantly ($t = 3.52$, $p < 0.01$) during the nestling period. Both sexes lost weight significantly during the nestling period (males $t = 3.524$, $p < 0.01$, females $t = 6.10$, $p < 0.001$). After fledging male and female weights were similar to those of birds feeding nestlings. Neither males or females gained weight before departure and there was no significant difference between departure and arrival weights.

Some female warblers started laying only a few days after arrival in the main study site, although others took a week or longer (Fig.11). Examination of weight data for females that started laying six days or less after arrival shows that these birds tended to have above average weights on or soon after arrival on the site. A female Willow Warbler that started her clutch three days after arriving in 1980 weighed 9.4 gms., which is about 1 gm. heavier than the mean weight for females at this time (this female was excluded

Table 19 The weights of adult Sedge Warblers in relation to migration and breeding in 1980.

	Arrival	One week after arrival to egg laying	Egg laying	Incubation	Nestling feeding	After young fledged	Departure
Females							
mean	11.7	12.1	13.7	11.5	10.7	11.2	11.1
S.D.	0.64	0.56	0.45	0.28	0.15	0.66	0.41
sample size	10	7	9	10	6	5	5
Males							
mean	11.2	11.4	11.8	12.1	11.3	11.4	11.3
S.D.	0.19	0.53	0.43	0.44	0.28	0.57	0.29
sample size	8	10	10	7	6	6	6

Arrival : weights measured up to one week after arrival

Departure : weights measured no more than four days before departure

from Table 17). Another female Willow Warbler that started laying six days after arrival weighed 9.0 gms. on the day she arrived in the site in 1981.

A female Whitethroat that started laying three days after arrival in 1979 weighed 17.3 gms. on the day she arrived in the site, which is over 3 gms. heavier than the mean arrival weight for most female Whitethroats. Also in 1979, another female that started laying six days after arriving weighed 17.2 gms. on the day she appeared in the site. In 1980 a female Whitethroat weighed 16.6 gms. four days after arrival; two days later she began to lay. In 1981, when female Whitethroats generally spent only two to eight days between arrival and egg laying, four birds weighed within six days of arrival all had weights above the mean arrival weight found in 1980 (which excluded the early bird mentioned above) ranging from 14.4 gm. to 16.6 gms.

The weights of juveniles before leaving the main study site did not show any evidence of weight gains which would be expected if they were about to embark on a long migratory flight (Berthold 1975). Since all the young Willow Warblers reared in the site left before August, and before they had completed post juvenile moult, samples of juveniles captured on or after the 6th August 1980, and around or nearing completion of post juvenile moult, were examined. These birds were particularly numerous in the case of Willow Warblers and, as they had all completed growth of their remiges, they could be sexed on the basis of wing length (males $>$ 66 mm. and females $<$ 66 mm, intermediate birds not used). Male weights (mean 9.2 gms. SD 0.46, n = 33) were not significantly different from the weights of breeding adult males around departure from the valley (mean 9.2 gms., SD 0.28, n = 9). Female weights (mean 8.2 gms. SD 0.27, n = 37) were also

similar to the weights of breeding adult females weighed prior to departure (mean 8.4, SD 0.27 n = 10).

Some young Whitethroats and Sedge Warblers reared in the study area were still present in August, but numbers were low, so weights from all three seasons were combined. Juveniles of these species cannot be reliably sexed, since the wing lengths of males and females overlap greatly, so comparisons with the adults were made with the sexes combined. As with the young Willow Warblers there was no evidence of significant weight gains in August. Weights of juvenile Whitethroats (mean 13.5 gms. SD 0.36 , n = 27) were not significantly different from the adults (mean 13.4 gms. SD 0.40, n = 10) while young Sedge Warblers (mean 10.5 gms. SD 0.43, n = 26) were even lighter than the older birds (mean 11.2 gms. SD 0.345, n = 11; $t = 4.65$, $p < 0.001$).

3:5 Weight changes in nestlings

The weight increases of some Willow Warbler nestlings are shown in Fig.26, which shows mean weights and confidence limits per day. Weight ranges within a brood were wide throughout the nestling period, and often became more marked as the chicks grew, probably due to the difference in size between the sexes.

In all species there was a very rapid period of growth up to day six or seven, and then a more gradual rise up to day 11, by which time weights had normally peaked and were either maintained or showed insignificant changes (Figs. 26-28). Day eleven was therefore chosen for comparison of the weights of chicks between years. Also fledging sometimes took place one or two days early and taking weights on the day of fledging might have risked losing data from some broods.

Table 20 shows data on the weights of Willow Warbler chicks over three years. Comparisons between years show that mean weights were lowest in 1979, but only significantly lower than in 1981 ($t = 2.45$, $p < 0.02$). Comparison of the weights of chicks from the three late Willow Warbler broods (mean 9.8 gms. SD 0.96, $n = 12$) showed no significant difference in weights compared to more normally timed broods (mean 9.86, SD 0.86, $n = 159$). Comparison of the mean weights of chicks from broods of six or more with broods of five or less showed no significant differences. Mean weights of Whitethroat pulli were also highest in 1981 (Table 21) but not significantly heavier than in 1980. In 1979 mean chick weights were significantly lighter than in 1980 and 1981 (1979-80 $t = 2.43$, $p < 0.02$, 1979-81 $t = 3.25$, $p < 0.01$). Late (second brood) Whitethroat chicks (mean 12.0 gms., SD 0.82, $n = 12$) were significantly lighter than chicks from more normally

Figure 26

Mean weights of Willow Warbler nestlings with 95% confidence limits and sample sizes 1979-81.

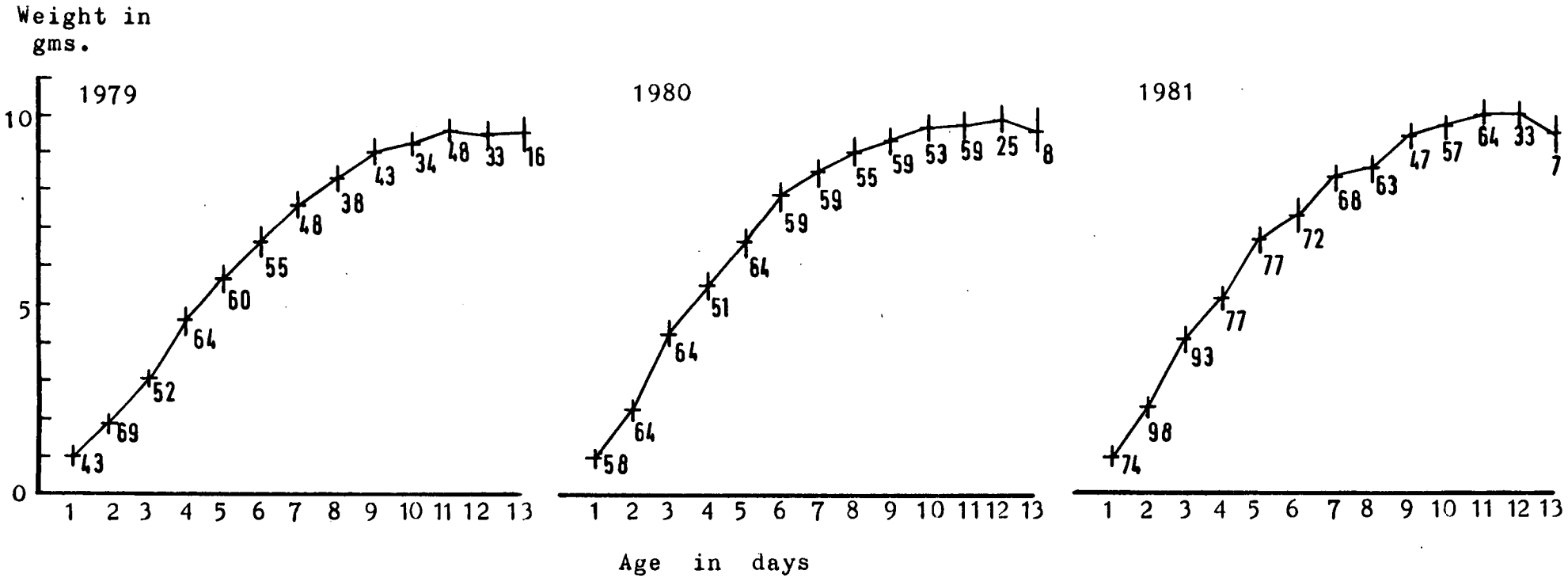


Figure 27
Mean weights of Whitethroat nestlings with 95% confidence limits and sample sizes 1979-81.

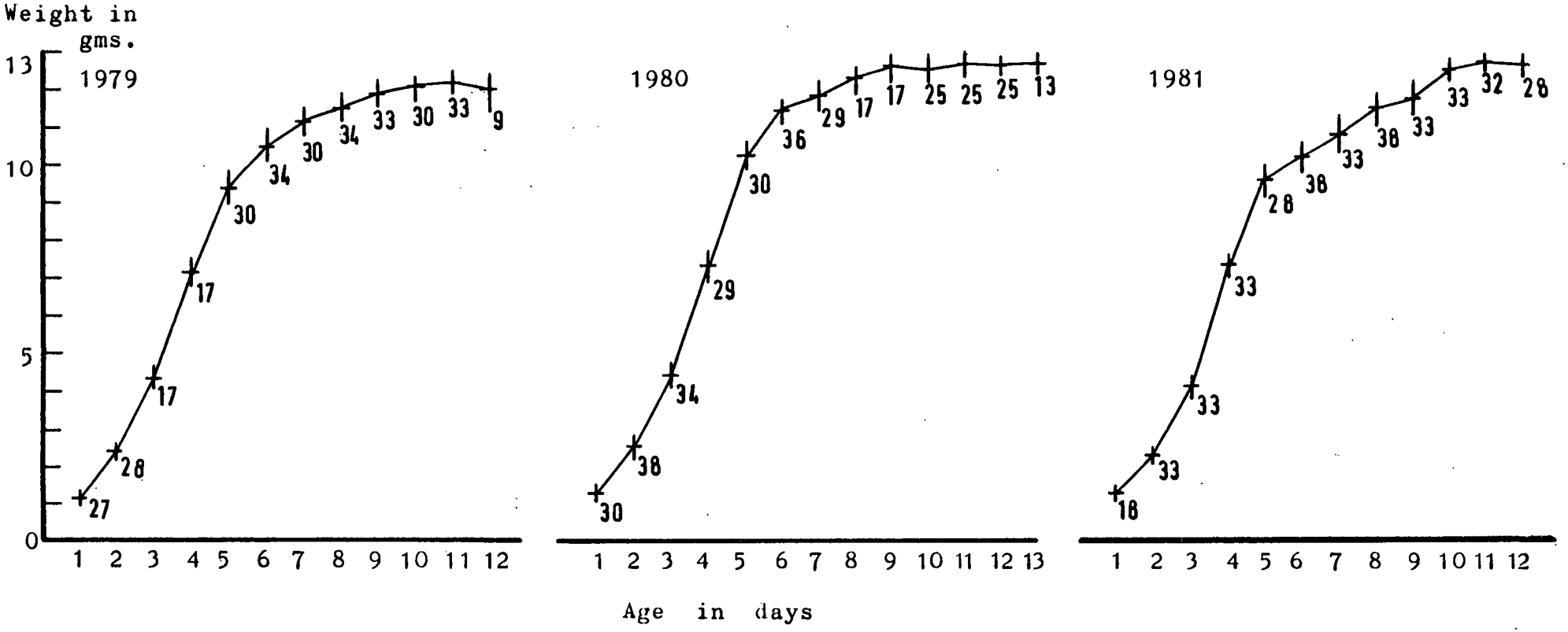


Figure 28

Mean weights of Sedge Warbler nestlings with 95% confidence limits and sample sizes 1979-81.

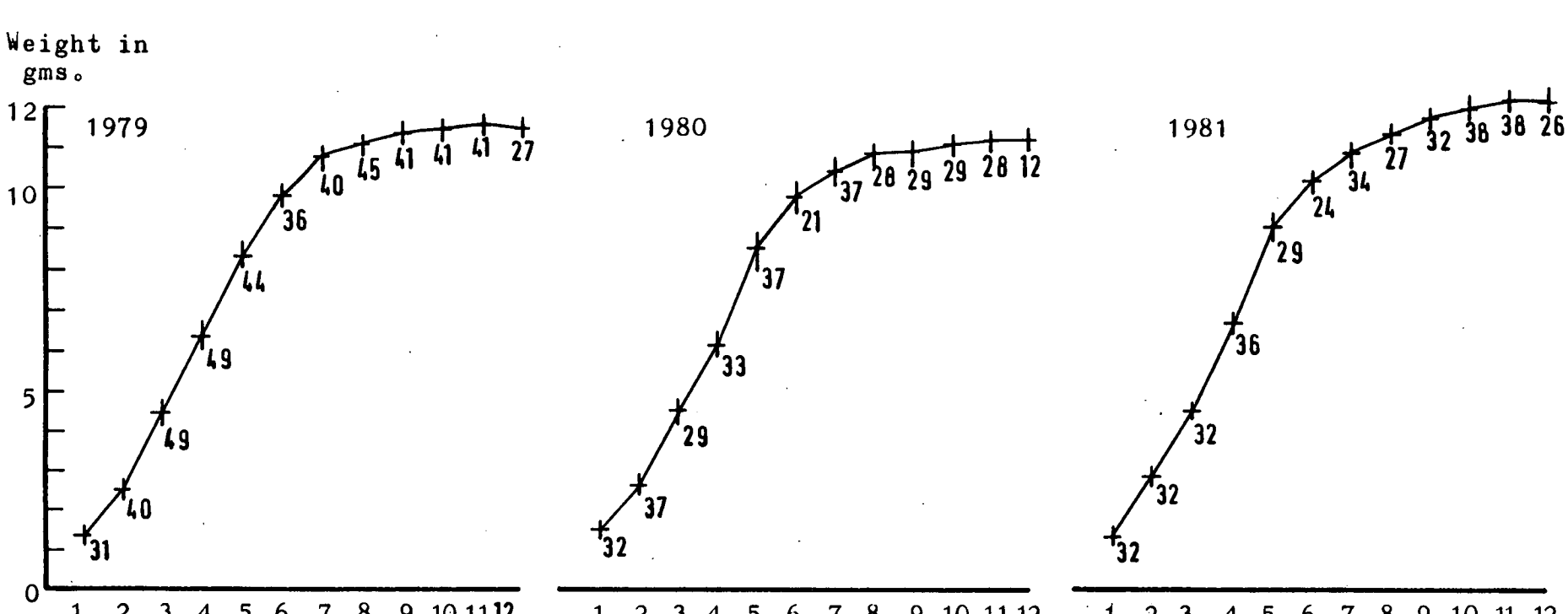


Table 20 The weights of nestling Willow Warblers at eleven days old 1979-81.

	Number of broods	Number of chicks	Mean weight of chicks	S.D.
1979	9	48	9.6	0.860
1980	11	59	9.8	0.875
1981	12	64	10.0	0.839

Table 21 The weights of nestling Whitethroats at eleven days old 1979-81.

	Number of broods	Number of chicks	Mean weight of chicks	S.D.
1979	9	33	12.1	0.876
1980	6	25	12.6	0.579
1981	7	32	12.7	0.623

Table 22 The weights of nestling Sedge Warblers at eleven days old 1979-81.

	Number of broods	Number of chicks	Mean weight of chicks	S.D.
1979	9	41	11.5	0.379
1980	7	28	11.2	0.374
1981	8	38	12.1	0.504

timed broods (mean 12.6 gms. SD 0.72 , n = 79; 1979-81 t = 2.56, p $<$ 0.02). Mean weights of Sedge Warbler chicks (Table 22) were also highest in 1981 when they were significantly heavier than in 1979 or 1980 (1979/81 t = 5.9, p $<$ 0.001, 1980/81 t = 7.9, p $<$ 0.001). 1979 was also higher than 1980 (t = 3.2, p $<$ 0.001). Later Sedge Warbler chicks (mean 11.6 gms. SD 0.62, n = 26; from clutches started more than one standard deviation after the mean first egg date each year) were not significantly lighter than chicks from earlier broods (mean 11.7, SD 0.56, n = 81).

3:6 Summary

All but two Willow Warbler nests were on the ground. Whitethroats and Sedge Warblers nested in herbs or low shrubs with Sedge Warbler nests higher above the ground than Whitethroats. Most birds were single brooded though one male Willow Warbler was polygamous and a minority of Whitethroats tried to rear second broods with different mates. Only Sedge Warblers laid replacement clutches when the original clutch was lost. Clutch size tended to decrease later in the season. Few eggs failed to hatch and few chicks starved. Most losses of eggs and chicks were due to mammalian predation, probably mostly by weasels. Overall more chicks were lost than eggs. The number of fledged young per pair of Sedge Warblers ranged from 2.8 to 3.8 over three years. With Willow Warblers the number of fledged young per breeding male ranged from 2.9 to 4.2 and per breeding female from 2.7 to 3.9 over three years. With Whitethroats the number of fledged young per breeding male ranged from 2.8 to 4.0 and per breeding female ranged from 2.5 to 4.0 over three years. Females of all species were significantly heavier when egg laying than at other times. Females which started laying within six days of arrival on the site were heavier than the average arrival weights for their species. No warblers showed any evidence of pre migratory weight gains in late summer. Nestling weights tended to be lowest in 1979 and highest in 1981. In Whitethroats nestlings from late broods tended to be lighter than earlier broods; in other species there were no significant differences.

Chapter 4 Return rates and local movements

4:1 Methods

Since all the adults which bred or attempted to breed in the main study site were uniquely colour ringed it was possible to measure their return rates in later years. All nestlings that survived to the appropriate age were given a colour ring unique to the year and a B.T.O. ring; any that were located in later years were captured, identified from the metal ring and a unique colour combination added. Although all the breeding adults and their progeny were ringed this was impossible with other classes of birds that visited the site. Some adults that failed to secure territories in spring were colour ringed, although an unknown number of birds could have visited the site for brief periods, and escaped capture. A small number of adults which visited the site, possibly after breeding elsewhere, were colour ringed. These birds were given a year colour rather than a unique combination. The largest category consisted of juveniles which appeared in the site in summer but had not been reared on the main study site. Samples of these birds, many of which spent relatively little time in the site, were caught and given a striped colour ring which was only unique to the year.

Rhodamine B dye was used on nestlings reared in the main study site. It was applied prior to fledging, with each brood receiving a unique colour pattern. Picric acid, which is often used to mark plumage due to its long life, was found to be unsuitable as it did not show up well in the field.

To investigate local movements some adults, and many more juveniles, were caught in mist nets at other sites, especially in 1980 when sample catches of juveniles at five sites up to seven

kilometres from the main study site were colour dyed using harmless alcohol based dyes of four different colours: mauve, blue, red and dark green. These birds were also given striped colour rings (different to those used in the main study site) since these dyes only lasted for a few weeks.

In 1981 samples of juveniles which visited the main study site were colour dyed on eight consecutive weekends between 27th June and 15th August, using different colours or combinations, to try to measure turnover within the site.

The same route that passed through all the breeding territories was walked daily throughout the period that warblers were present on the main study site. This allowed data on the numbers of marked and unmarked birds of each species to be collected on a standardized basis.

Besides the daily visits to the main study site in 1979-81 the surrounding countryside was censused for all warbler species in all three years, and in 1982, using tape lures. Details of the census procedure are given in Ch.7:1. The area covered was extended each season from 14.0 km^2 in 1979 to 16.2 km^2 in 1982. Although most work in the main study site took place between 1979-81 the site was also visited in 1982 to check on return rates. The use of a tape recorder meant that male warblers could be examined for colour rings fairly easily and at least some females also responded to the tape, though less demonstratively than males.

4:2 Return rates and ages of the breeding birds

The return rates of breeding adults to the main study site are shown in Table 23. These data provide estimates of survival rates between one breeding season and the next, though such estimates are minima, as it is not known whether all the birds that did not return had died. The checks carried out in the surrounding countryside each spring using a tape recorder showed that one male and three female Willow Warblers and one male Whitethroat had returned to territories up to 1200 metres away from the main study site. This information meant that return rates for male and female Willow Warblers and male Whitethroats from 1979 to 1980 and for female Willow Warblers from 1980 to 1981 had to be revised. Since so few (5) birds were located in other sites in successive years compared to the number of adults colour ringed in the main site in spring (168) and the many birds seen over up to 16.22 km^2 of surrounding countryside (though this census was biased in favour of males which responded more vigorously to the tape recordings than females) it does seem that breeding adults, or at least adult males, are highly site tenacious. In most years a higher percentage of males than females returned to the study site, though the differences were not significant.

Male Willow Warblers showed a significantly higher return rate than male Sedge Warblers in 1981 (Fisher's Exact Test $p = 0.046$). In 1980 female Whitethroats had a significantly higher return rate than female Sedge Warblers (Fisher's Exact Test $p = 0.032$). Otherwise there were no significant differences between species in return rates

Although percentage return rates suggested some year to

Table 23 The percentage of the breeding population returning over three years.

		1979-80	1980-81	1981-82
Willow Warbler	male	47,53(15)	57(14)	37(19)
	female	46,54(13)	20,40(15)	35(20)
Whitethroat	male	20,30(10)	44(9)	25(8)
	female	64(11)	0(10)	0(8)
Sedge Warbler	male	25(12)	10(10)	30(10)
	female	17(12)	40(10)	20(10)

1. Figures in parentheses are breeding bird numbers in the previous year.
2. Where two figures are shown the lower is the return rate to the main study site and the higher the revised figure since a bird(s) returned to a site in the surrounding area.

year variations, especially with Whitethroats and Sedge Warblers, there were no statistically significant differences in annual return rates in any species.

Table 24 shows the return rates of breeding adults in relation to breeding success. Apart from male Willow Warblers in 1981, and female Whitethroats in 1981 and 1982, a higher percentage of successful birds returned to the study site the next year than birds which had failed to fledge young. However differences were only statistically significant with female Willow Warblers (Fisher's Exact Test, $p = 0.05$) and female Sedge Warblers (Fisher's Exact Test, $p = 0.05$).

Only with Willow Warblers did any adult birds stay long enough on the study site to complete all or most of their moult (Ch.2). A significantly higher percentage (46.2%) of the Willow Warblers that stayed to moult on the site returned the next year than those which left to moult elsewhere (22.2%, $X^2 = 3.71$, $p < 0.05$). Also failed breeders were significantly less likely to moult in the study site (61.7% of failed breeders did not stay to moult, 10% of successful breeders did not stay to moult, $X^2 = 25.9$, $p < 0.001$), but of those birds that did stay to moult the proportion of failed breeders that returned the next year was similar (42.8%) to the proportion of successful breeders that returned (47.2%).

Mortality of adults in the breeding season was apparently low. Only two birds were definitely known to have died; both were Willow Warblers in mist nets. Two others disappeared while breeding attempts were underway. Both were female Whitethroats, one prior to laying and one during incubation, probably killed by a predator.

Table 24 Comparison of the return rates of failed and successful breeders.

			Percentage of failed birds to return	Percentage of successful birds to return
Willow Warblers	males	1980	20 (5)	66.6 (9)
		1981	75 (4)	40 (10)
		1982	25 (8)	50 (10)
	females	1980	25 (4)	55.5 (9)
		1981	25 (4)	27.2 (11)
		1982	10 (10)	50 (10)
Whitethroats	males	1980	0 (3)	28.6 (7)
		1981	25 (4)	33.3 (6)
		1982	0 (2)	28.5 (7)
	females	1980	0 (2)	87.5 (8)
		1981	0 (4)	0 (6)
		1982	0 (2)	0 (6)
Sedge Warblers	males	1980	0 (4)	37.5 (8)
		1981	0 (3)	14.2 (7)
		1982	0 (2)	37.5 (8)
	females	1980	0 (4)	25 (8)
		1981	0 (3)	57.1 (7)
		1982	0 (2)	25 (8)

The numbers of birds returning from a previous year are shown in parentheses.

The site was occasionally visited by at least one Sparrowhawk Accipiter nisus, the only avian predator in the area likely to kill adult warblers, but, apart from one bird killed in a mist net, no warblers were seen to be taken by hawks and no male birds disappeared while holding territory, although they were relatively conspicuous then. Once the young fledged it became impossible to tell whether a bird that disappeared had left the site or been killed, but no attacks by hawks on warblers were witnessed, and there is no obvious reason why they should become more vulnerable at a time when females are no longer sitting on eggs and their behaviour becomes more secretive than when males are singing and displaying, or both sexes are feeding noisy young.

Since ringing had been carried out in the main study site prior to 1979 the ages of several birds were known precisely, and minimum ages known for others (Svensson 1975). Table 25 shows the age structure of the breeding birds. The maximum age recorded for Willow Warbler males was five years, and for females four years; for Whitethroat males it was seven years and for females three years; for Sedge Warbler males it was six years and for females three years.

Table 25 Age structure of the breeding warbler population 1979-1982

			Age in years							
			U	1	2	3	4	5	6	7
Willow Warbler	male	1979	7	1	(3)	(3)	1			
		1980	4	2	1(4)		(2)	1		
		1981	2	5	2(5)	1(2)		(2)		
		1982	7	2	3(2)	(1)	1(1)			
	female	1979	12		(1)					
		1980	7	1	(6)	(1)				
		1981	12	2	2(1)	(2)	(1)			
		1982	7		2(4)	3	(3)			
Whitethroat	male	1979	4	3				(2)	(1)	
		1980	4	2	(1)				(1)	(1)
		1981	3		(4)	(1)				
		1982	3		1(3)					
	female	1979	8		(3)					
		1980	3		(3)	(4)				
		1981	7	1						
		1982	7							
Sedge Warbler	male	1979	6	1	(2)	(1)		(2)		
		1980	4	2		(1)	(1)		(2)	
		1981	10					(1)		
		1982	6		(4)					
	female	1979	12							
		1980	8		(2)					
		1981	6		(3)	(1)				
		1982	7		1(2)					

Notes U=unknown

Numbers in parentheses refer to birds which were at least the age shown in the respective column e.g. 1(4) in column 2 means that in 1980 one male Willow Warbler was known to be 2 years old and another 4 were at least 2 years old

4:3 Recruitment to the breeding population and local movements

Tables 26 to 28 show the origins of birds recruited into the breeding population each year. Twelve adult Willow Warblers joined the breeding population. Only three of these (all females) were birds that had been ringed elsewhere. The other nine included two males that had tried to hold a territory unsuccessfully in a previous year, four males and three females that arrived to moult in late summer and returned to breed the next year; of these moulting birds one had been reared in the site and three others had visited it two years previously. Only three of the nestlings ringed in the main study site in the previous year returned to breed there but a further nine birds that were ringed as free flying juveniles joined the breeding population next spring. Four of these birds had been caught in the main study site in summer though definitely not reared there. The other five were ringed at sites within 2 km of the main study site. The largest category (40) was of unringed birds, although it is likely that many of these were also one year old, and at least some of them may have visited the site in the previous summer but avoided capture.

Unringed birds also predominated in recruits to the breeding populations of Whitethroats (Table 27) and Sedge Warblers (Table 28). None of the 193 ringed nestlings which fledged returned to the main site and only two out of 75 juvenile Whitethroats and three out of 74 juvenile Sedge Warblers ringed in summer returned. All five were ringed in the main study site though none were reared there. One male Sedge Warbler that had failed to hold a territory in 1981 returned to breed in 1982 while three adult Whitethroats that had visited the main study site for

Table 26 Origins of Willow Warblers recruited into the breeding population each year.

		1980	1981	1982
Nestling from previous year	male		1	1
	female	1		
Free flying juveniles*	male	2	4	1
	female		2	
Adults which came to moult in the main study site	male		2	2
	female			3
Adults which failed to secure territory in previous year	male	1	1	
	female			
Adults from elsewhere*	male			
	female		1	2
Unknown origin and age	male	4	3	7
	female	7	12	7
Total	male	7	11	11
	female	8	15	12

* Free flying juveniles include birds mist netted in the main study site (4) in summer though not reared there and birds caught at other sites in the surrounding countryside (5).

** Birds ringed as adults in a previous year at a site outwith the main study site and not known to have visited it.

Table 27 Origins of Whitethroats recruited into the breeding population each year.

		1980	1981	1982
Nestling from previous year	male			
	female			
Free flying juvenile*	male			1
	female		1	
Adults which came to moult in the main study site	male			1
	female			
Adults which failed to secure territory in previous year	male	1	1	
	female			
Unknown origin and age	male	6	3	3
	female	3	7	7
Total	male	7	4	5
	female	3	8	7

* Both juveniles were caught in the main study site in summer though reared elsewhere.

Table 28 Origins of Sedge Warblers recruited into the breeding population each year.

		1980	1981	1982
Nestling from previous year	male			
	female			
Free flying juvenile*	male	2		
	female			1
Adults which failed to secure a territory in previous year	male			1
	female			
Unknown origin and age	male	4	9	6
	female	8	6	7
Total	male	6	9	7
	female	8	6	8

* All juveniles were caught in the main study site in summer though reared elsewhere.

short periods in a previous year returned to breed. The ratio of unringed birds among the recruits was much higher for these two species than in Willow Warblers (unringed:ringed; Whitethroat, 29:5; Sedge Warbler 40:4, Willow Warbler 40:24).

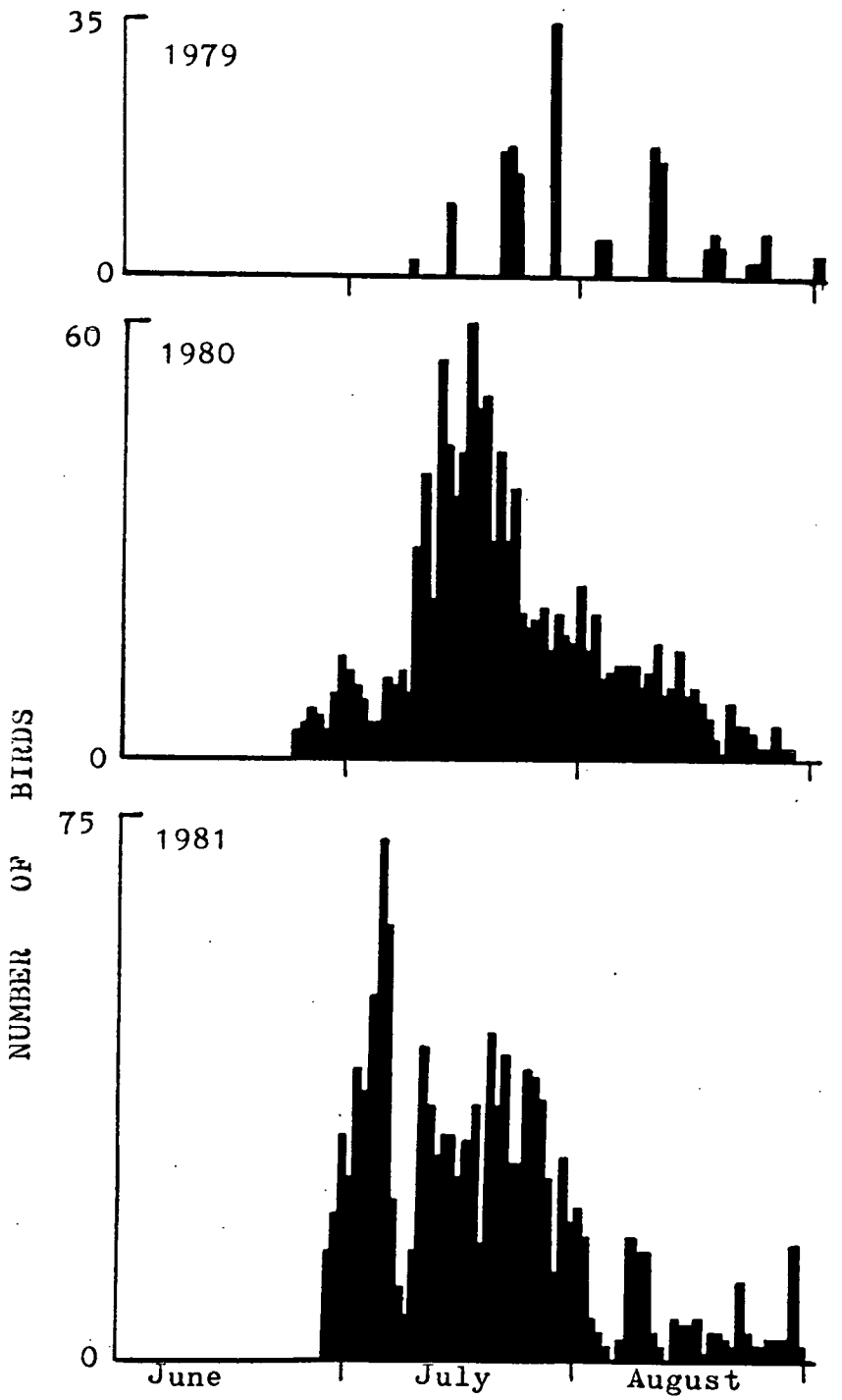
The return rate of nestlings to the main study site in a later year was only 1.9% for Willow Warblers and zero for the other two species, but this gives too low an estimate of the survival rate of the nestlings over their first winter, since four Willow Warblers and one Sedge Warbler were seen holding territories up to 3.5 kilometres from the site in later years and a further, unknown, number may have survived to breed elsewhere. The major source of recruits to the breeding population in the main study site appeared to be from birds reared elsewhere (Tables 26 - 28). Nine Willow Warblers, two Whitethroats and three Sedge Warblers ringed as free flying juveniles returned to breed in the main study site when one year old. Nine of these birds had visited the main site as juveniles though none were reared in the site. A further 20 Willow Warblers, one Whitethroat and two Sedge Warblers ringed as juveniles were located in the larger study area in a later year. Altogether 29 Willow Warblers returned to the larger study area out of 581 juveniles ringed, three Whitethroats returned out of 113 juveniles ringed and four Sedge Warblers returned out of 101 juveniles ringed. Return rates of juveniles were slightly higher than the return rates of the nestlings fledged from the main study site (Willow Warbler 5.0%: 4.4%; Whitethroat 2.7%: 0 nestlings returned, Sedge Warbler 3.9%: 1%). These rates are still relatively low indicating either that the juveniles disperse more widely than the adults, or that they suffer higher mortality or, more likely, a combination of the two. The numbers of young

birds which visited the main study site in summer during post fledging dispersal were relatively high, especially with young Willow Warblers, and it was impossible to ring them all. Figures 29 to 31 show the results of counts of these juveniles. The higher totals for Willow warblers than for the other two species reflects the greater abundance of the former in the surrounding countryside (Ch.7). The slightly different year to year patterns shown in Figures 29-31 reflect differences in fledging dates over the three seasons e.g., in 1981, when first egg dates tended to be earlier (Ch.2), counts of juveniles peaked earlier than in previous years. Wandering juveniles (i.e. birds that visited the site but were not hatched there) first appeared around or soon after the time the first nestlings fledged in the main study site, but all the birds reared in the site had left well before the end of the wandering period shown in Figures 29-31, with a tendency for the nestlings to leave the site around the time that peak counts of wandering juveniles were obtained.

The maximum number of juvenile warblers recorded in the main study site on any one day was 72 Willow Warblers, ten Whitethroats and 18 Sedge Warblers. However, more birds passed through the site than were present on any one occasion. Table 29 shows that the number of juveniles caught each summer was always higher than the daily counts and, in the case of Willow Warblers, higher than the number of nestlings reared in the site.

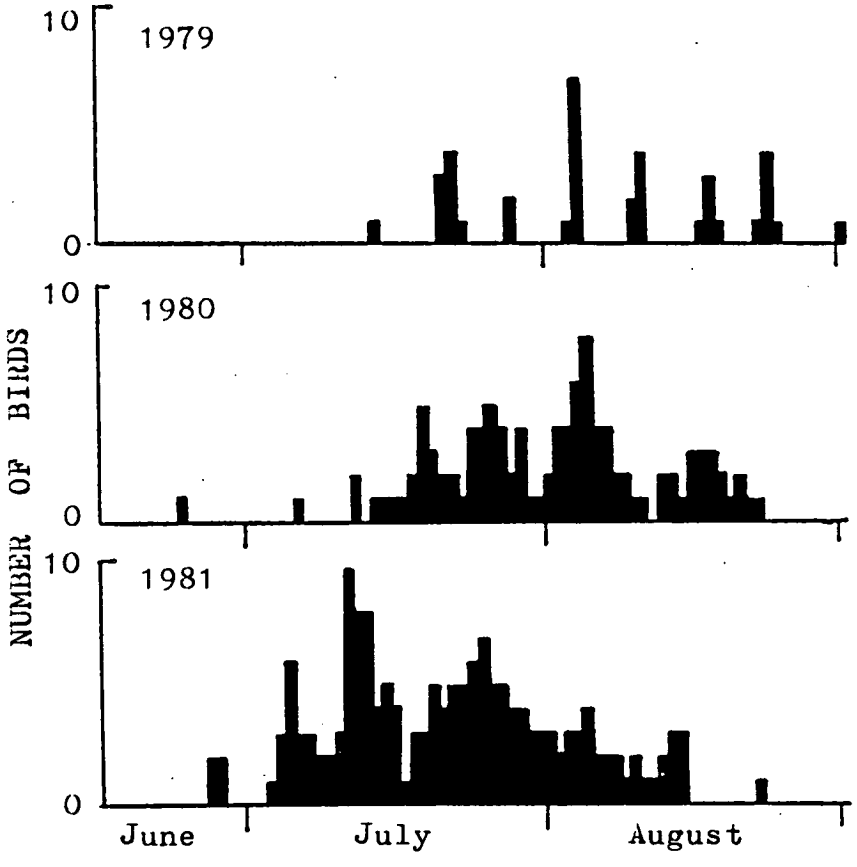
Table 30 shows that most juvenile Willow Warblers which visited the site spent less than seven days there though in the early part of the summer birds tended to stay longer. Although the catching and colour marking process might be expected to encourage birds to leave, the high proportions present within 24 hours of marking suggests that birds did not leave the site as an immediate response

Figure 29 Counts of juvenile Willow Warblers that visited the main study site but were not reared there 1979-81.



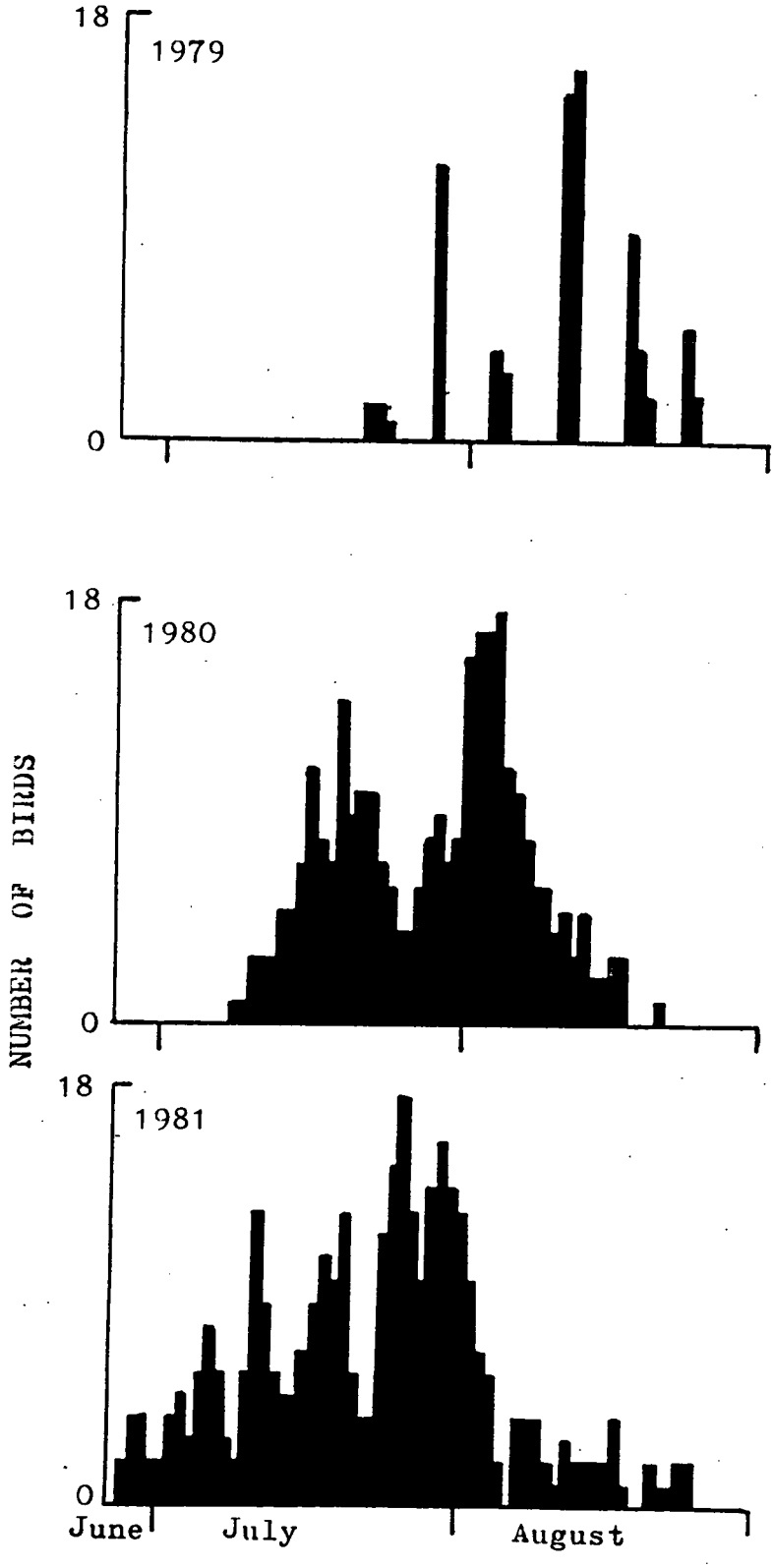
Counts were carried out up to three times per week in 1979 but daily in 1980 and 1981.

Figure 30 Counts of juvenile Whitethroats that visited the main study site but were not reared there 1979-81.



Counts were carried out up to three times per week in 1979 but daily in 1980 and 1981.

Figure 31 Counts of juvenile Sedge Warblers that visited the main study site but were not reared there 1979-81.



Counts were carried out up to three times per week in 1979 but daily in 1980 and 1981.

Table 29 Comparison of the number of wandering juveniles caught per year with daily counts and the number of nestlings reared in the main study site.

		No. of nestlings fledged	Max.daily count of wandering juvs.	No. of wandering juvs. ringed per year
Willow Warbler	1979	48	35	98
	1980	59	60	122
	1981	53	72	88
Whitethroat	1979	33	7	33
	1980	25	8	23
	1981	32	10	19
Sedge Warbler	1979	37	16	24
	1980	28	18	19
	1981	38	18	31

Wandering juveniles were birds that visited the main study site in summer but were not reared there.

to capture. Also the tendency for later birds to stay for shorter periods (no bird marked after 24th July stayed for longer than 20 days) which was also found with birds fledged in the site (Ch.2) suggests that the movements of the colour dyed birds were not atypical of the rest. Table 30 strongly suggests that the number of juvenile Willow Warblers which moved through the site during the summer was much higher than the maximum (72) seen on any one day. The results of dye marking juvenile Whitethroats (Table 31) and Sedge Warblers (Table 32) suggest an even shorter stay by the juveniles of these species, with only one Whitethroat staying more than 20 days and all Sedge Warblers leaving within a week.

Table 33 shows that young Willow Warblers moved at least 3.5 km. during their post fledging period. Juvenile Whitethroats and Sedge Warblers were present at other sites in much smaller numbers than Willow Warblers so it is not surprising that fewer sightings were obtained of these species. Even so three Whitethroats and two Sedge Warblers (15% and 9.5% of those that were colour marked) were seen at the main study site just under a kilometre from where they were colour dyed.

Table 30 The time spent by wandering juvenile Willow Warblers in the main study site in 1981.

Date of colour dyeing	Number colour dyed	Maximum number of dyed birds present within 24 hours *	2-6	7-13	14-20	21-27	28-34	35-41	42-48	49-55	56-62	63-69
			Number of dyed birds remaining for different time periods (in days) after marking									
27th June	11	9	6	10	1	1	0	0	2	2	0	0
3rd July	18	7	7	2	0	0	0	0	0	0	0	
10th July	11	10	6	4	0	0	0	0	0	0		
17th July	14	8	10	1	0	0	0	0	0			
24th July	11	7	5	1	1	0	0	0				
31st July	10	10	0	0	0	0	0					
7th August	6	4	4	0	0	0						
14th August	3	3	3	2	0							

* At least four hours after colour marking.

Wandering juveniles were birds that visited the main study site in summer but were not reared there.

Table 31 The time spent by wandering juvenile Whitethroats in the main study site in 1981.

Date of colour dyeing	Number colour dyed	Maximum number of dyed birds remaining for different time periods (in days) after marking						
		present within 24 hours *	2-6	7-13	14-20	21-27	28-34	35 or more days
27th June	2	0	0	1	0	0	0	0
3rd July	3	3	0	3	1	0	1	0
10th July	3	2	0	0	0	0	0	
17th July	2	1	0	0	0	0		
24th July	1	1	0	0	0			
31st July	2	2	0	0				
7th August	2	2	0					
14th August	2	2						

* At least four hours after colour marking.

Wandering juveniles were birds that visited the main study site in summer but were not reared there.

Table 32 The time spent by wandering juvenile Sedge Warblers in the main study site in 1981.

Date of colour dyeing	Number colour dyed	Maximum number of dyed birds remaining for different time periods (in days) after marking		
		present within 24 hours *	2-6	7 or more days
27th June	3	3	0	0
3rd July	1	1	1	0
10th July	11	7	4	0
17th July	5	3	3	0
24th July	3	3	1	0
31st July	3	1	0	0
7th August	3	3	0	0
14th August	2	2	0	0

* At least four hours after colour marking.

Wandering juveniles were birds that visited the main study site in summer but were not reared there.

Table 33 Movements of colour dyed warblers between sites in 1980

	Site A	Site B	Site C	Site D	Site E
Distance from the main study site	0.8kms.	1.25kms.	2.0kms.	3.5kms.	7.0kms.
Willow Warbler					
Numbers ringed	108	24	5	23	46
Numbers appeared at the main study site	15(13.8%)	3(12.5%)	1(20%)	1(4.3%)	0
Whitethroat					
Numbers ringed	20	0	0	0	2
Numbers appeared at the main study site	3(15%)	0	0	0	0
Sedge Warbler					
Numbers ringed	21	0	1	0	0
Numbers appeared at the main study site	2(9.5%)	0	0	0	0

4:4 Life expectancy and survival

The proportions of breeding adults that were recorded in later years, either in the main study site or the larger study area, allow minimum annual adult survival rates to be calculated assuming adult mortality is independent of age.

Over three years the known survival rates for breeding Willow Warblers were 47.9% for males and 41.7% for females. This means that each breeding season a male would need to produce 0.52 successors, and a female 0.58 successors, to maintain the population in which the oldest male should reach an age of eight years and the oldest female seven years. In fact the oldest two male Willow Warblers in this study were at least five years old (originally ringed as birds of unknown age) and the four oldest females were at least four years old (also ringed as birds of unknown age). The annual output of fledged young over three years averaged 3.6 per breeding male and 3.4 per breeding female. This means that the mortality of young Willow Warblers over their first winter could reach 70.8% for males and 65.0% for females without adversely affecting recruitment into the breeding population. However the recorded return rate of all young Willow Warblers (i.e. ringed either as nestlings or free flying juveniles) to the larger study area was only 4.9% which would not be adequate to maintain the population, as it gives a shortfall of 43.4% in males and 50.2% in females. Alternatively, the recorded return rate for young Willow Warblers was well below their true survival rate (probably because young birds returned to breed outwith the larger study area of 14.00 to 16.22 km^2 that was searched for colour marked birds each spring) which, given the lack of evidence for decline in the Willow Warbler population as a whole, seems more likely.

The proportions of adult Whitethroats (males 33.3%, females 24.1%) and Sedge Warblers (males 21.9%, females 25.0%) that were known to have returned in a later year were lower than with Willow Warblers. With Whitethroats this means that an average of 0.67 young birds per breeding male and 0.76 young birds per breeding female would need to be available as recruits to the breeding population if it is to be maintained. Over three years the average annual output of fledglings per male was 3.5 and per female was 3.1. Even if these young birds had the same survival rate as that estimated for adults from known return rates, then recruitment to the breeding population would be 9% too low for males and 38.5% too low for females, implying that the population is threatened with extinction, with females disappearing first in twelve years time. The known return rate for Whitethroats ringed as nestlings or juveniles was 1.5% which is clearly inadequate to maintain the population. Comparison of the maximum ages reached by Whitethroats in this study (one male was at least seven and four females were at least three) shows that the maximum ages (five years for males, four years for females) predicted from the proportions of adults known to return in later years may be too low.

Return rates of adult Sedge Warblers gave minimum survival rates of 21.9% for males and 25.0% for females. This means that 0.78 successors per breeding male and 0.75 successors per breeding female would be needed to maintain the population. Over three years average annual output per pair (there were no complications due to mate changing or polygamy in Sedge Warblers) was 3.2 fledglings i.e. 1.6 per breeding adult. As with Whitethroats, even if these young birds had the same survival rate as that estimated for adults,

too few (42.9% with males; 34.8% with females) would be available to maintain the breeding population which would effectively become extinct in ten years (when the last males would disappear, although females would be present for another four years). The return rate of Sedge Warblers ringed as nestlings or juveniles was only 2.5%. Maximum ages estimated from return rates of adult Sedge Warblers were only four years for both sexes. In the study the oldest known female was at least three years old and two males were known to be at least six years old.

4:5 Summary

46% of male Willow Warblers, 33% of female Willow Warblers, 30% of male Whitethroats, 24% of female Whitethroats, 22% of male Sedge Warblers and 25% of female Sedge Warblers returned to the main study site in a later year. A few Willow Warblers and Whitethroats returned to other sites up to 1.2 kms away and some of the recruits to the breeding population in the main study site were known to be older than one year. The return rate of birds ringed as nestlings in the main study site was 1.9% for Willow Warblers and zero for the other species, though others were known to have returned to territories up to 3.5 km from the main site. Return rates of all ringed juveniles to the larger study area were 5.0% for Willow Warblers, 2.7% for Whitethroats and 3.9% for Sedge Warblers. Adults that bred successfully were not significantly more likely to return than those that failed, although with Willow Warblers birds that moulted on the site were more likely to return than those that did not. A few birds that had visited the site, but did not breed there, did so in a later year. With all species juveniles that had not been reared in the main study site visited it during the summer. Observation of colour marked birds indicated a rapid turnover for most of these birds, and suggested they were involved in a post fledging, wandering phase, with distances up to 3.5 kms recorded. Young Willow Warblers were particularly numerous in summer and the number ringed each year was greater than the number fledged in the site. It was estimated that 70.8% of young male Willow Warblers and 65.0% of young female Willow Warblers that fledged could die during their first winter without the population as a whole being adversely affected. Return rates of Whitethroats and Sedge Warblers were such that, unless they were well below their true

survival rates, both species were in decline. Maximum ages recorded were at least five years for male Willow Warblers and at least four years for female Willow Warblers, at least seven years for male Whitethroats and at least three years for female Whitethroats, at least six years for male Sedge Warblers and at least three years for female Sedge Warblers.

Chapter 5 Warbler feeding ecology

5:1 Methods for invertebrate sampling

This programme was designed to give information on the relative biomass of potential warbler prey and it is stressed that the data presented do not constitute a complete description of the invertebrate fauna of the various plant species. Twelve vegetation types were selected for sampling: hawthorn, birch, willow, elder, rose, bramble, gorse, broom, nettle/bishopweed mixture, nettle, rosebay willowherb and grass. These vegetation types were chosen as they made up well over 90% of the plant cover in the main study site (Fig.1) and previous experience indicated that they included those plant species most used by feeding warblers. The study site also included a small number of tall deciduous trees, mainly along part of the boundary fence. These were occasionally visited by some Willow Warblers as they formed convenient song posts; their scarcity and position meant that they were only occasionally used for feeding. The overgrown orchard at one end of the main study site held several fruit trees. These were not sampled either since warblers in that area fed predominantly in hawthorn, nettle and other native species which were colonizing the previously cultivated ground.

In 1979 two methods of sampling the invertebrates in the vegetation were carried out: water trapping, which has been used in studies of feeding warblers in southern England and France (Bibby & Green 1981), and a form of sweep netting. Water traps consisted of 5 inch basal diameter plastic trays half filled with water, to which a few drops of detergent were added, and fixed in place within each of the vegetation types to be sampled. One water trap sample involved leaving a fresh trap for seven days before emptying and renewing the liquid. Sweep netting involved

using a specially constructed net consisting of a strong steel frame 25 x 25 cms. square with a wooden handle. Nylon mesh (1 mm diameter) was stitched round the steel frame and a linen collecting bag stitched to the bottom. This design of net allowed sweeping of all types of vegetation, including hawthorn and bramble, which would tear a conventional entomologist's sweep net. Samples were taken in six different areas of hawthorn, two of birch, two of willow, five of elder, two of rose, five of bramble, four of gorse, two of broom, two of nettle/bishopweed mixture, three of pure nettle, four of willowherb and five grass areas. The unequal number of samples from different plant species reflects the variation in abundance of different vegetation types within the site. Once taken each sample was transferred to a killing jar and then to a dry container. Each sweep netting sample involved taking ten consecutive sweep while moving slowly through a patch of vegetation. Sweep netting might be expected to be biased against very mobile invertebrates, such as some flies, or species that cling tightly to stems and branches. However, water trapping gave similar results to sweeping, suggesting that the latter method was adequate for the purposes of this study (see Figs. 32-35). Since water traps proved vulnerable to spilling due to birds, such as thrushes or pigeons landing on them (even when nailed to trees), or disturbance by mammals (probably foxes) trapping was discontinued in favour of sweep netting. Sweep netting was carried out weekly between early April and mid September in the three years 1979-81. As some invertebrates were likely to be more or less active, and therefore catchable, at different times of day, or in response to weather, sweep netting was carried out in late mornings in dry weather; this occasionally meant postponing sampling for 24 hours.

Samples were sorted into Orders of invertebrates except for snails which were all classed as Mollusca. Invertebrates were further divided into groups of the same or similar species and then into 2 mm. size classes for weighing. Twenty invertebrates from each size class of each taxon were then placed in a thermostatically controlled oven maintained at 60°C until three consecutive weighings indicated that a constant dry weight had been achieved. The mean weight for each taxon of organisms was calculated and the resulting weights used to calculate total dry weights for each sample. This saved separately drying and weighing all the invertebrates in each sample.

5:2 Observations of feeding warblers

Warblers were watched while feeding to determine the vegetation types from which they obtained their prey and, where possible, obtain data on the prey eaten by adults themselves and fed to their young.

Adult warblers were watched using close focussing 8 x 30 binoculars from either good vantage points (which were readily available due to the uneven ground) or whilst watching feeding birds from as little as 2.5 metres. Comparison of the feeding rates and behaviour of birds watched from close range and from more distant vantage points indicated that the birds did not change their behaviour in response to the observer, except when he was close to the nest. When near nests a minimum of 6 metres distance was required, otherwise the parent birds did show signs of concern at the observer's presence. Each year from 1979-81 observations were made on specific pairs of colour marked birds, as well as on birds encountered on a route walked daily which passed through all the warbler territories in the main study site. Each year eight individuals of each species were selected for daily study. All the species of vegetation which were sampled for invertebrates were represented in these birds' territories. Feeding observations were also obtained from another eight Whitethroats, 13 Willow Warblers and11 Sedge Warblers in 1979, nine Whitethroats, 16 Willow Warblers and nine Sedge Warblers in 1980 and six Whitethroats, 21 Willow Warblers and nine Sedge Warblers in 1981. Observations were made between 0500 and 0900 and 1700 and 2100 hours B.S.T. as these were the most practical times to carry out daily observations and the times when peak feeding activity occurred (Appendix D1-12). Total effective observation time per species per season was between 20 and 30 hours. Individual observations involved watching a bird until

lost from sight and usually lasted between 80 and 120 seconds. A stopwatch was used to measure the time spent on different activities and a small tape recorder used to record the activities. This meant that the time spent feeding could be separated from time spent doing other things e.g. singing or preening. It also meant that data were obtained on the rates at which birds attempted to capture prey. Prey taken was classified into size categories of less than 5mm, 5-10mm and greater than 10mm. Five feeding methods were recorded. These were:

stand pecking - the bird pecked food from a leaf or twig without moving its position

climb pecking - the bird picked food from stems whilst climbing up the stems

hop pecking - prey was caught as the bird hopped along twigs or stems only stopping briefly when large prey were encountered

leap catching - birds leaped towards prey catching it in mid air and landing on another perch

flycatching - birds caught flying prey and landed on the same perch

The time spent in each vegetation type was also noted.

At four points in the breeding season (before laying, incubation, feeding nestlings and feeding fledged young) a pair of birds of each species was watched throughout a day from 0500-2100 hours B.S.T. to confirm peak feeding times and to get some information on the time spent on feeding diurnally and on other activities through the breeding period. On these twelve days it was impractical to maintain the intensity of observations possible during the shorter periods when data on prey choice and feeding

methods were acquired. The aim of day long observation was simply to allocate the birds' behaviour into broad categories i.e. feeding, preening, resting, singing, nest building and incubating. This meant that the observer could occupy a vantage point further from the birds than was needed for more intensive studies. Some categories of behaviour, e.g. incubation, did not necessitate constant observation. There was some overlap between singing and feeding which was overcome by using the stopwatch and tape recorder. If a bird was briefly hidden from view it was presumed to be carrying out the activity seen before and after its disappearcnce e.g. when a feeding bird was obscured by foliage. However if the activity changed, or if the disappearance lasted for more than 15 seconds, then the time when the bird was not visible was disregarded.

Faecal samples were collected to provide a check on the reliability of field observations since they have been shown to give a reliable picture of the diet of insectivorous passerines (Davies 1977). This was important since from 25 to 34% of the prey captured could not be identified. Faecal samples were collected from adults caught in mist nets and from nestlings during daily nest checks. Samples were preserved in alcohol for later examination under a binocular microscope and an estimate made of the number of organisms involved from the identifiable parts. Most parts could be identified by comparison with whole organisms. As a further check on the field observations nestlings between five and eight days old were collared in 1981 using loops made from string and rubber tubing. Collars were left on for 30 minute periods and 33 food parcels from Whitethroat nestlings, 19 from Sedge Warblers and 28 from Willow Warblers were collected. The samples collected in this way contained both large and small items suggesting that few, if any, food items had been

lost either by swallowing or by falling from the bird's gapes. Both faecal results and collaring results were used to confirm the results obtained by watching adult warblers collecting food for their young.

5.3 Invertebrate biomass throughout the season

The results of the sweep netting programme are shown in Figures 32-34 and the results from water trapping in Figure 35. Similar results were obtained by both methods suggesting that neither method gave any unduly biased picture of the relative biomass of potential invertebrate prey. The proportion by weight of each invertebrate group that occurred in ten of the twelve vegetation types through the season are shown in Appendix A1-10. Broom and grass are not shown in Appendix A as they were rarely used by feeding warblers. All vegetation types showed some seasonal variation but there were marked differences between plant species in their invertebrate biomass and in the timing of the peaks in invertebrate populations.

The least seasonal variation was found in the biomass of invertebrates associated with the lower growing shrubs and creepers (Fig.33). In this group peaks only reached 13-17 mgs. dry weight per sample compared to minimum samples of 1 to 3 mgs. The two evergreen species, gorse and broom, peaked earlier than the deciduous rose and bramble, with the earlier flowering gorse ahead of broom. The most important groups of invertebrates associated with gorse were Coleoptera, mainly Curculionidae, and Araneae (Appendix A5). The important groups associated with broom were also Coleoptera and Araneae and to a lesser extent Diptera. Rose and bramnle attracted aphids which, because they produced "honeydew," in turn attracted Diptera, especially around late June and July when the plants were flowering (Appendix A6 and A7).

The invertebrate biomass of the most important trees and tall shrubs are shown in Figure 32. All these species, except elder,

Figure 32 The invertebrate biomass in the tree and tall shrub layer 1979-81. Mean weights and ranges are shown. The horizontal lines show the nestling periods for Willow Warblers, Whitethroats and Sedge Warblers.

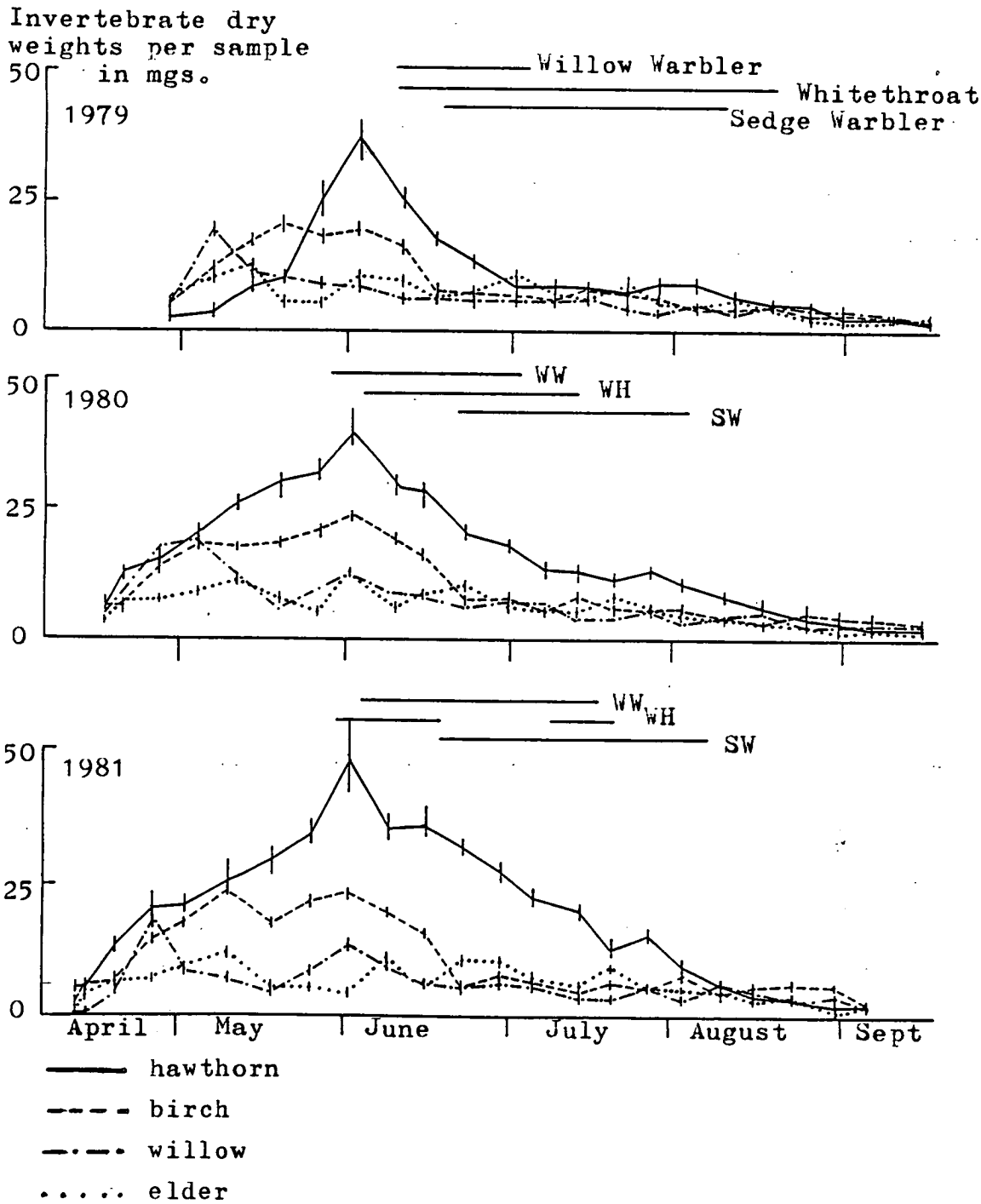


Figure 33 The invertebrate biomass in the small shrub and creeper layer 1979-81. Mean weights and ranges are shown. The horizontal lines show the nestling periods for Willow Warblers, Whitethroats and Sedge Warblers.

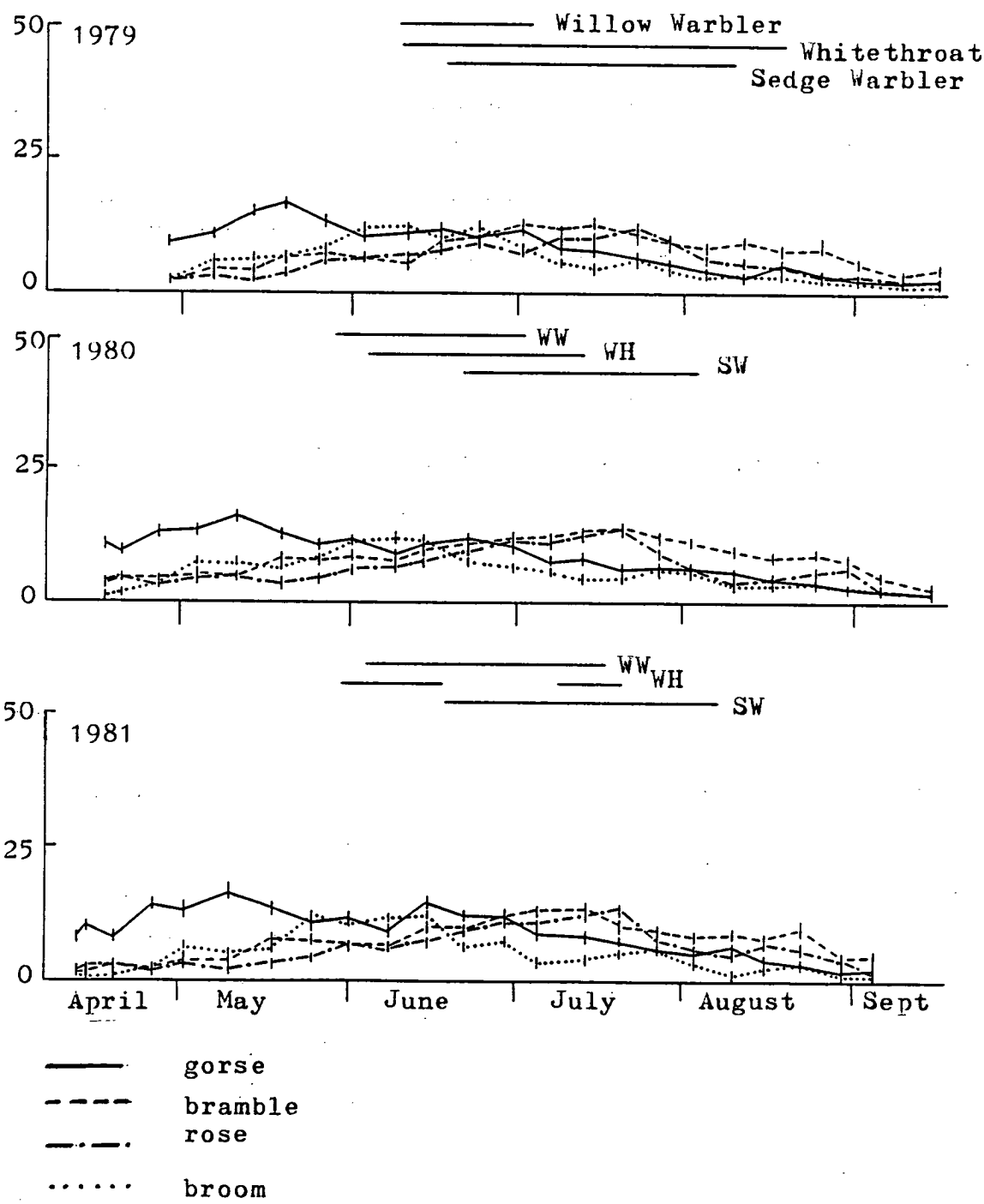


Figure 34 The invertebrate biomass in the herb layer 1979-81. Mean weights and ranges are shown. The horizontal lines show the nestling periods for Willow Warblers, Whitethroats and Sedge Warblers.

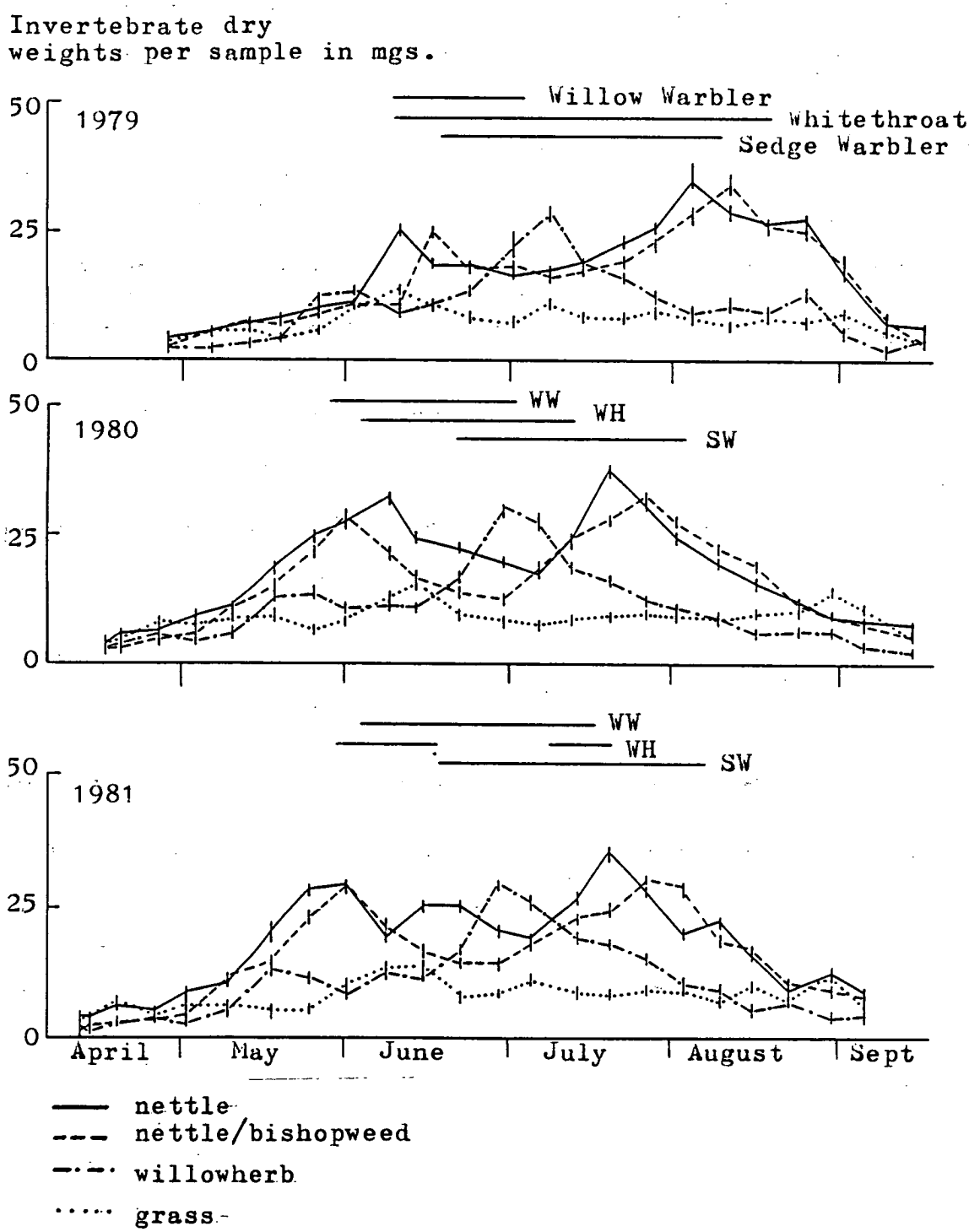
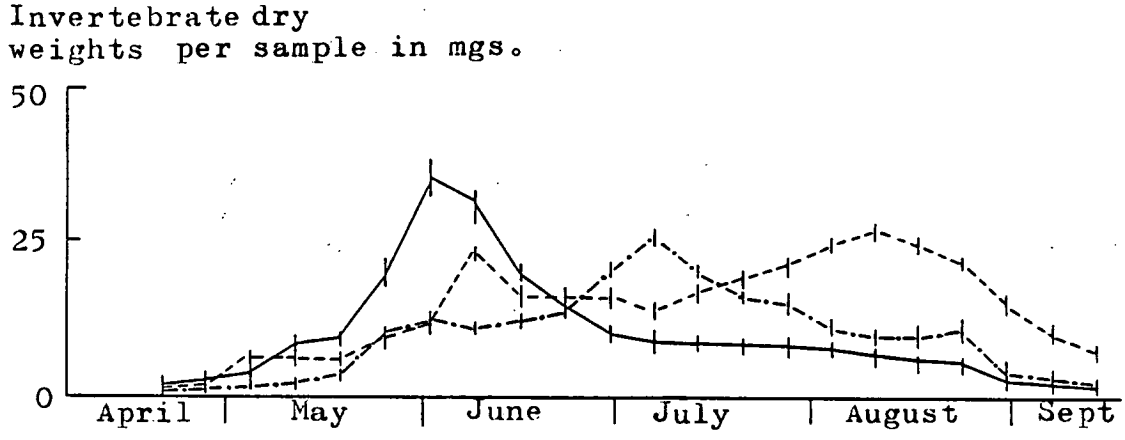


Figure 35 The invertebrate biomass of hawthorn, nettle and willowherb in 1979 based on samples from 13 water traps. Mean weights and ranges are shown.



	Number of water traps
—— Hawthorn	6
-·-·- Willowherb	4
---- Nettle	3

produced markedly higher invertebrate weights per sample than gorse, broom, rose or bramble. There was variation in the seasonal pattern between species with willow the earliest, peaking around the end of April and start of May, and birch and hawthorn reaching peaks about a month later. Over three years hawthorn samples weighed 34% higher than those from birch, 55% higher than those from willow and 56% higher than those from elder. Elder provided mainly Hemiptera (aphids) and Diptera as well as large numbers of Collembola but very few caterpillars (Appendix A4) Willow showed an early peak as insects were attracted to the flowers which opened prior to the leaves. Diptera and Coleoptera were the important groups of insects on willow at this time (Appendix A3). The invertebrate biomass of birch was greater than willow, the important groups being Diptera, Hemiptera and Lepidoptera larvae with numbers of large Coleoptera, especially Weevils (Appendix A2). The large peak shown by hawthorn was caused by green caterpillars which increased in numbers and size up to late May and early June with a decline in numbers as the season progressed. Hemiptera, especially aphids, increased into July and, because they produced "honeydew," they in turn attracted large numbers of Dipterans (Appendix A1).

In 1979 peak invertebrate weights occurred later for all tree and shrub species than in 1981 and total biomass was considerably lower over the season for the most important species, hawthorn, as caterpillars were less numerous ($t = 2.44$, $p < 0.02$). There was no significant difference in total invertebrate biomass between 1980 and the other two years.

The biomass available from all the trees and shrubs declined markedly as the season progressed but the pattern varied between species. In two out of the three years Willow produced a second

peak around the end of May due to aphids, which fed on the growing leaves, and Dipteran flies. Elder, which was the latest of the group to flower, peaked later than the others but was relatively unimportant due to its impoverished invertebrate fauna. Birch and hawthorn, which were the most important species in terms of potential warbler prey, showed declines throughout June, although in June estimates of biomass from these two species were still well above those of April or July. Birch declined rather more steeply than hawthorn. By the end of July samples from both species had dropped to around 10 mgs. dry weight, similar weights to samples from late April when the trees were only starting growth. By the end of August weights dropped even more to values comparable to those from the "bud burst" stage in April.

The field or herb layer (Fig.34) showed a reverse pattern to the trees and taller shrubs with peak invertebrate biomass occurring later in the summer. Samples from grasses were lower in biomass than the three other common herbs sampled, all of which were either taller and/or broader leaved than any of the grass species. Of these tall herbs, nettle beds and patches of nettle mixed with bishopweed reached a peak around early June in all three seasons. Biomass then dropped off, but rose again sharply in July to a second, higher peak as the plants become senescent, finally falling off rapidly by the end of August. Sample weights from willowherb showed only one seasonal peak early in July.

As with the trees the herb layer showed year to year variation with 1979 later than 1980 and 1981 by around ten days. However total biomass was not significantly lower in 1979 than 1980 or 1981.

The important groups of invertebrates associated with the first peak of nettles in late May and early June were Coleoptera, Diptera

and Hemiptera with small amounts of caterpillar. The later peak around late July was associated with large numbers of Hemiptera and Diptera (Appendix A8). The nettle and bishopweed areas showed similar invertebrate associations with Hemiptera and Diptera being the most important potential prey and with a slightly larger biomass of caterpillars (Appendix A9). The later season peaks also contained large numbers of small moths. The willowherb peak occurred when the plants flowered in early July and lay between the two peaks of nettle. The important invertebrates on willowherb were Dipterans and Hemipterans (Appendix A10). The grass samples showed no major peaks and held mainly Aranaea, larger Hemiptera and Coleoptera. Comparison of the plant species that held the largest biomass of potential invertebrate prey showed that, besides peaking later, the herb layer held proportionately less caterpillars but more beetles, bugs, flies and spiders than the trees and shrubs.

5:4 The use of vegetation by the warblers

The birds' use of the main vegetation types over three years is shown in Figures 36-38. The pattern for all three species was similar throughout the three years. There was a marked difference between Willow Warblers and the other two species but Whitethroat and Sedge Warbler showed a more similar pattern. Overall Willow Warblers spent 85% of their feeding time in trees and tall shrubs compared to 48% for Whitethroat and 47.5% for Sedge Warblers. The three species spent relatively little time feeding in the small shrubs and creepers with Willow Warblers spending 7%, Sedge Warblers 7% and Whitethroats 8% of their time there. Willow Warblers spent considerably less time in the herb layer (8%) than Whitethroats (44%) and Sedge Warblers (45.5%).

Besides these overall differences between the species the relative proportions of time spent in the different vegetation types varied throughout the season. All the warbler species used the low shrub/creeper layer less than either the tall shrub or the herb layer. The low shrubs and creepers were used most in April and May when all three warbler species utilized gorse. Broom, rose and bramble were infrequently used and have been combined on Figures 36-38. Broom was rarely used by any of the three species. Willow Warblers virtually abandoned the low shrub layer for a period in late May - early June. They used it again, though only to a minor extent, later in the summer when they sometimes fed in wild rose. Whitethroats and Sedge Warblers did use this layer throughout the season but also spent more time in it in May than in later months. Of the total time Whitethroats spent in the low shrub/creeper layer 6.5% was spent in it in May and 1.5% over the rest of the season. Sedge Warbler showed a similar pattern with 5.7% of the time in May and 1.3% over the rest of the season.

Figure 36 The proportion of time spent by adult Willow Warblers feeding in different plant species 1979-81.

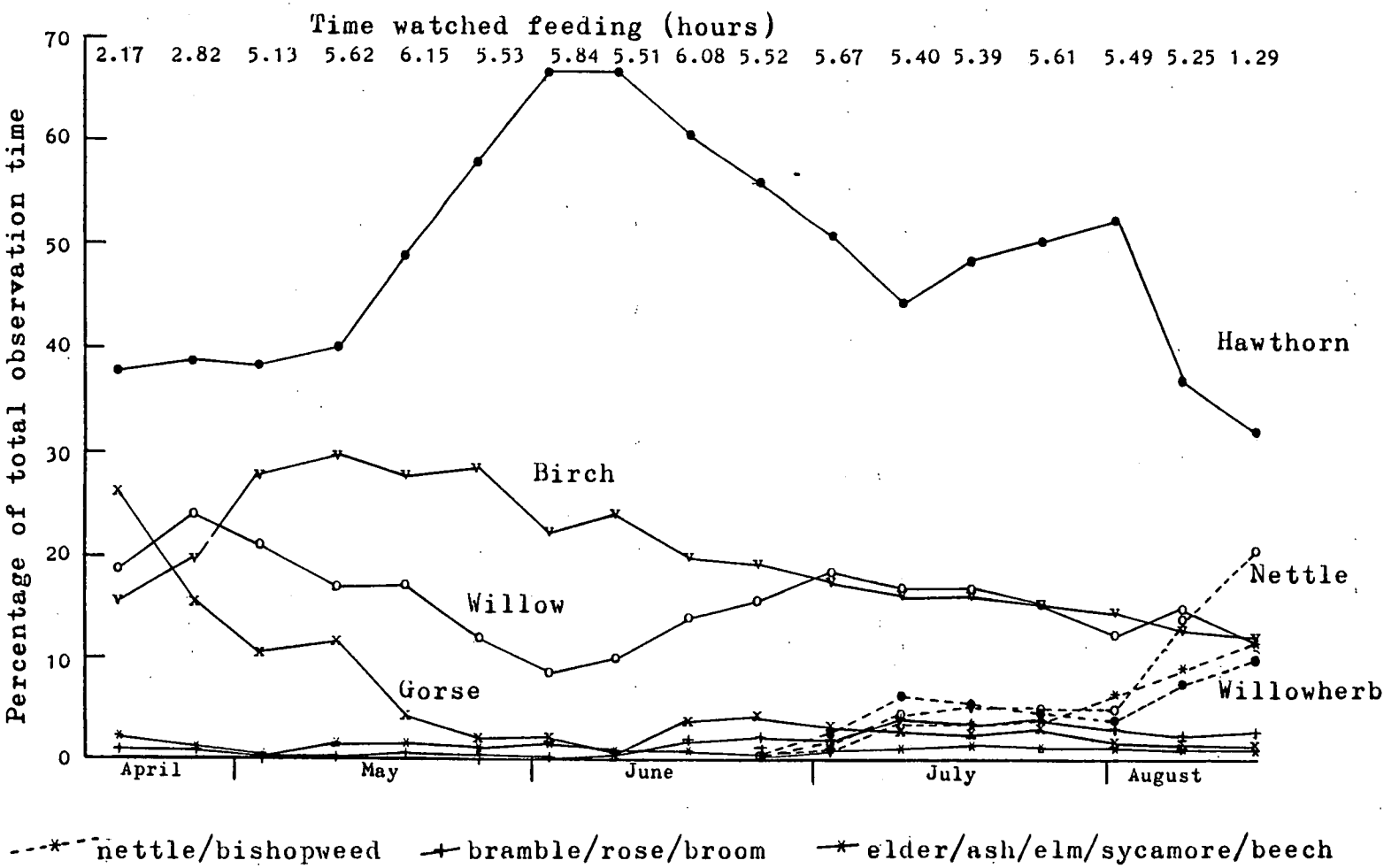


Figure 37 The proportion of time spent by adult Whitethroats feeding in different plant species 1979-81.

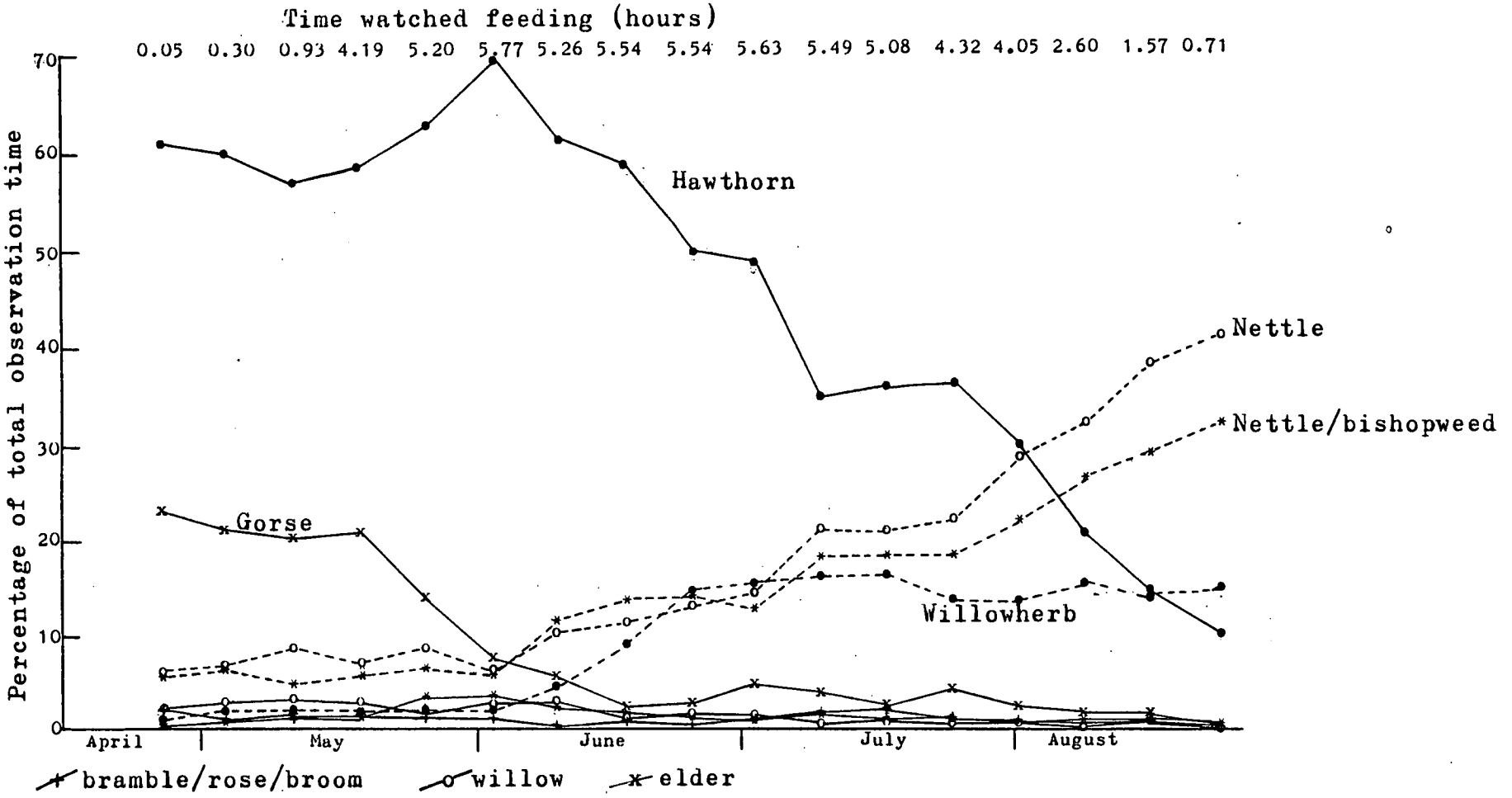
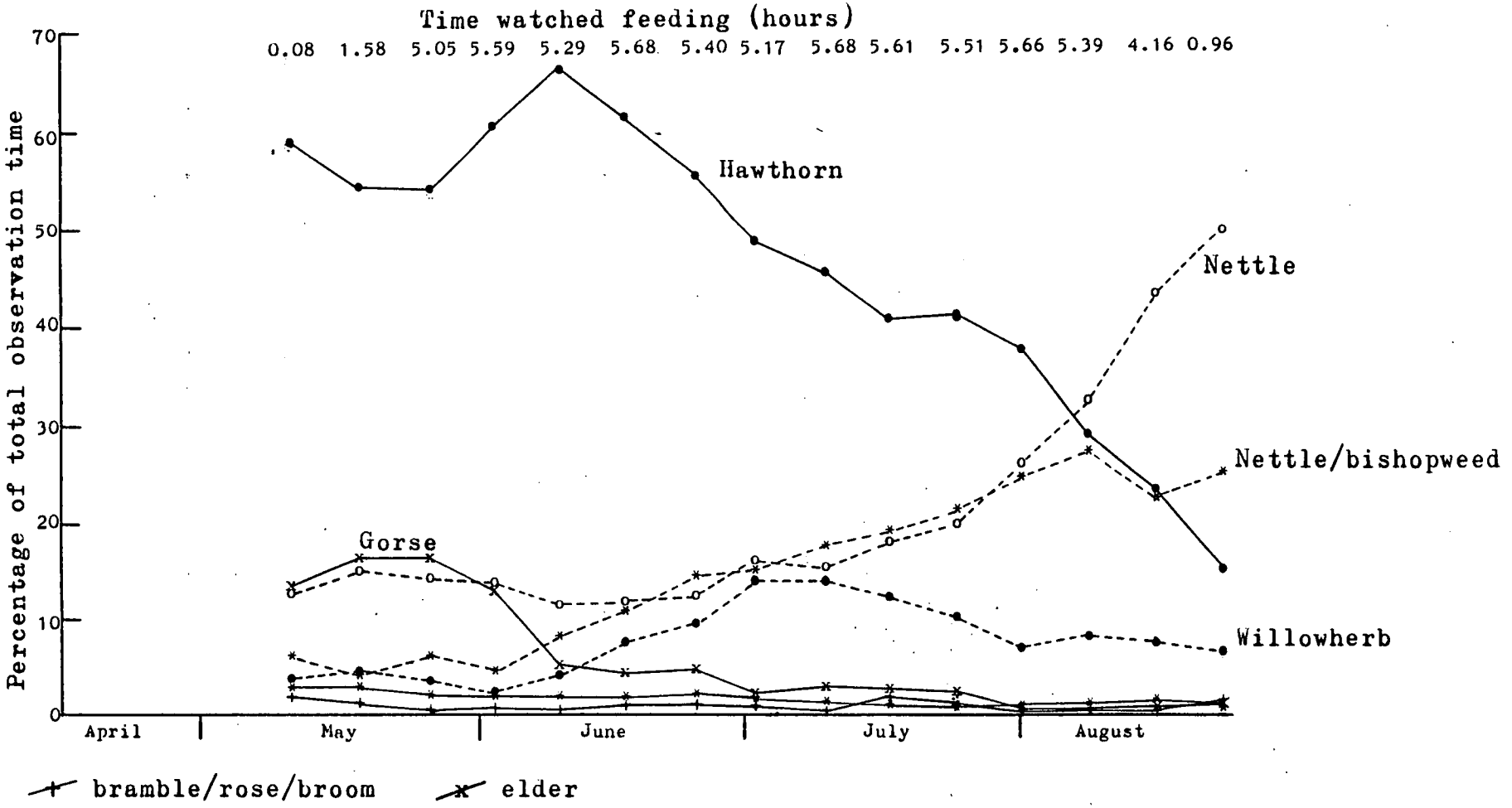


Figure 38 The proportion of time spent by adult Sedge Warblers feeding in different plant species 1979-81.



Both Whitethroats and Sedge Warblers spent a considerable amount of time feeding in tall shrubs, especially in spring. In May Whitethroats spent 67% and Sedge Warblers 59% of their time in tall shrubs but by late summer this dropped to less than 20%. When feeding in tall shrubs both Whitethroats and Sedge Warblers were virtually confined to hawthorn, although willow was sometimes used by Whitethroats. Neither species used birch, which was extensively utilized by Willow Warblers, as were hawthorn and willow.

All three warbler species made progressively more use of the herb layer, with the exception of grass, as the season progressed, but in different proportions. Willow Warblers did not utilize this layer at all until late June. They used it increasingly towards the end of the summer up to a maximum of 44% of the time that they were watched feeding in August. They then used the tall shrubs rather less, although even in August Willow Warblers spent over 30% of their time in hawthorn, and over 10% of their time in birch and willow. Both Sedge Warblers and Whitethroats used the herb layer throughout the season but increasingly so in late summer. In May Whitethroats spent around 15% of their time feeding in nettle and nettle/bishopweed mixture. Sedge Warblers spent around 20% of their feeding time in nettle or nettle mixture and around 4% of their feeding time in willowherb in May. Both species made increasing use of the herb layer through the summer. Their use of willowherb peaked in July around 14-16%. Nettle, either alone or in mixed stands with bishopweed, was the most important part of this layer. Sedge Warblers spent 34% of their feeding time there in July and over 75% of their time there in August. Whitethroats spent around 40% of their time there in July and just over 70% in August.

5:5 Feeding methods

Although the three warbler species overlapped considerably in their use of the vegetation there were significant differences in their choice of feeding methods. Table 34 shows the percentage of observed capture attempts by each of the three species using the five feeding methods recorded in the study.

Willow Warblers mostly fed by stand pecking (43%) and hop pecking (36%) typically when they took slow moving prey from hawthorn and birch leaves. Willow Warblers also used leap catching (5%) and flycatching (16%) from near the tops of tall shrubs and trees. Willow Warblers were never seen climb pecking.

Whitethroats' most common feeding method was hop pecking (61%) which usually involved hopping along branches and catching prey without stopping. Stand pecking (30%) was also important with climb pecking (9%) rather less so. Under 1% of Whitethroats' capture attempts involved leap catching. Whitethroats were not recorded flycatching.

Sedge Warblers most common feeding method was also hop pecking (40%) but stand pecking (33%) and climb pecking (23%) were also important. Climb pecking was mainly observed in the herb layer, where birds pecked at food as they climbed up stems. A limited proportion of capture attempts (3%) involved leap catching and even fewer (0.3%) involved flycatching.

Interspecific comparisons (Table 34) show that flycatching was only important to Willow Warblers since Sedge Warblers only rarely used this technique and Whitethroats were never seen flycatching. Leap catching was a relatively unimportant method for all three species but Willow Warblers and Sedge Warblers both used leap catching significantly more than Whitethroats.

Table 34 Comparison of the use made of different feeding methods by warblers 1979-81.

Feeding methods	Percentage of total capture attempts 1979-81						
	Willow Warbler		Whitethroat		Sedge Warbler		Willow Warbler
Stand pecking	43 (51906)	X^2=3810.4	30 (28099)	X^2=271.3	33.5 (33018)	X^2=2063.7	43 (51906)
Climb pecking	-		9 (8430)	X^2=6617.8	22.6 (22275)		-
Hop pecking	36 (43456)	X^2=13027.8	60.8 (56948)	X^2=7995.1	40.4 (39819)	X^2=446.0	36 (43456)
Leap catching	5 (6036)	X^2=4312.4	0.2 (187)	X^2=2531.4	3.2 (3154)	X^2=437.9	5 (6036)
Flycatching	16 (19314)		-		0.3 (296)	X^2=16423.1	16 (19314)
Total capture attempts	(120712)		(93664)		(98562)		(120712)

All figures in parentheses are numbers of capture attempts

All Chi squared tests are significant ($p<0.001$)

Climb pecking was never seen in Willow Warblers and was used significantly more by Sedge Warblers than by Whitethroats.

For all three species stand pecking and hop pecking were the most frequently used feeding techniques. Willow Warblers used stand pecking significantly more than either of the other two species; Sedge Warblers used stand pecking significantly more than Whitethroats. Whitethroats used hop pecking significantly more than either Willow Warblers or Sedge Warblers; Sedge Warblers used hop pecking significantly more than Willow Warblers.

Although Whitethroats used hop pecking significantly more than Sedge Warblers hop pecking was the most commonly used technique with both species. It was investigated further by comparing the capture rate of the two species when hop pecking. Whitethroat (mean 0.53 capture attempts per second per week $\pm$ SE 0.009, 17 weeks) were significantly faster than Sedge Warbler (mean 0.43 capture attempts per second per week $\pm$ 0.007, 15 weeks, Mann-Whitney U-test two tailed $p < 0.05$). By contrast when climb pecking, the technique which Sedge Warblers used more often than the other species, Sedge Warblers (mean 0.44 capture attempts per second per week $\pm$ 0.007, 15 weeks) had a significantly higher capture attempt rate than Whitethroats (mean 0.30 capture attempts per second per week $\pm$ 0.011, 17 weeks; Mann-Whitney U-test two tailed $p < 0.05$).

5:6 Prey selection by adult warblers

The prey items seec to be taken by adult warblers are shown in Figs. 39-41. Since examination of each year separately showed a similar pattern all three years have been combined in Figs.39-41. The results of examination of faeces collected from trapped birds are shown alongside the results from observation of feeding birds in Appendix B1-3. Nothing was found in the faeces to suggest that field observation produced an unrepresentative picture of what the birds were actually eating and, since the samples of faeces were necessarily much smaller than data obtained from watching birds, the latter have been used in seasonal and interspecific comparisons.

The invertebrate groups most frequently eaten by feeding birds were Hemiptera, Diptera, Coleoptera (mainly adults) and Lepidoptera (mainly larvae).

Dipterans were eaten more than any other type of invertebrate by adult Willow Warblers, forming more than 40% of observed prey items throughout the season, and over 50% from late April to late May and from the second half of June until the end of the season. (Fig.39). Willow Warblers mainly took Dipterans from hawthorn, birch and willowherb later in the season (Appendix A1-3, A10, Appendix B1). Hemipterans were also frequently eaten, especially when the males arrived in April(34%), and in July and August when Hemipterans constituted up to 39.7% of observed Willow Warbler prey. They were proportionately less important in May and June (10-22% of observed prey). This period coincided with the peak in caterpillars on hawthorn (Appendix A1); the proportion of Lepidoptera eaten by Willow Warblers rose from under 2% in April to around 20% in early June, dropped to around 10% at the end of June and under 5% in July and August. Hemipterans (mainly adult aphids) were taken by

Figure 39 The proportions of different invertebrate groups eaten by adult Willow Warblers 1979-81.

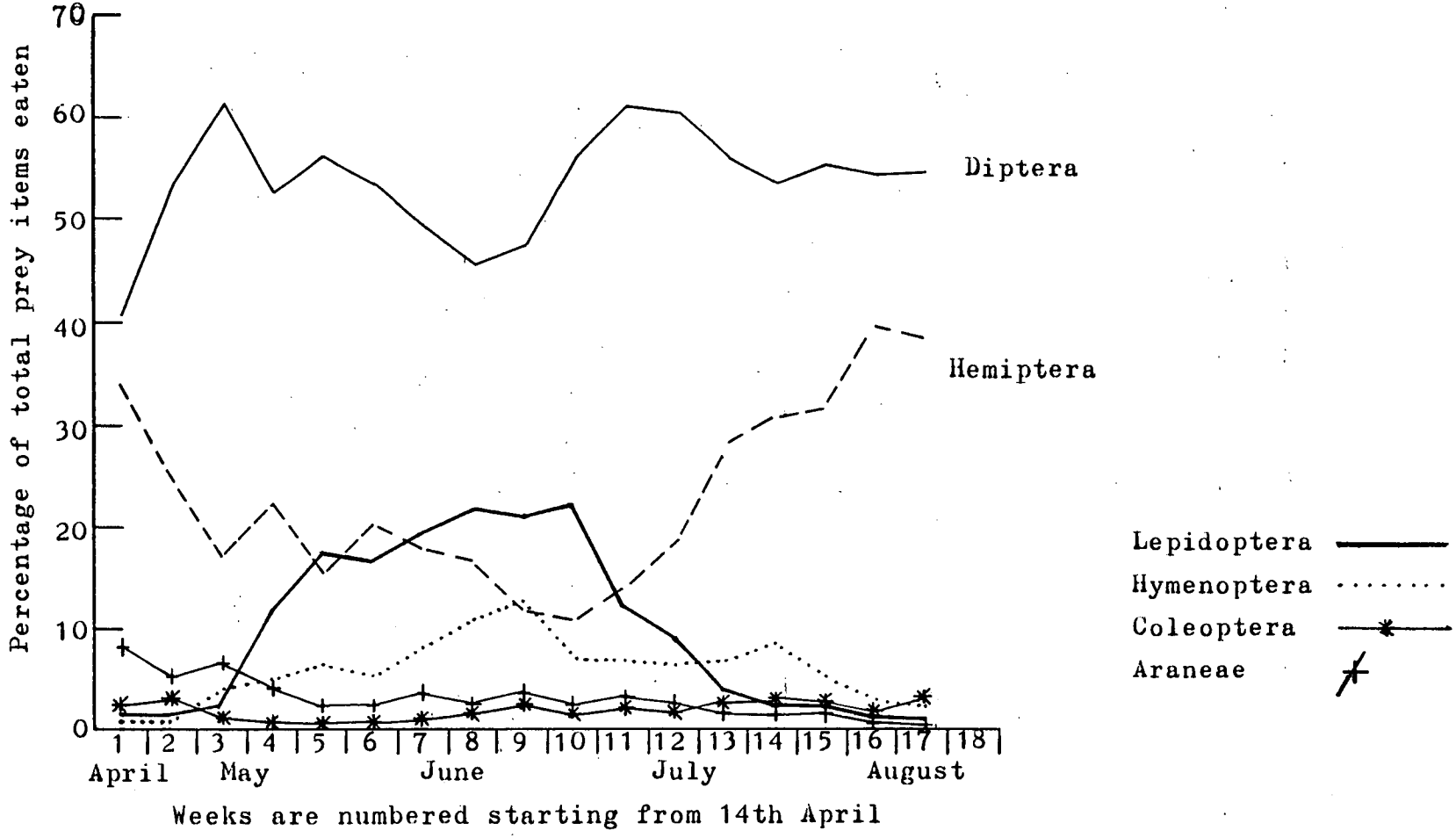


Figure 40 The proportions of different invertebrate groups eaten by adult Whitethroats 1979-81.

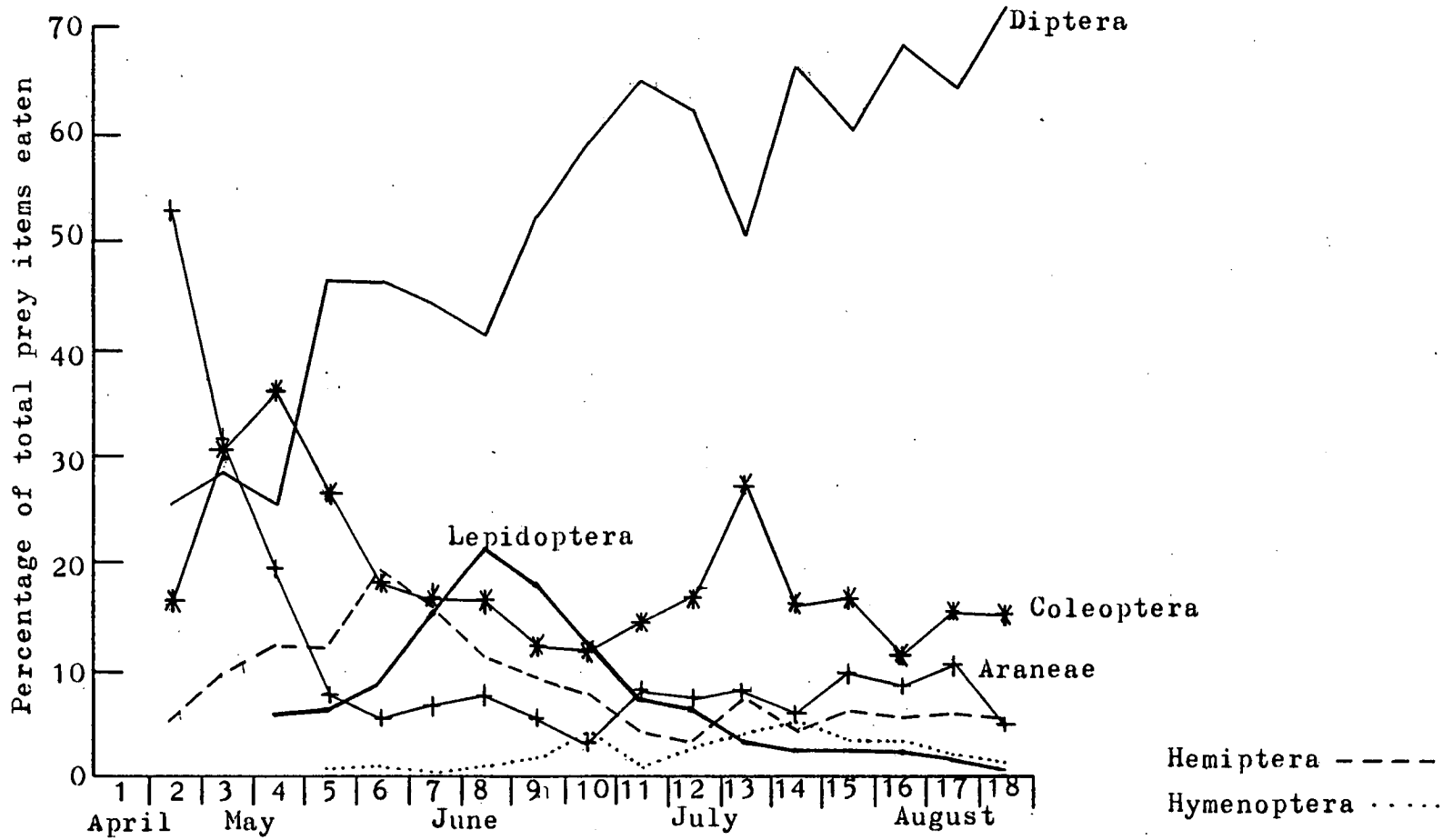
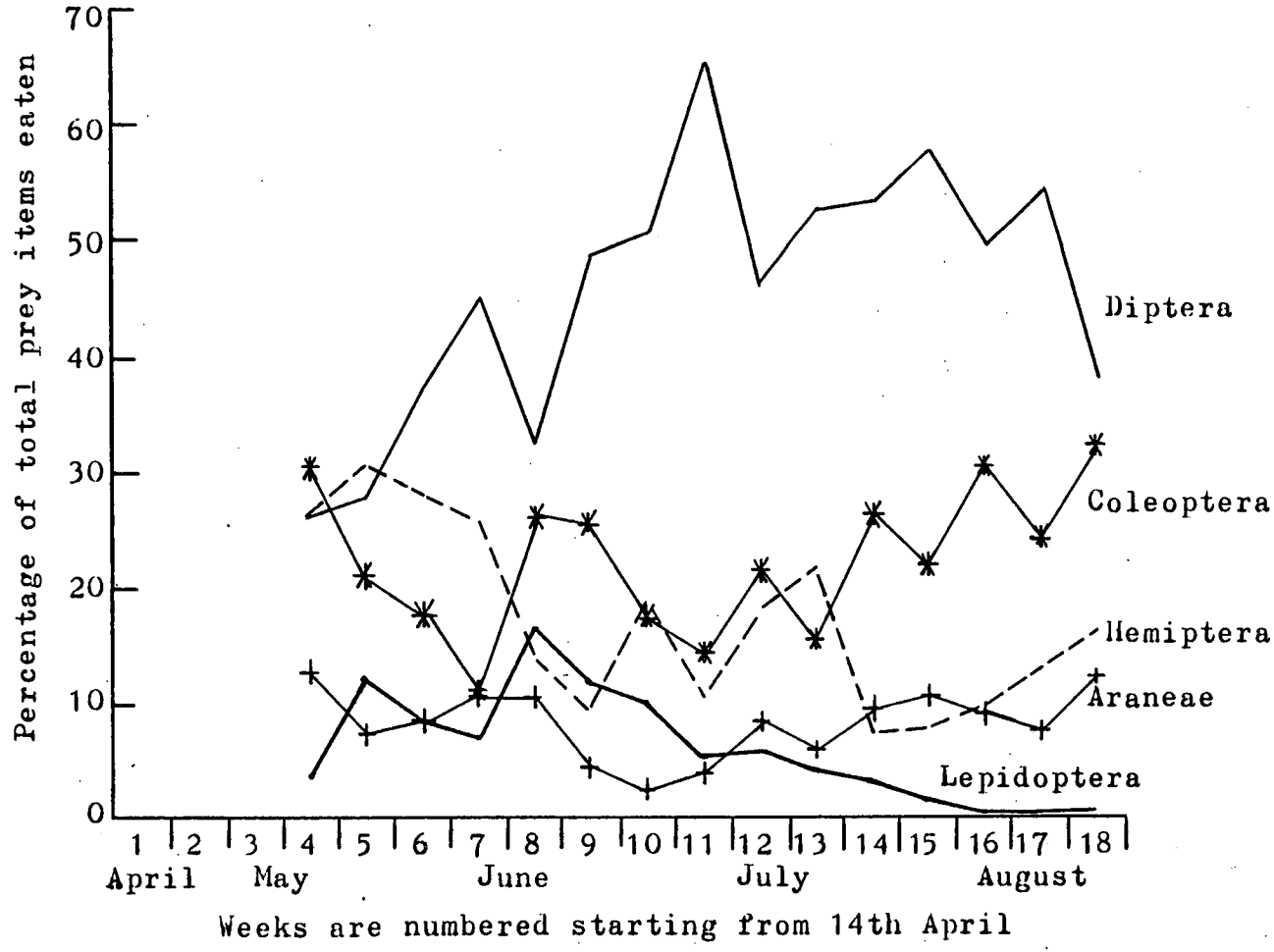


Figure 41 The proportions of different invertebrate groups eaten by adult Sedge Warblers 1979-81.



stand or hop pecking from new leaf growth on hawthorn, birch and willow in April especially by male Willow Warblers (which were the first birds to arrive) and again from around mid July till the end of the season when aphid numbers again built up in the tree and tall shrub layer and in the herb layer.

Lepidoptera were nearly always eaten as larvae, primarily obtained from hawthorn by stand pecking, although small moths were eaten as adults later in the season from the herb layer by hop or leap catching.

Willow Warblers also ate small amounts of Araneae and Collembola mainly in early spring. Collembola were taken from crevices in the rough bark of elder whereas the spiders were often taken from gorse. Other groups taken in small quantities by Willow Warblers were Molluscs - only very occasionally eaten - and Dermaptera and Hymenoptera, the latter mostly in the form of Ichneumons, and sometimes ants, which were taken in small quantities throughout the season.

Adult Whitethroats are more Diptera than any other prey, the proportion of observed prey items rising from 25% at the end of April to 72% by mid August (Fig.40). They obtained Diptera mainly by hop catching from hawthorn early in the season and from the herb layer later in the season (Appendix A1, A8-10, Appendix B2). Whitethroats took many spiders on their arrival in the study area, principally from gorse (Appendix A5), but also from hawthorn and willow (Appendix A3) and very occasionally from grass, but the proportion dropped rapidly (52 to 19%) by early May and to under 10% by mid May and for the rest of the season the second most frequently taken prey by Whitethroats were Coleopterans (11-36%). The proportion of Lepidoptera taken reached 20% in

early June, a similar proportion to Willow Warblers, but this figure was maintained for a shorter period in Whitethroats than Willow Warblers. Whitethroats obtained Lepidopteran larvae from hawthorn by stand pecking and, later in the season, large Lepidopteran larvae were obtained from nettle beds by stand and climb pecking methods. Some moths and occasional butterflies were caught later in the season from the herb layer by leap catching and hop pecking. Hemiptera were taken by Whitethroats, but normally constituted under 10% of their diet, except in May when the proportion taken rose to 19.5% when large numbers of bugs, such as Miridae and froghoppers, were present in the tall shrub and herb layers. These were usually taken by hop catching. In late summer Whitethroats also took insignificant amounts of Dermaptera and Molluscs.

Sedge Warblers most frequent prey were also Diptera (Fig.41) which formed between 26% and 65% of observed prey items. They obtained these by hop pecking and, later in the season, stand pecking for the larger craneflies. Sedge Warblers also took many Hemipterans in May (up to 30% of their prey) but in June, July and August the proportions of Hemipterans in their diet dropped to around 20% or less. Coleopterans (11-30%) were important to Sedge Warblers throughout the season and taken by stand and climb pecking mainly from nettle (Appendix A8). Lepidoptera were taken less often by Sedge Warbler than the other warblers forming up to 16.7% of Sedge Warbler prey in early June but well under 10% after mid June. Lepidoptera were taken by stand pecking from hawthorn (Appendix A1) and climb pecking from nettle and willowherb. Spiders formed from 2-13% of Sedge Warbler prey throughout the season and were mainly taken from

nettle and hawthorn.

Comparisons of the use made by the three species of warbler of the five most important invertebrate groups (Table 35) showed that Willow Warblers took significantly more Diptera, Hemiptera and Lepidoptera than both Whitethroats and Sedge Warblers. Whitethroats took significantly more Coleoptera and Araneae than Willow Warblers and significantly more Lepidoptera and Diptera than Sedge Warblers. Sedge Warblers took significantly more Coleoptera than either Willow or Whitethroats and significantly more Hemiptera than Whitethroats. There was no significant difference in the proportions of Araneae taken by Sedge Warblers and Whitethroats. However Sedge Warblers took significantly more of the smaller Araneae (< 5mm) than Whitethroats, whereas Whitethroats took significantly more Araneae in the 5-10mm size class than Sedge Warblers.

Table 35 Comparisons of the numbers of the five most important invertebrate groups seen to be taken by Willow Warblers, Whitethroats and Sedge Warblers 1979-81.

	Willow Warbler		Whitethroat		Sedge Warbler		Willow Warbler
Hemiptera	4559.3	$X^2=965.4$	1353.9	$X^2=258.3$	2144.7	$X^2=204.9$	4559.3
Lepidoptera	1924.1	$X^2=19.5$	1137.5	$X^2=13.5$	922.1	$X^2=67.7$	1924.1
Diptera	10551.8	$X^2=11.6$	7042.9	$X^2=97.9$	5894.8	$X^2=198.2$	10551.8
Coleoptera	359.5	$X^2=2922.2$	2572.3	$X^2=24.9$	2754.3	$X^2=3439.4$	359.5
Araneae	598.1	$X^2=441.5$	1118.7	NS	1053.1	$X^2=425.3$	598.1
size classes 5mm			415.7	$X^2=89.4$	604.7		
5-10mm			612.3	$X^2=35.5$	441.7		

The mean number of individuals of each invertebrate group seen to be taken each year are shown.

Chi squared values are significant ($p<0.001$) except where marked NS (not significant).

5:7 Invertebrate prey fed to the young

The results of collaring chicks to collect samples of the invertebrate prey adult warblers fed to their young are shown in Appendix C1-C3, along with the results of analysis of nestling faeces and field observation of prey collected as food for the nestlings and newly fledged young. The results for all three methods were similar therefore observations of food collected by the adults to their young were used in the interspecific comparisons since more data were available from this method than with the other two.

There were interesting differences between the food given to the young (Figs. 42-44) and that eaten by the adults at the same part of the breeding season (Figs. 39-41). Generally the food given to the young consisted of the larger invertebrate species or size classes. Although some of the food eaten by the adults could not be identified it is extremely unlikely that this caused the difference apparent between Figs. 42-44 and Figs.39-41 since the prey that could not be identified were mainly the smaller invertebrates.

Comparisons of the proportion of the invertebrate groups most frequently taken showed that with Coleoptera, Lepidoptera and Hemiptera the differences between the three species of warblers held for both adults and young (Tables 35, 36). Willow Warblers fed significantly more Lepidoptera and Hemiptera to their young than either Whitethroats or Sedge Warblers. Sedge Warblers fed their young significantly more Coleoptera than did Willow Warblers or Whitethroats and significantly more Hemiptera than did Whitethroats. Whitethroats gave their young significantly more Coleoptera than Willow Warblers did and significantly more Lepidoptera than Sedge

Figure 42 The proportions of different invertebrate groups collected by adult Willow Warblers for their young 1979-81.

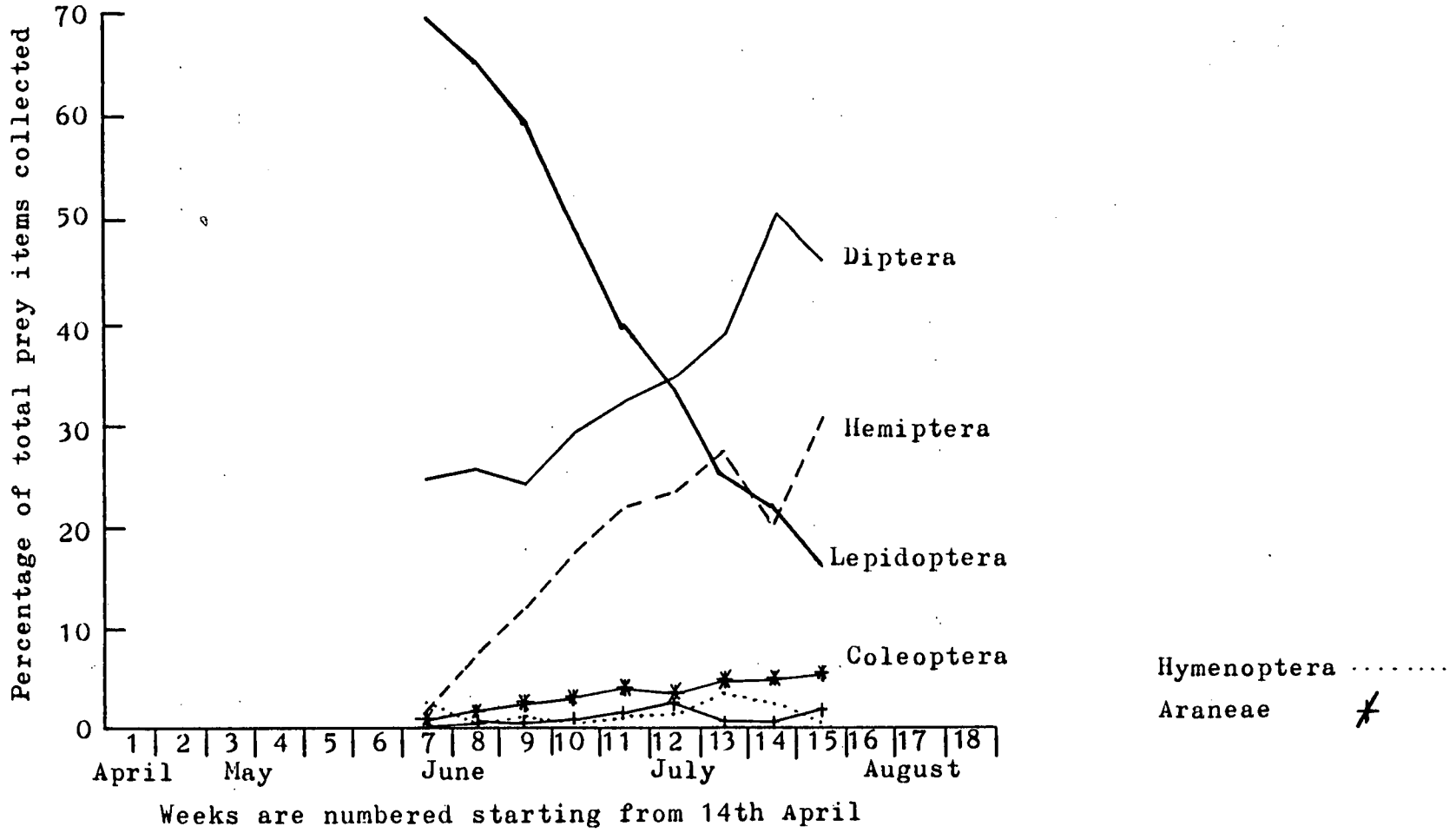


Figure 43 The proportions of different invertebrate groups collected by adult Whitethroats for their young 1979-81.

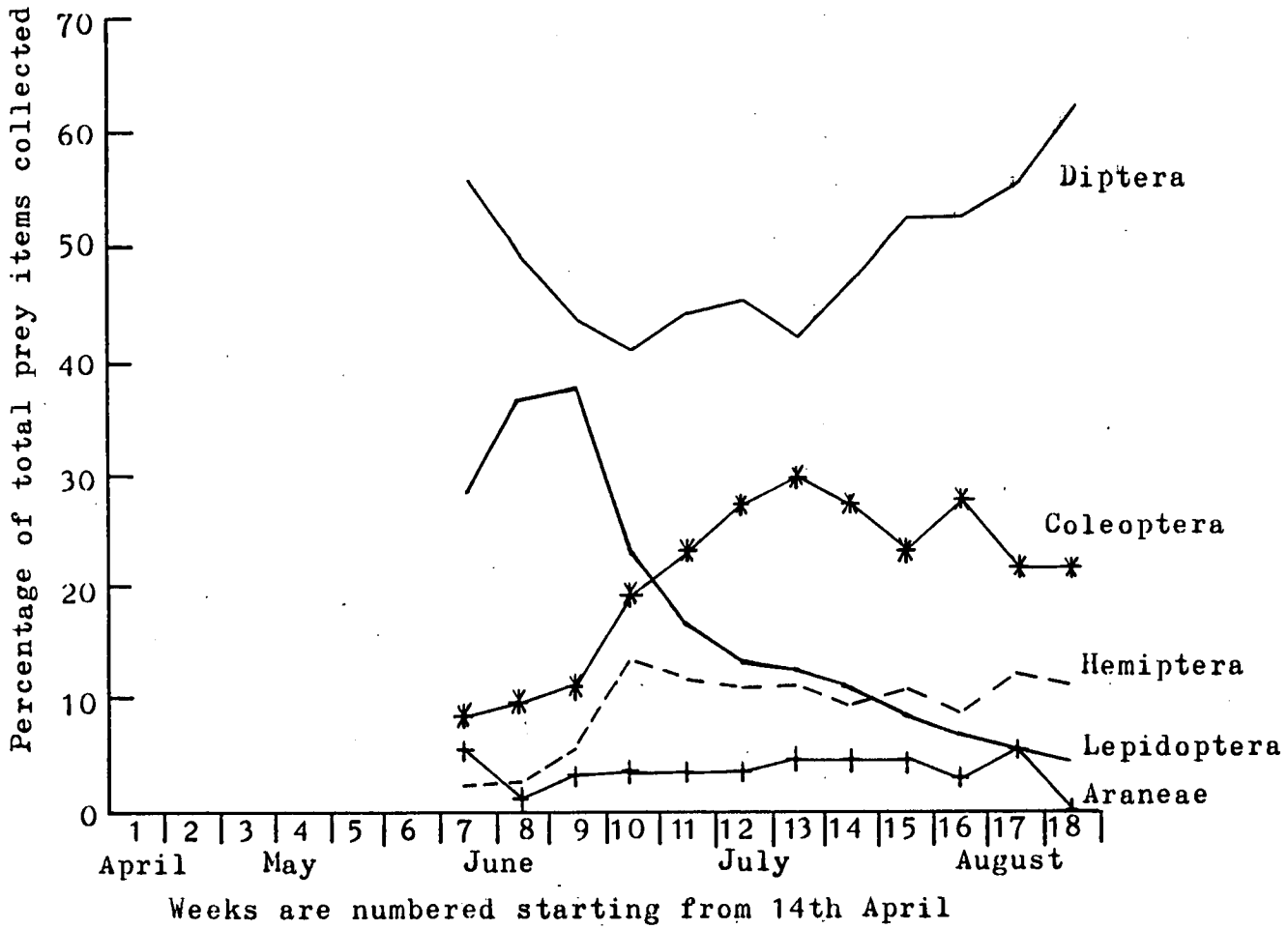


Figure 44 The proportions of different invertebrate groups collected by adult Sedge Warblers for their young 1979-81.

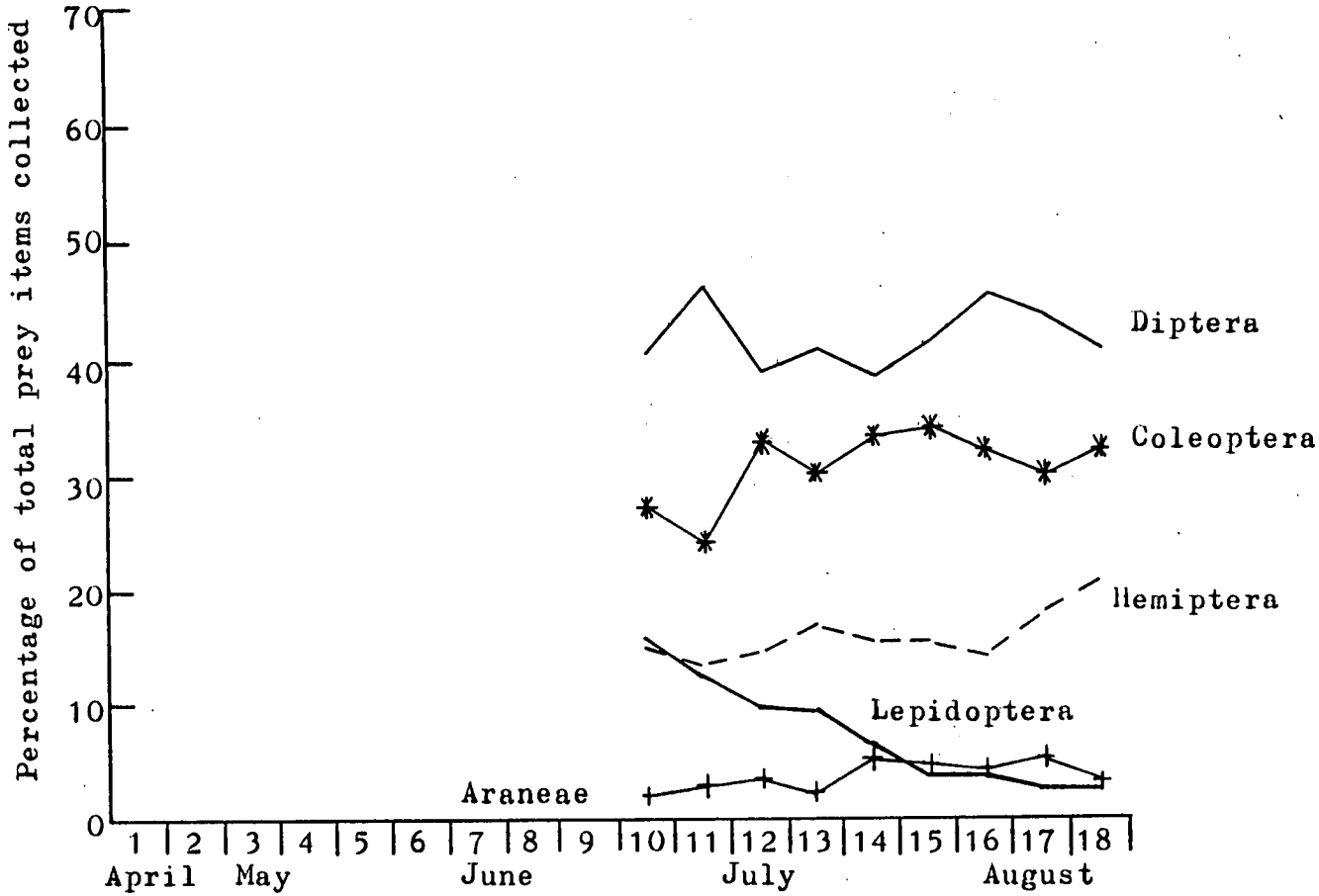


Table 36 Comparison of the numbers of the four most important invertebrate groups collected by adult warblers for their young 1979-81.

	Willow Warbler		Whitethroat		Sedge Warbler		Willow Warbler
Hemiptera	1305.3	(275.24)	681.7	(133.51)	1172.3	(29.04)	1305.3
Lepidoptera	2798.3	(866.12)	1334.0	(298.01)	645.6	(2032.32)	2798.3
Diptera	2396.8	(54.65)	2993.1	(1.20,NS)	3141.8	(72.44)	2396.8
Coleoptera	249.2	(987.04)	1550.8	(169.82)	2299.2	(1788.85)	249.2

The mean number of individuals of each invertebrate group seen to be taken each year are shown.

Chi squared values are shown in parentheses and are all significant ($p<0.001$) except where marked NS (not significant).

Warblers. However with Diptera the pattern was different. There was no significant difference between Sedge Warblers and Whitethroats in the amount of Diptera fed to their chicks but there was in the size of Dipteran prey; Sedge Warblers fed a significantly greater proportion of Diptera less than 5mm in length (X^2 = 1102.52, $p < 0.001$) and Whitethroats significantly more in the 5-10mm and greater than 10mm classes to their young (5-10mm X^2 = 822.23, $p < 0.001$, > 10mm X^2 44.58, $p < 0.001$). Sedge Warblers and Whitethroats both fed significantly more Diptera to their young than Willow Warblers which was the opposite to the feeding pattern of the adults themselves.

This change was due to the different proportions of prey that the adults fed to their young compared to what they consumed themselves. Willow Warblers fed less Diptera to their young than the other two species since they increased the numbers of Lepidoptera given to the chicks to a maximum of 70% of prey items at the end of May (the corresponding figure for adult prey at this time was 19.7%). Diptera were still an important chick food, especially for later broods, since the proportion of Diptera fed to young Willow Warblers rose from 24% in early June to around 50% in late July. The only other important food source for young Willow Warblers was Hemiptera, which increased in importance as caterpollars declined, reaching a maximum of 30% of the prey items collected for the young in the second half of July.

In general Willow Warblers tended to collect higher proportions of fewer invertebrate types for their young than they ate themselves. Two groups, Collembola and Dermaptera, were taken by adults but never seen to be fed to young or recorded in faeces of young. Willow Warblers collected significantly more Lepidoptera and Coleoptera

for their young than they took themselves in the same time period but ate significantly more Hemiptera and Diptera than they collected for their chicks (Table 37).

Whitethroats also collected a higher proportion of Lepidoptera for their chicks than they took themselves, though unlike Willow Warblers Lepidoptera (maximum proportion 36.8%) never outnumbered Diptera (maximum 62.7%) in the proportions of prey items seen to be collected for the chicks. As with Willow Warblers the proportions of Lepidoptera collected for the chicks decreased throughout the breeding season while the proportions of Diptera (41-62.7%) and Coleoptera (8.4-29.9%) increased. Hemiptera featured less prominently in the diet of Whitethroat chicks (around 10% for the later part of the season) as did small numbers of Araneae (1.9-5.3%).

Comparison of the prey collected for young Whitethroats with that eaten by the adults showed that significantly more Lepidoptera, Hemiptera and Coleoptera were taken for the chicks which in turn received significantly fewer Diptera than were eaten by the adults (Table 37).

The most frequent prey items collected for young Sedge Warblers were Diptera (around 40%) and Coleoptera (around 30%) with smaller proportions of Lepidoptera, which decreased during the breeding season (15 to <3%), Hemiptera, which increased later in the season, (14.9-21%) and even fewer Araneae (<5%). Young Sedge Warblers received significantly more Lepidoptera, Hemiptera and Coleoptera than were eaten by the adults which in turn ate significantly more Diptera; this pattern was similar to Whitethroats but the proportions were significantly different between the two species (see above and Table 37).

Table 37 Comparison of the numbers of the four most important invertebrate foods eaten by adult Willow Warblers, Whitethroats and Sedge Warblers with the numbers collected for their young.

	Hemiptera		Lepidoptera		Diptera		Coleoptera	
	adult	young	adult	young	adult	young	adult	young
Willow Warbler	1938.0	1305.3	1062.6	2798.3	4877.8	2396.8	201.9	249.2
	(16.17)		(1758.45)		(592.21)		(26.65)	
Whitethroat	805.6	681.7	895.0	1334.0	5511.6	2993.1	1665.2	1550.8
	(5.98, $p<0.01$)		(302.75)		(402.16)		(46.88)	
Sedge Warbler	760.7	1172.3	184.1	645.6	3138.1	3141.8	1368.9	2299.2
	(18.87)		(169.11)		(176.65)		(88.44)	

The mean number of individuals of each invertebrate group seen to be taken each year are shown.

Chi squared values are shown in parentheses and are all significant ($p<0.001$) or $p<0.01$ where marked.

5:8 The proportion of time spent on feeding and other activities

The results of watching individual pairs of Willow Warblers, Whitethroats and Sedge Warblers throughout a day at four important stages of their breeding seasons are shown in Appendix D1-12. All three species spent more time feeding in the mornings between 0700 and 1100 hours B.S.T, despite seasonal changes in the timing of dawn, than earlier in the morning, or from late morning to early evening. Another peak in feeding activity also occurred in the evening. There were differences between the sexes in the proportion of time spent on different actibities associated with the breeding season. Only males sang and only females incubated. There were also differences between males and females in the amount of time spent feeding. In the pre incubation period females of all three species spent more time feeding than males. (Sedge Warbler $X^2 = 9.29$, $p < 0.01$, Whitethroat $X^2 = 36.07$, $p < 0.001$, Willow Warbler $X^2 = 22.92$, $p < 0.001$). During incubation this was reversed and females spent less time feeding than males. (Sedge Warbler $X^2 = 22.66$, $p < 0.001$, Whitethroat $X^2 = 21.47$, $p < 0.001$, Willow Warbler $X^2 = 41.19$, $p < 0.001$).

When young were in the nest both males and females spent more time feeding (up to 98%) than at any stage of the breeding cycle; even so there was still a decrease (to 60-80%) between 1100 and 1500 hours though less so than at other stages. Females of all three species spent significantly more time feeding when their young were in the nest than during the pre incubation phase (Sedge Warbler $X^2 = 45.74$, $p < 0.001$, Whitethroat $X^2 = 55.13$, $p < 0.001$, Willow Warbler $X^2 = 104.97$, $p < 0.001$) and males of all three species spent significantly more time feeding when they had nestlings than when the hens were on eggs (Sedge Warbler $X^2 = 118.78$, $p < 0.001$, Whitethroat $X^2 = 72.40$, $p < 0.001$

Willow Warbler $X^2 = 93.12$, $p < 0.001$). At this time male song also dropped off dramatically. When feeding fledged young the proportion of time spent feeding was still high but less so than when young were in the nest. (males: Sedge Warbler $X^2 = 27.5$, $p < 0.001$, Whitethroat $X^2 = 16.47$, $p < 0.001$, Willow Warbler $X^2 = 29.52$, $p < 0.001$; females: Sedge Warbler $X^2 = 35.74$, $p < 0.001$, Whitethroat $X^2 = 19.88$, $p < 0.001$, Willow Warbler $X^2 = 33.53$, $p < 0.001$).

5:9 Summary

In late April and May all species fed more in evergreen shrubs, such as gorse, than they did after deciduous or herbaceous species had leafed out. Invertebrate biomass in the trees and taller shrubs peaked in late May or early June, largely due to caterpillars, when all species spent a greater proportion of their feeding time there than at other times of year. Willow Warblers spent a higher proportion of time feeding in trees and tall shrubs than Whitethroats or Sedge Warblers. Invertebrate biomass declined in trees and tall shrubs from around mid June as caterpillars pupated, though other invertebrates, notably flies and bugs, were taken from this layer throughout the summer, especially by Willow Warblers. The most important tree or tall shrub species to feeding warblers was hawthorn, followed by birch and willow. The invertebrate biomass in nettles showed two peaks, one in June around flowering, and a higher peak in July or early August, as the plants senesced. Willowherb biomass peaked in early July. These herbs held few caterpillars but more bugs, beetles, flies and spiders than the tall shrubs and trees. All three warbler species increased their feeding time in the herbs as the season progressed though Whitethroats and Sedge Warblers fed there more often than Willow Warblers. The three species showed significant differences in feeding methods. Willow Warblers used stand pecking more than the others. Sedge Warblers used stand pecking more than Whitethroats. Whitethroats used hop pecking more than the others. Sedge Warblers used hop pecking more than Willow Warblers. Climb pecking was mostly used by Sedge Warblers and flycatching mostly by Willow Warblers. The most important groups of prey taken by all warblers were adult Diptera, Hemiptera and Coleoptera and the larvae of Lepidoptera.

Willow Warblers took more Diptera, Hemiptera and Lepidoptera larvae than the other species. Whitethroats took more Coleoptera than Willow Warblers and more Lepidoptera and Diptera than Sedge Warblers. Sedge Warblers took more Coleoptera than Willow Warblers and more Hemiptera than Whitethroats. Adult warblers fed different proportions of prey species to their young than they ate themselves. In general the interspecific differences found in prey eaten by adults were maintained in the prey fed to their young. However Willow Warblers fed significantly less Diptera to their young than the other two species due to the high proportion of Lepidoptera larvae they collected for their chicks.

Chapter 6 Warbler territories

6:1 Methods

The territories of male Willow Warblers, Whitethroats and Sedge Warblers were mapped in the three seasons 1979-81 in the main study site from late April (depending on arrival dates) through May and, in the case of Whitethroats and Sedge Warblers, in June. Points where each male bird sang were plotted on copies of the 1:2500 scale map of the site (Fig.2). The positions of females were also noted. Movements of birds outwith their own territories and clashes with other birds were noted though neither of these were at all common. The outermost points for each singing male were joined up by straight lines to give an estimate of territory size which was measured using a planimeter. In the three years 1979-81 and in 1982 other warbler species were colour ringed in the main study site although time did not permit their territories to be mapped in detail. However it was possible to allocate birds of the five species involved to either the grazed or ungrazed ends of the study site.

Vegetation was mapped in the main study site on copies of a 1:1250 scale map. A tape measure and coloured crayons were used in the field to plot the different vegetation types (Ch.5: Figs. 36-38) known to be used by feeding warblers on maps. Areas not utilized by warblers were also mapped and notes made of their characteristics e.g. grazed areas. Areas were then calculated from the maps using a planimeter. All measurements using the planimeter were carried out three times to improve accuracy.

6:2 Territory size and composition

The territories of breeding male Willow Warblers, Whitethroats and Sedge Warblers from 1979-81 are shown in Table 38. There was considerable variation in territory size. Mean territory size was largest with Whitethroats (annual means 3621-5050 m^2).

Whitethroats were the only species to show any degree of overlap although fighting was rarely (five occasions in 1979-81) observed between overlapping males. Whitethroat territory sizes were therefore calculated with and without the overlap areas.

Since overall territory size could be affected by areas of ground of little or no use to feeding warblers the areas of the vegetation types known to be used by feeding warblers (Figs.36-38) were also calculated and are shown in Table 39. Field observation indicated that breeding warblers collected food for themselves and their nestlings almost exclusively from within their territories until the young fledged; there were only nine records of breeding adults outwith their then territories in three years during incubation or while feeding nestlings. Though individual territories showed variation there were differences in the areas of different vegetation types between territories of the three species. Willow Warblers used nettle and willowherb less than the other species (Figs.36-38). Willow Warbler territories contained significantly smaller areas (annual means 242-326 m^2) of herbs than either Whitethroat territories (annual means 1203-1301 m^2) or Sedge Warbler territories (annual means 1050-1145 m^2) in all three years (Table 39). There was a significant correlation between the size of Willow Warbler territories and the area of herbs within them in only one year (Fig.47). Throughout the season Willow Warblers used trees and tall shrubs more often than Sedge Warblers and Whitethroats (Figs. 36-38). Whitethroats spent slightly more time than Sedge Warblers'

Table 38 The sizes of Willow Warbler, Whitethroat and Sedge Warbler territories 1979-81.

		1979	1980	1981
Willow Warbler	range	1980-4200	1679-3500	1710-3680
	mean	2709.3	2569.2	2712.6
	S.D.	957.4	519.1	665.9
	n	14	14	19
Whitethroat	range	2980-6120	4390-6040	3800-5500
with overlap*	mean	3621.3	5050	4852.5
	S.D.	1098.7	515.7	637.8
	n	8	9	8
no overlap	range	2660-5370	2630-5750	3240-5350
	mean	3317.5	4054.4	4310.0
	S.D.	933.9	1026.5	768.6
	n	8	9	8
Sedge Warbler				
	range	2700-3470	2700-3870	3000-4000
	mean	2958.3	3226.0	3474.0
	S.D.	228.7	442.5	296.3
	n	12	10	10

All areas are in m^2. * these figures were not used in comparisons. Overall Willow Warblers had significantly smaller territories than Whitethroats or Sedge Warblers (Willow Warbler x Whitethroat $t=5.87$, $p<0.001$; Willow Warbler x Sedge Warbler $t=3.75$, $p<0.001$) and Sedge Warblers had significantly smaller territories than Whitethroats ($t=3.62$, $p<0.001$). The territories of three unmated males and one whose female was killed before laying were not included as their boundaries were imprecise.

Table 39 Comparisons of the areas of the main vegetation types used by feeding warblers in each territory 1979-81.

	1979			1980			1981		
Willow Warbler	A	B	C	A	B	C	A	B	C
range	1460-2550	0-650	50-850	1129-2800	0-550	50-790	1100-2900	0-590	25-600
mean	1966.4	268.6	326.4	1756.3	200.0	242.1	1868.9	217.9	247.1
S.D.	360.6	217.1	283.4	468.7	150.6	243.9	533.2	159.6	194.4
	t=3.48 p<0.01	t=2.12 p<0.05	t=5.47 p<0.001	NS	t=4.72 p<0.001	t=7.24 p<0.001	NS	t=3.75 p<0.001	t=11.15 p<0.001
Whitethroat									
range	750-2150	350-780	900-2150	760-2120	290-1200	890-1950	1110-2500	280-750	930-1670
mean	1296.2	458.7	1203.7	1441.1	698.9	1211.1	1551.2	497.5	1301.2
S.D.	493.9	141.2	432.5	493.9	328.2	369.2	488.0	192.4	259.7
	NS	NS	NS	NS	NS	NS	t=2.38 p<0.05	NS	NS
Sedge Warbler									
range	750-1500	200-700	250-1650	700-1550	350-800	850-1550	750-1440	400-800	950-1900
mean	1064.2	441.7	1083.3	1150.0	555.0	1050.0	1116.0	595.0	1145.0
S.D.	209.6	170.3	384.5	253.3	151.7	201.4	219,1	134.3	275.3
	t=7.33 p<0.001	t=2.15 p<0.05	t=5.54 p<0.001	t=3.56 p<0.01	t=5.43 p<0.001	t=8.22 p<0.001	t=4.13 p<0.001	t=6.15 p<0.001	9.83 p<0.001
Willow Warbler									
mean	1966.4	268.6	326.4	1756.3	200.0	242.1	1868.9	217.9	247.1

All areas are in m^2. * Whitethroat territories do not include areas of overlap.

A = Tall shrubs and trees:ie. all tree species and hawthorn, willow and elder.

B = Low shrubs and creepers:ie. gorse, broom, bramble and rose.

C = Herbs:ie. nettle, nettle/bishopweed, and willowherb.

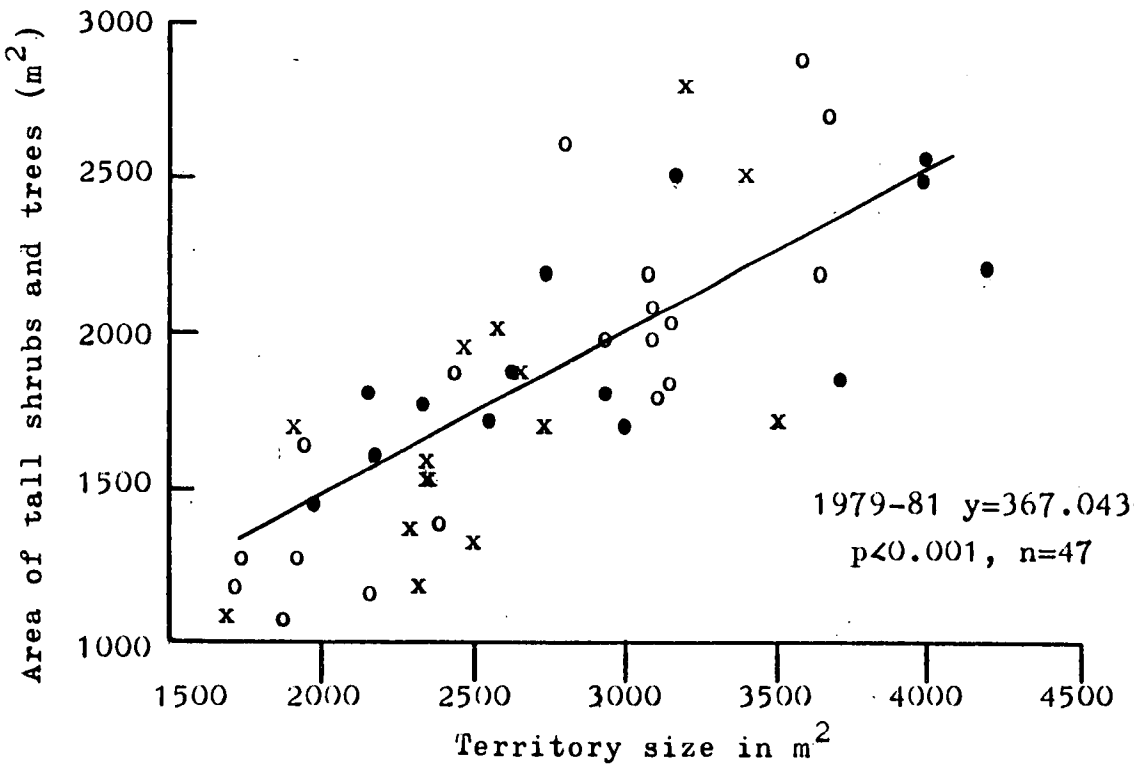
feeding in shrubs (Figs. 37 and 38). Willow Warbler territories contained significantly more trees and tall shrubs (annual means 1756-1966 m^2) than Sedge Warblers (annual means 1064-1150 m^2) in all three years; Willow Warbler territories usually contained more trees and tall shrubs than Whitethroats' (annual means 1296-1551 m^2) though the difference was only significant in 1979 (Table 39). In all three years there was a significant correlation between the size of Willow Warbler territories and the area of trees and tall shrubs within them (Fig.45). In one out of three years there was a significant correlation between the size of Whitethroat territories and the area of trees and tall shrubs within them (Fig.48). There was no correlation between Sedge Warbler territory size and the area of trees and tall shrubs within each territory (Fig.51). Whitethroats and Sedge Warblers both used the herb layer for feeding more than Willow Warbler's (Figs. 36-38). There were no significant differences between Whitethroats and Sedge Warblers in the areas of herbs within their territories (Table 39). In 1979 there was a significant correlation between Whitethroat territory size and the area of herbs within each territory (Fig.50).

In two out of three years there was a significant correlation between Sedge Warbler territory size and the area of herbs within each territory (Fig.53). Of the three major vegetation categories low shrubs and creepers were used less by feeding warblers than either tall shrubs and trees or herbs (Figs. 36-38). Of the low shrubs gorse was used more than the others though mainly for a relatively short spell after the birds' arrival in spring. Whitethroats spent more time feeding in gorse than Sedge Warblers and both species used gorse more than Willow Warblers(Figs.36-38). There were no significant differences between the areas of low

shrubs and creepers in the territories of Sedge Warblers and Whitethroats in any of the three years. Both species' territories contained significantly larger areas of low shrubs and creepers than Willow Warbler territories in all three years (Table 39). The only significant correlation between territory size and area of low shrub and creeper was with Whitethroats in 1980 (Fig.49).

A further point about the territories of all three species was the very marked difference between the two parts of the main study site. The ungrazed, herb rich section held from 30-32 territories between 1979-81 whereas the grazed end held only three to five territories over the same period. Figure 54 shows the distribution of the territories of all three species per year and also demonstrates the considerable degree of overlap between the three species, especially in the ungrazed scrub. Over the three years only 4-5% of the ungrazed area was not utilized by breeding warblers, 28-30% was occupied by at least one species, up to 44% by two species and up to 23% by all three species. Only 2446 to 2880 m^2 of the ungrazed section was not used by Warblers; and consisted of 830 to 1281 m^2 (29-45%) grass, 710-1320 m^2 (29-46%) tall shrubs and trees, 220-460 m^2 (7.6-18.8%) low shrubs and creepers and 410-510 m^2 (14-18%) herbs. By contrast in the grazed section from 64.3% to 81.4% of the area was not used over the three years 1979-81 and, since only Willow Warblers were represented by more than one territory, interspecific overlap was greatly reduced (1979) or absent (1980 and 1981). Although some 53% of the grazed section was short grass, and clearly unattractive to breeding warblers, a considerable area (7753-13478 m^2) of tall shrubs was also not used. This consisted of two hedges (predominantly hawthorn) along two sides of the

Figure 45 Comparison of territory size and the area of tall shrubs and and trees within each Willow Warbler territory 1979-81.

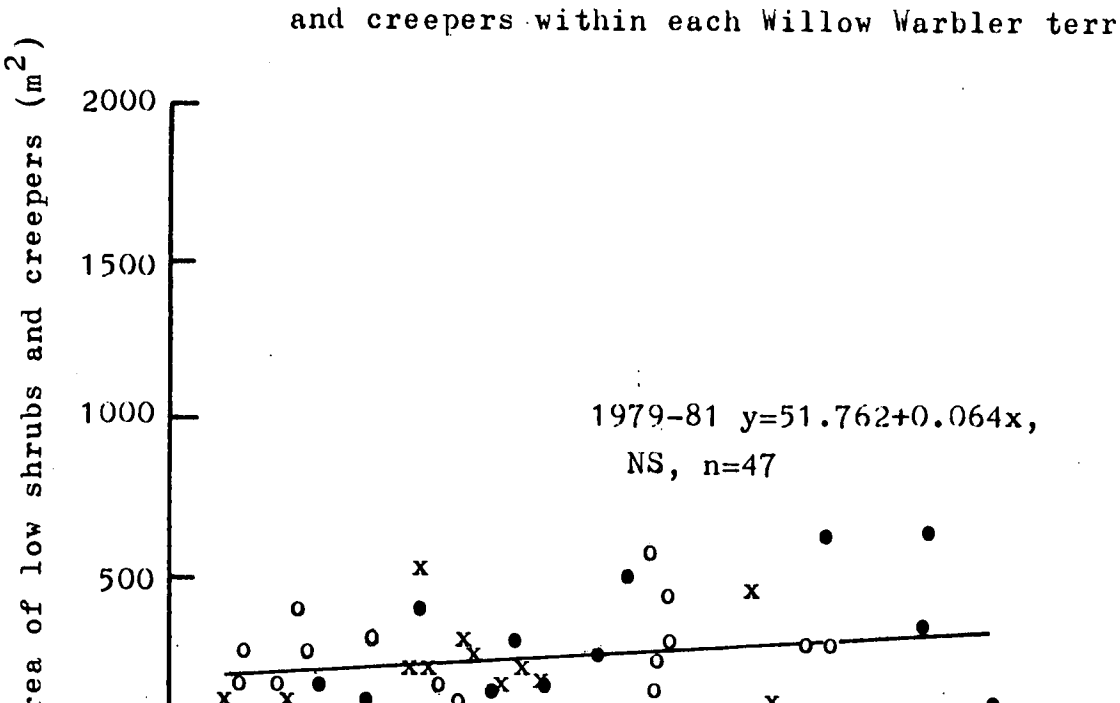


● 1979 y=906.206+0.357x, p<0.01, n=14

x 1980 y=134.604+0.631x, p<0.01, n=14

o 1981 y=9.620+0.685x, p<0.001, n=19

Figure 46 Comparison of territory size and the area of low shrubs and creepers within each Willow Warbler territory 1979-81.

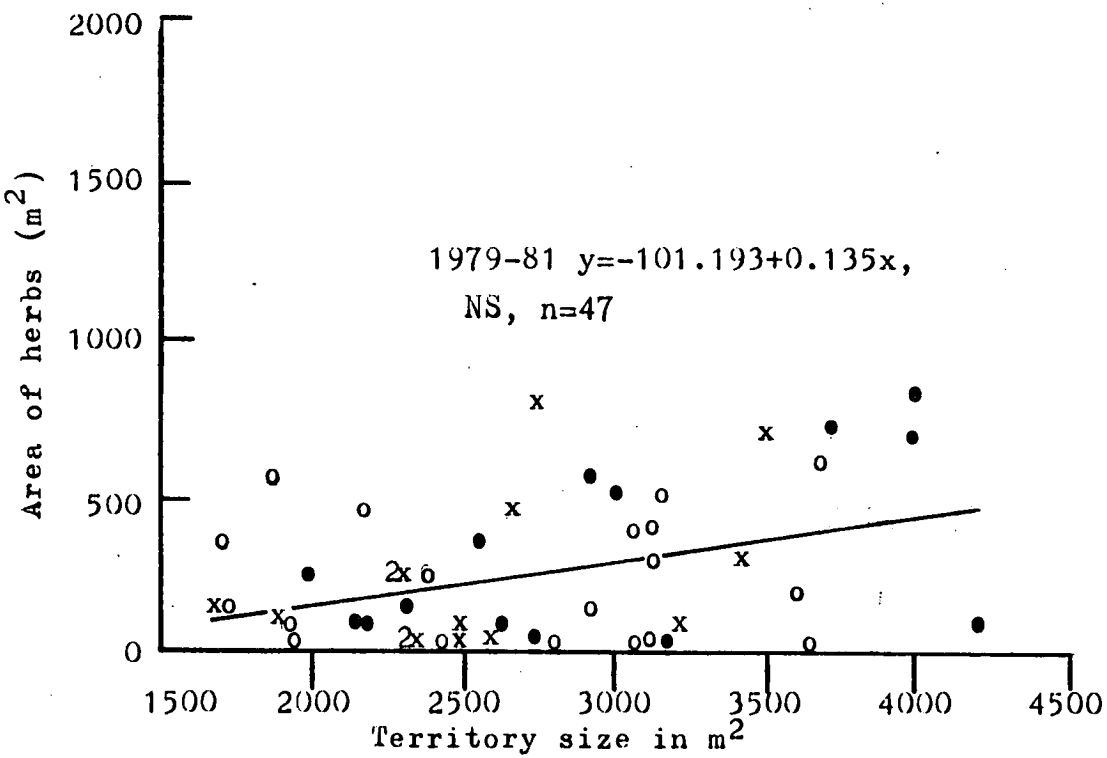


• 1979 y=-121.203+0.131x, NS n=14

x 1980 y=117.790+0.032x, NS, n=14

o 1981 y=216.942+0.0004x, NS, n=19

Figure 47 Comparison of territory size and the area of herbs within each Willow Warbler territory 1979-81.

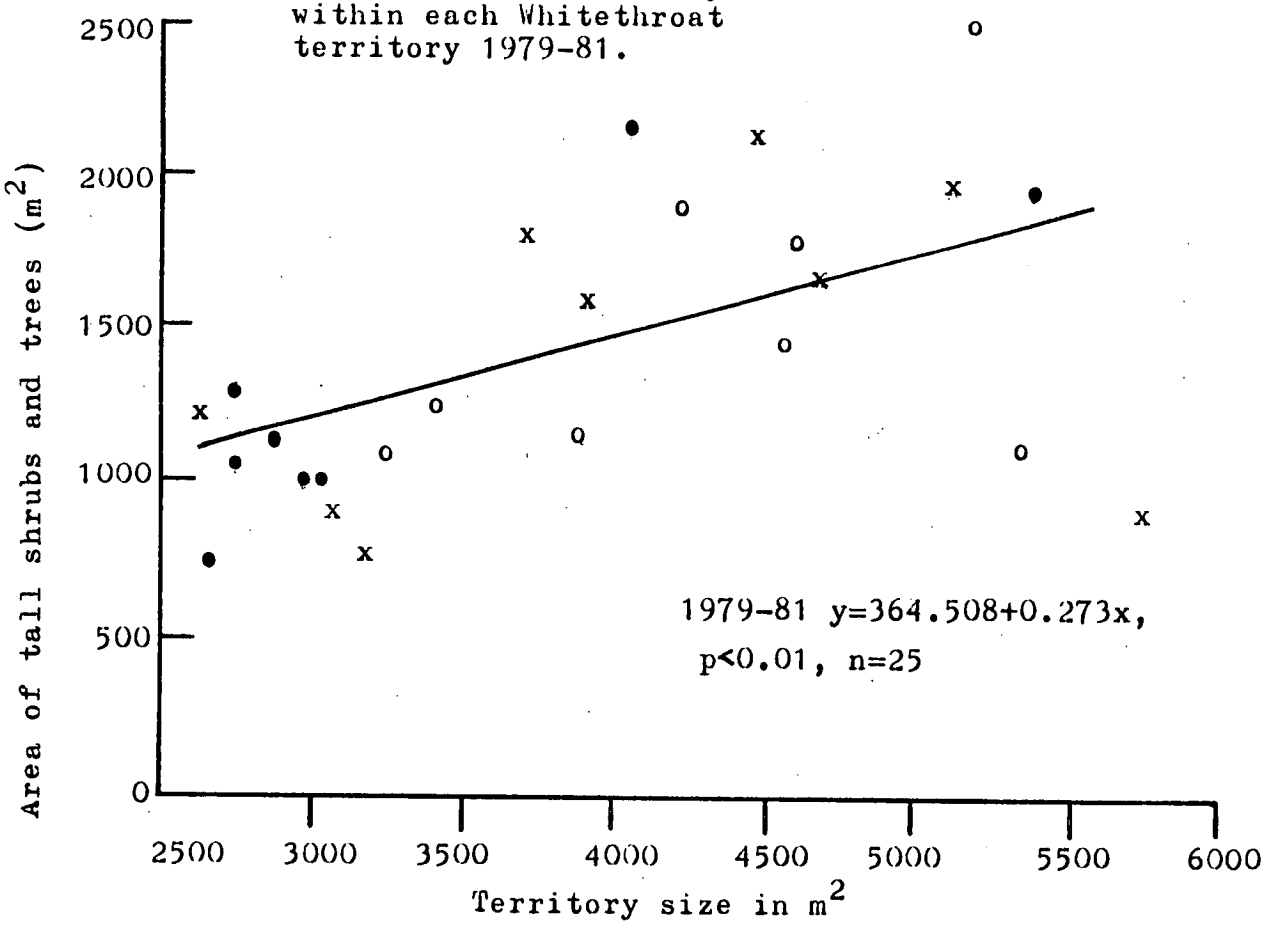


• 1979 y=-308.186+0.214x, p<0.01, n=14

x 1980 y=-326.420+0.221x, NS, n=14

o 1981 y=215.813+0.012x, NS, n=19

Figure 48 Comparison of territory size and the area of tall shrubs and trees within each Whitethroat territory 1979-81.

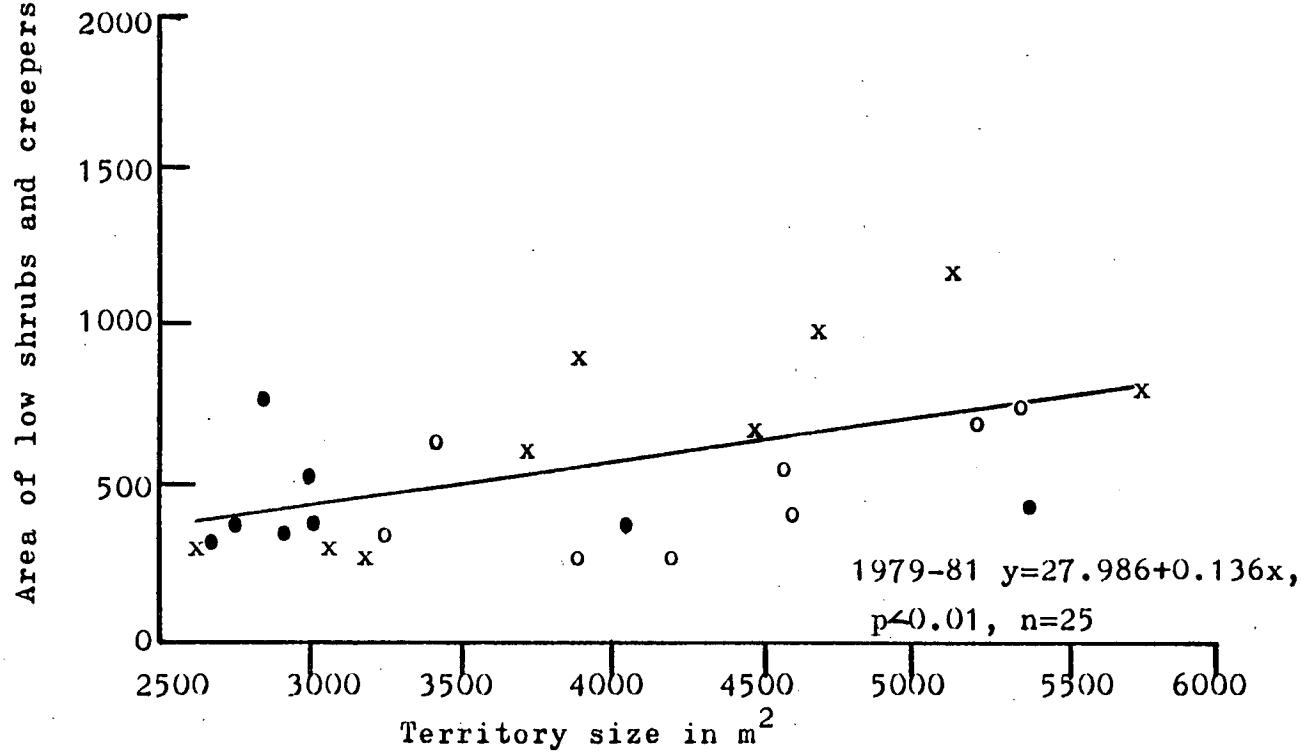


● 1979 y=-158.429+0.439x, p<0.05, n=8

x 1980 y=848.749+0.146x, NS, n=9

o 1981 y=172.705+0.320x, NS, n=8

Figure 49 Comparison of territory size and the area of low shrubs and creepers within each Whitethroat territory 1979-81.

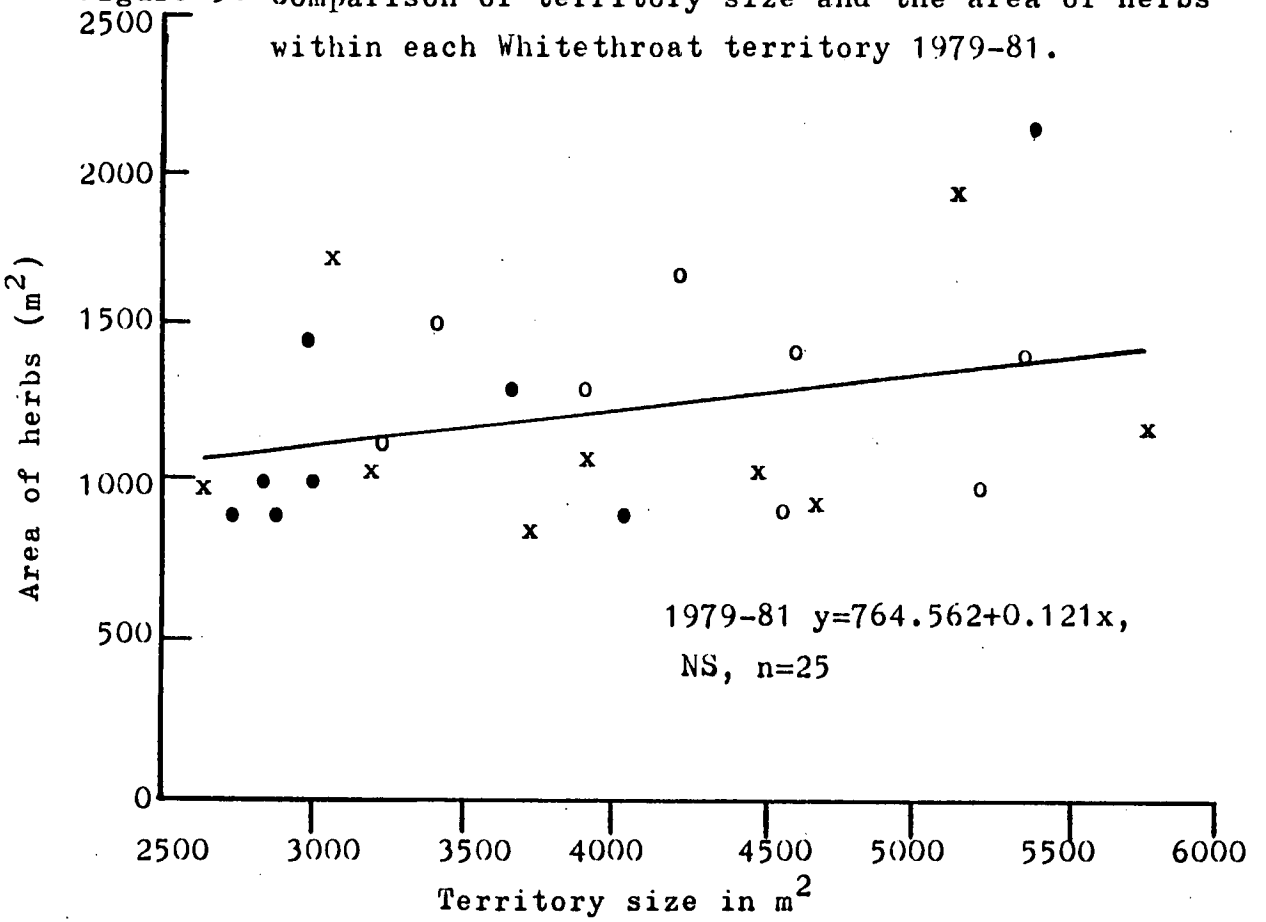


● 1979 y=508.702+0.015x, NS, n=8

x 1980 y=-350.502+0.259x, p<0.01, n=9

o 1981 y=-92.084+0.137x, NS, n=8

Figure 50 Comparison of territory size and the area of herbs within each Whitethroat territory 1979-81.

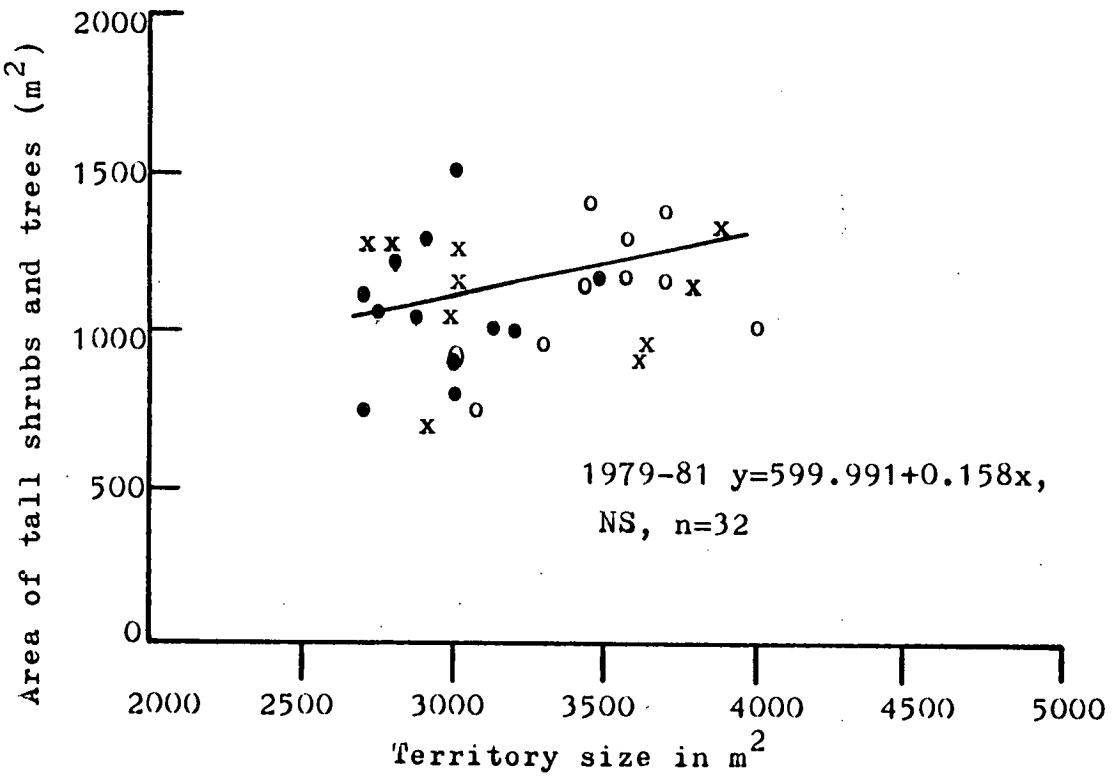


● 1979 y=97.740+0.333x, $p<0.05$, n=8

x 1980 y= 907.389+0.075x, NS, n=9

o 1981 y=1524.180+0.052x, NS, n=8

Figure 51 Comparison of territory size and the area of tall shrubs and trees within each Sedge Warbler territory 1979-81.

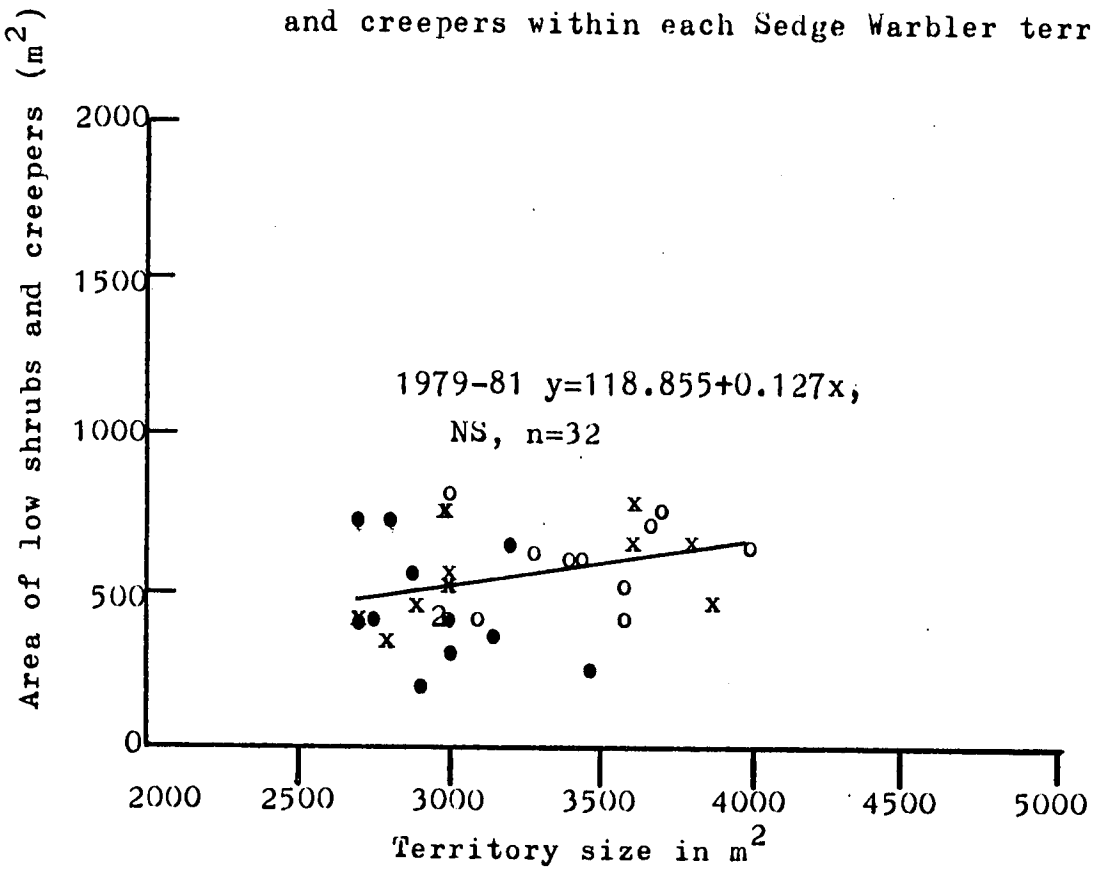


• 1979 y=672.081+0.133x, NS, n=12

x 1980 y=763.599+0.120x, NS, n=10

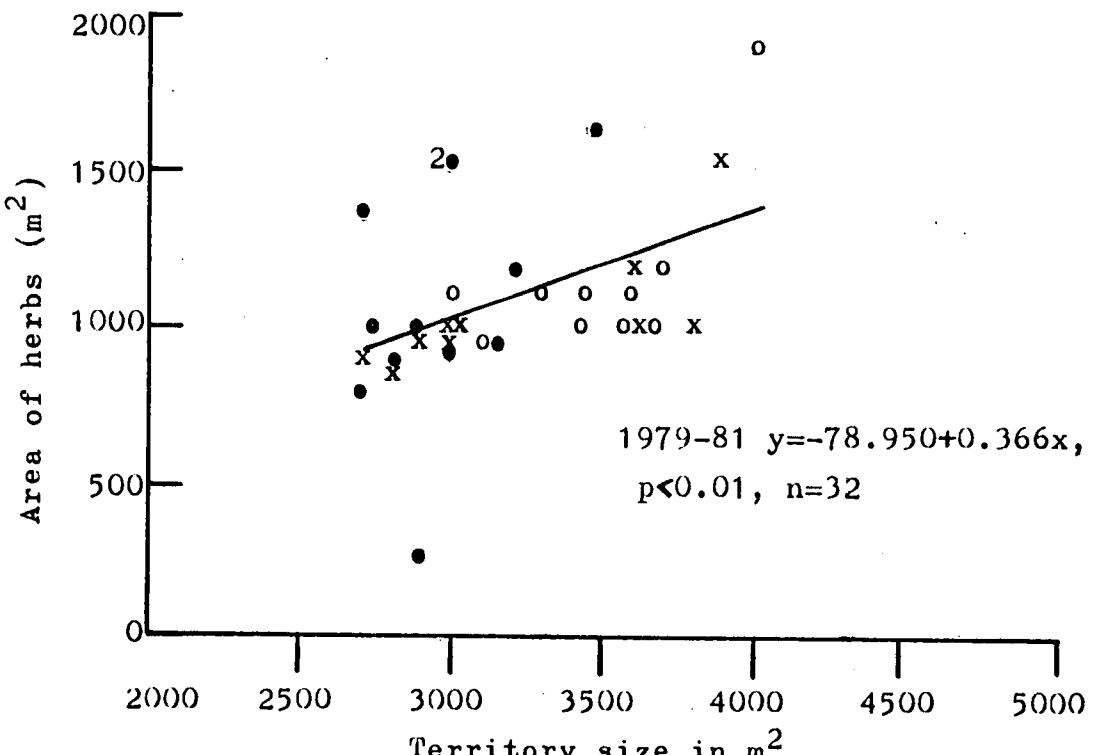
o 1981 y=-109.776+0.353x,NS, n=10

Figure 52 Comparison of territory size and the area of low shrubs and creepers within each Sedge Warbler territory 1979-81.



• 1979 y=1257.192+0.276x, NS, n=12
x 1980 y=25.643+0.164x, NS, n=10
o 1981 y=552.347+0.012x, NS, n=10

Figure 53 Comparison of territory size and the area of herbs within each Sedge Warbler territory 1979-81.

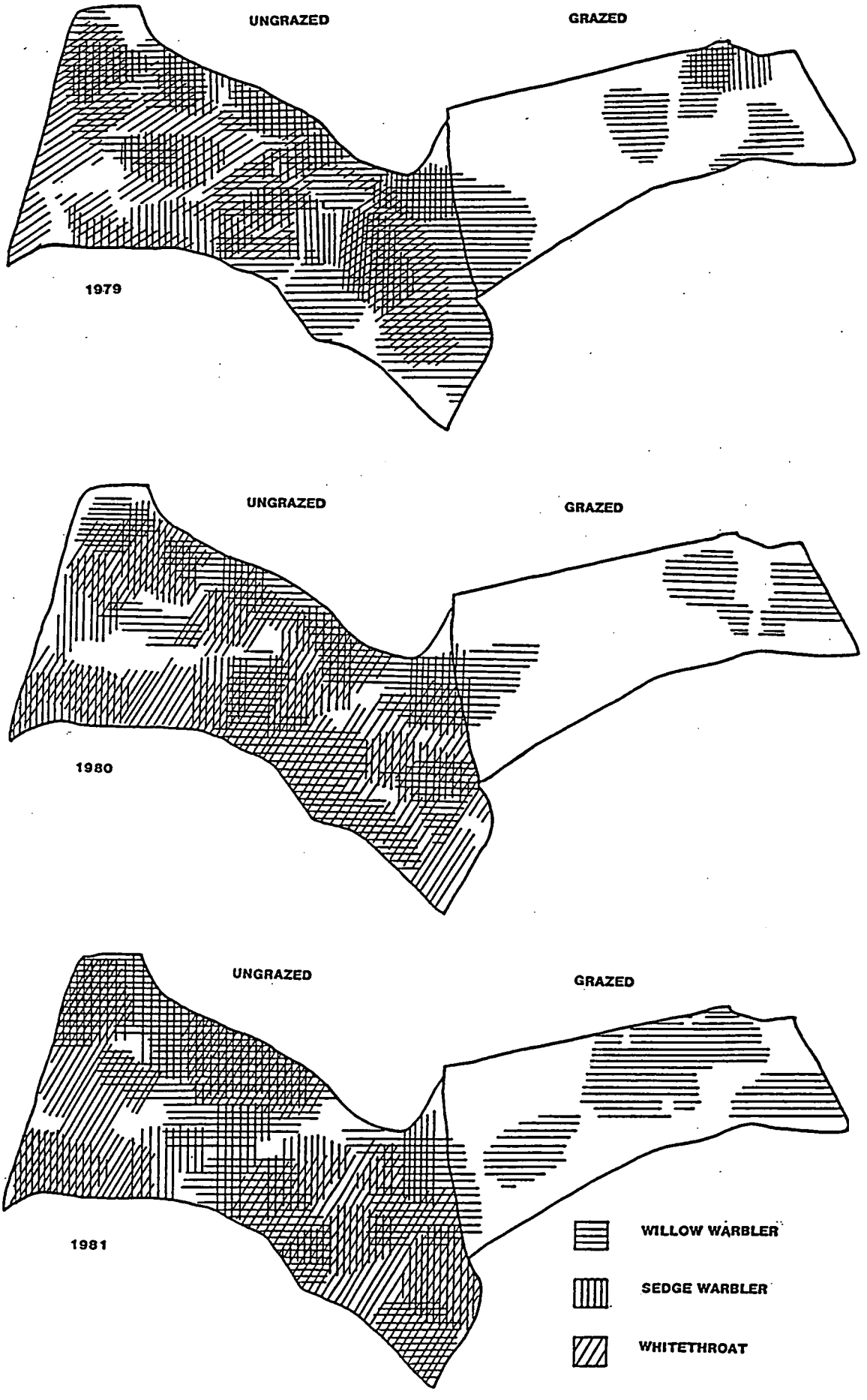


• 1979 y=-1117.384+0.744x, NS, n=12

x 1980 y=-72.046+0.348x, p<0.02, n=10

o 1981 y=-948.968+0.603x, p<0.05, n=10

Figure 54 The areas used as territories by Willow Warblers, Whitethroats and Sedge Warblers in the main study site 1979-81.



grazed area and two areas of thicket, again largely composed of hawthorn. All these areas were characterized by a dense growth of shrubs which, together with the effects of grazing animals, prevented herbs or creepers becoming established. Internally these thickets contained only woody stems and leaf litter. The only area within the grazed section that contained more than one warbler species was a steep bank, which was relatively difficult for animals to reach, and contained bramble, rose and nettle as well as hawthorn. The small areas of nettle (350 m^2 in total) present in the grazed part lay entirely within warbler territories in all three years. These data suggest that the numbers and variety of warblers that a site can support is linked to a diverse vegetation structure and that shrubs and trees alone support many fewer warblers than areas with a well developed field layer.

The ungrazed scrub also held more territories of the five scarcer warbler species.* Table 40 shows that from four to seven males of up to five species held territories in the ungrazed section from 1979-82 whereas at most three males from this group held territory in the grazed section. On three occasions a male Lesser Whitethroat and a male Willow Warbler held territories that overlapped the boundary between the grazed and ungrazed sections.

* These were Grasshopper Warbler Locustella naevia
Lesser Whitethroat Sylvia curruca
Garden Warbler Sylvia horin
Blackcap Sylvia atricapilla
Chiffchaff Phylloscopus collybita

Table 40 Warbler territories 1979-82 for the ungrazed west section and the grazed east section of the main study site.

West section - 5.8 hectares					East section - 4.6 hectares			
1979	1980	1981	1982		1979	1980	1981	1982
2	2	1	0	Grasshopper Warbler	0	0	0	0
11	10	10	10	Sedge Warbler	1	0	0	0
0.5*	0.5*	0.5*	2	Lesser Whitethroat	0.5*	0.5*	0.5*	0
10	9	8	7	Whitethroat	0	0	0	0
1	2	3	1	Garden Warbler	0	1	0	0
0	2	2	3	Blackcap	0	1	1	1
0	0	0	1	Chiffchaff	0	0	0	1
11.5*	11	13.5*	12.5*	Willow Warbler	3.5*	3	5.5*	4.5*
36	36.5	38	36.5	Total	5	5.5	7	6.5

Birds that overlapped the boundary between the west and east sections of the main study site are marked thus *.

6:3 Summary

Willow Warbler territories contained significantly larger areas of trees and tall shrubs than Sedge Warbler territories in three years and Whitethroats in one year. Whitethroat and Sedge Warbler territories contained significantly larger areas of herbs and low shrubs or creepers than those of Willow Warblers in three years. There were no significant differences between Whitethroats and Sedge Warblers in the areas of herbs and low shrubs or creepers within their territories. Whitethroat territories contained significantly larger areas of trees and tall shrubs than Sedge Warbler territories in one year. There were significant correlations in three years between Willow Warbler territory size and the area of trees and tall shrubs within each territory and in one year between territory size and the area of herbs in each territory. With Whitethroats there was a correlation in one year between territory size and the area of trees and tall shrubs within each territory, in one year between territory size and the area of low shrubs or creepers within each territory and in one year between territory size and the area of herbs within each territory. Sedge Warblers showed significant correlations in two years between territory size and the area of herbs within them. Grazed scrub with thickets held many fewer warblers of a reduced range of species than an area of similar size with a complex structure and well developed field layer.

Chapter 7 Warbler distribution in the surrounding countryside

7:1 Methods

All species of warblers were censused in areas around the main study site (Fig.2) to provide information on return rates and dispersal (Ch.4) and on the numbers of warblers in different habitats. The demands of the work in the main study site meant that this work had to be confined to a census of territorial males and limited the amount of data that could be collected on the habitats they occupied.

A considerable literature has developed on bird census methods although most studies have compared different methods, e.g. line transects versus territory mapping, rather than checking census methods against a colour ringed population (see Oelke 1980 for a recent review). It is generally accepted that, even within the passesines, different groups and species differ so markedly in their behaviour that no single method will provide the same degree of census accuracy with all bird species (Svensson 1980). Field trials have shown the mapping method to be superior to others in Scottish woodlands (Moss 1976). The current recommendations of the International Bird Census Committee (1969) are for a form of the mapping method (Enemar 1959) since this method is generally considered the best available, its principal drawback being the time involved. In Britain the BTO now recommend 10 visits between mid March (April in the North) and late June (Marchant 1983). Although this methodology is satifactory for monitoring annual population changes at small sites it can only be applied to larger areas at a considerable cost in time. Early in the course of this study it was noticed that male warblers were relatively easy to census between their arrival and pairing

since they sang vigorously throughout this period (Appendix D1-D3). After pairing song production by males decreased, although no species stopped singing completely as Catchpole (1977) found with Sedge Warblers in marshland in England. Even after pairing it was found that a male warbler would invariably respond to playback of his species' (and sometimes other species) song from a tape recorder, though the exact response varied between individuals. All males approached the tape recorder and sang, but some appeared more confident and aggressive, and the amount and intensity of song, and the distance they approached, varied.

Warbler censusing was carried out between May and early June to cover the period when males were likely to be singing vigorously (see Ch.2 for details of the timing of the breeding seasons). To make sure late arrivals were located, and to prevent transient birds affecting the census results, two visits were made to the census area at least 10 days apart. Most visits were carried out in the morning or evening and the midday-early afternoon period avoided since song was less frequent then (Appendix D1-D3). The procedure was to listen for singing males before and after switching on the tape. The tape was used in brief (usually 15-30 second) bursts to prevent drawing birds out of their territories. Continuous loop cassettes (1-3 minutes duration) were used with songs of all eight warbler species likely to be encountered. In the field tapes of all species at all likely to be found in that habitat were played, although in practice it was found that a brief burst of song triggered off a response both in other warblers and in several other songbirds as well. Tapes were played at least once per 50 metres, which allowed the position of the territorial males to be plotted, since they tended to move around singing in a

limited area provided the tapes were not played incessantly. Birds' positions were plotted on to 1:10560 scale maps with coloured pens; this scale proved easier to handle in the field than the 1:2500 scale normally used in British census work when all bird species are involved. Habitat details were also noted on the maps. Four main categories were used: woodland, farmland, former industrial land and farms and villages. In practice no warblers were found holding territory in the built up areas. These categories were further sub-divided. Farmland habitat was divided into hedgerows, hedges with occasional trees, hedges with more than 50% of their length taken up by trees (tree lines) and shelterbelts. In addition it was noted if the hedge or tree line was between fields, or bordering tracks or roads, and whether it had an adjacent ditch. Former industrial land was classified as ~~disused railway and~~ disused railway and other features e.g. siding or station. The presence of a ditch or stream along the railway was also noted. Disused coal bings were divided into those naturally regenerating and those (one only) which had been landscaped and planted by the local authority. Woodland was not sub divided since the woods censused were all a mixture of mature broadleaved trees, native and exotic conifers of various ages; no woods corresponding to the even aged monocultures which have caused controversy in some upland areas were found.

Before the birds arrived the larger study area was compared with Ordnance Survey maps to check for habitat changes, e.g. hedgerow removal, and changes noted on the maps in the field. Measurements were also taken of hedgerows and other linear features in the field, a minimum of ten measurements at regular intervals along the hedge at ground level being made to allow the mean width to be calaulated. In the case of coal bings, disused railway systems and woods areas were calculated from the maps using a planimeter.

7:2 Warbler distribution in different habitats

The results of the 1982 census of 16.22 km^2 of land around the main study site are shown in Table 41 along with the densities calculated for the main site. The amount of woodland, farmland (including hedges, tree lines and shelterbelts) and former industrial land (principally disused railways and coal bings) are also shown. Although most of the area surveyed was farmland relatively few warblers (6/km^2) occurred there. Many more (197/km^2) held territory in woodland and a considerable number (182/km^2) used the old railways and, to a lesser extent, the bings. The use made by the warblers of these habitats is examined further in Table 42 which shows that two of the hedgerow types contained no warblers at all. There was a marked tendency for warblers to appear on farmland when the hedgerows were larger than average. Only when between field boundaries were supplemented by a ditch or a tree line did they support warblers. Although it might seem that the extra height afforded by the tree line was responsible for the appearance of warblers the width of these boundaries should also be noted. Field hedges with individual trees were only around 0.3 metres wider than other field hedges, but tree lines were much wider, permitting a shrub and herb layer to develop. This was especially marked when a tree line was associated with a ditch. These tree lines usually held Willow Warblers with occasional Blackcaps. Hedges alongside roads and tracks were better than hedges which separated fields. Road and trackside hedges were usually much wider, though this varied considerably, as did their maintenance programme, though roadside hedges were more likely to have a neatly mown verge than hedges along the tracks, which often developed an abundant field layer and outgrowths of bushes and

Table 41 The numbers of warbler territories in 16.217 km^2 of countryside.

	Woodland	Farmland	Former industrial land	Main study site	Total
Area (km^2)	0.613	13.470	1.345	0.104	16.217
Grasshopper Warbler	-	-	2(1)	-	2(<0.5)
Sedge Warbler	9(15)	18(1)	56(42)	10(96)	93(6)
Lesser Whitethroat	-	2(<0.5)	9(7)	2(19)	13(<1)
Whitethroat	4(6)	24(2)	35(26)	7(67)	70(4)
Garden Warbler	8(13)	2(<0.5)	8(6)	1(10)	19(1)
Blackcap	11(18)	3(<0.5)	7(5)	4(38)	25(1)
Chiffchaff	1(2)	1(<0.5)	-	2(19)	4(<0.5)
Willow Warbler	88(143)	30(2)	128(95)	17(163)	263(16)
All Species	121(197)	80(6)	245(182)	43(413)	489(30)

Figures in parentheses show the density per km^2.
No warblers were found in 0.685 km^2 of built up land.

Table 42 The numbers of warblers in different habitats in 1982.

	Length (metres)	width	area (km^2)	warbler nos.	density/ km^2	Number of species
Mixed woodland						
1			0.104	30	288	6
2			0.055	11	200	4
3			0.063	15	238	4
4			0.391	65	166	6
Main study site scrub-grazed			0.046	6.5	141	7
Main study site scrub-ungrazed			0.058	36.5	629	3
Hedges tree lines and shelter belts						
Field hedge	7790	2.6	0.020	0	0	0
Field hedge plus ditch	1550	4.9	0.008	1	132	1
Field hedge with scattered trees	2510	2.9	0.007	0	0	0
Field tree line	2310	8.6	0.020	3	150	2
Field tree line plus ditch	3000	12.3	0.037	5	135	2
Farm track+hedge	8430	12.5	0.105	18	171	3
Farm track+hedge plus ditch	1725	12.0	0.021	4	193	2
Roadside hedge	7370	3.5	0.026	1	39	1
Roadside tree line	5210	17.8	0.093	14	151	3
Young shelter belt			0.038	15	395	5
Mature shelter belt			0.043	13	302	4
Scrub in field (grazed)			0.059	6	102	3
Derelict land						
Disused railway line			0.441	65	147	6
Disused railway line and stream			0.215	41	191	6
Disused railway line and sidings/bing			0.186	49	263	6
Regenerating coal bing			0.285	57	200	5
Planted coal bing			0.086	24	279	5
Disused quarry			0.132	9	68	3

creepers. Roadside tree lines held warblers at similar densities to field tree lines.

Although tree lines held warblers at densities of up to 150 per km^2 they were relatively poor in species. Only a few sections of hedgerow or tree lines held more than two species of warbler and the majority held one or none. Shelterbelts were rather more diverse; of the four examined one held two, two held four and one held five species of warbler. All shelterbelts and woodlands held warblers at densities of 166 or more per km^2, probably because all contained a variety of tree species and areas of shrubs and herbs. Species diversity was higher in woods than on farmland except for some shelterbelts since all woods held at least four species of warbler.

Some sections of the old railways and bings held very high numbers of warblers but overall they had lower densities than the woods. This was largely due to the amount of unsuitable habitat they contained. Some of the coal bings and the tracks of the old railways had either not yet been colonized by vegetation, or held a low growth of grasses and other plants which were unattractive to most birds, including warblers. With the railways former sidings and stations held more warblers than stretches of line because there was less space at the sides of the former track for scrub to develop.

7:3 Summary

Warbler territory density on farmland was 6/km^2 compared to 182/km^2 on former industrial land, 197/km^2 in mixed woodland and 629/km^2 in ungrazed scrub in the main study site. On farmland only shelterbelts, areas of scrub and larger than average hedges and treelines held warblers.

Chapter 8 Discussion

8:1 Introduction

All the warblers that breed in Scotland are long distance migrants. Most species, including Willow Warblers, Whitethroats and Sedge Warblers, winter in tropical Africa south of the Sahara Desert, although some Chiffchaffs and Blackcaps may winter around the Mediterranean (Zink 1973). This strategy has evolved relatively recently as changes in climate have allowed many species of insectivorous birds to colonize northern Europe, but created an increasingly wide desert barrier which must be overflown twice each year if the birds are to combine the advantages of reduced competition and temporarily abundant food in the breeding season with freedom from the effects of winter cold (Moreau 1972). Clearly the long distances involved, which include a minimum of 1500 kms of desert and a variable amount of open sea, depending on the birds' routes, impose a considerable strain on species which, unlike Swifts, Apus apus, and hirundines, do not fly for long distances, except when on migration. At least three factors are likely to affect migrant warblers: weather conditions during the journey, their ability to build up sufficient reserves for the flight and the condition of their plumage which could affect flying efficiency. In addition the timing of migration is likely to be linked to seasonal variations in the food supply in both the breeding and wintering areas.

Although this study has concentrated on the biology and ecology of warblers in a breeding site the results obtained can only be properly discussed in the light of these other important factors in the birds' lives.

8:2 The timing of arrivals.

There is experimental evidence that the timing of migration in warblers is endogenously controlled by circannual rhythms, which naturally are of less than a calendar year's duration, but subject to modification by environmental factors such as changing day length (see reviews by Gwinner 1981 and Berthold 1984). This means that birds will leave Africa around the same time each year, although their passage northwards is liable to disruption by the weather they encounter en route. The numbers of northbound migrants seen in spring in Morocco (Smith 1968) and southern Spain (Nisbet, Evans & Feeny 1961) seems to vary according to weather conditions, while further north radar evidence (Parslow 1969) has shown that in April and May the movement of small passerines migrating into and through southern England is affected by precipitation, cloud cover, temperature and the speed and direction of the wind.

In this study several birds often arrived in the main study site at the same time, whereas on other days no new arrivals were recorded, suggesting that they had moved north in waves in response to the weather conditions they encountered en route to the site. Certain weather conditions, notably combinations of strong northerly winds and below average temperatures, were associated with periods when warblers were unlikely to arrive on the site, although it is stressed that a full account of the effect of weather on the birds' spring migration is outwith the scope of this study as it necessarily requires weather data from a series of stations to the south of the study site, ideally supplemented by radar observations of migrating birds. There was some evidence from this study that weather conditions became less inhibiting to migrants later in the spring. For example some Willow Warblers arrived in May when maximum

daily temperatures failed to reach 10°C, although none had arrived during similar conditions in April. Such a pattern might be explained by the urgency of individual birds to reach a breeding site around the time of year dictated by an internal "clock" (Gwinner and Berthold, ops.cit.). Birds which arrived earlier than average did so during particularly favourable weather conditions, as when an anticyclone gave light winds and above average temperatures, or during southerly or south westerly airflows.

With the exceptions of Whitethroats and Sedge Warblers in 1981 there were significant differences in the mean arrival dates of males and females of all three species. Since males all acquired territories before they acquired mates, it seems reasonable to conclude that the purpose of early arrival by males is to secure a territory, especially since it has been shown that in several species of birds (and other animals) territory holders are usually successful in disputes with later incomers (Davies 1978). However, in this study a three year old Willow Warbler was able to displace a one year old male holding territory for the first time. If this pattern is at all common it means that older birds would not necessarily find it advantageous to arrive significantly earlier than one year olds, as recorded with Reed and Sedge Warblers in reed beds in England (Catchpole 1972). In this study some at least of the earliest males to arrive on the site were one year old birds. It may be that some inexperienced birds are more likely to arrive early, either in response to temporarily favourable conditions for migration, or because these individuals are genetically predisposed to migrate before the rest of the population. Such genetic variation could be advantageous when climatic changes result in early springs on the breeding grounds, but obviously are likely to lead to the deaths of the individuals

concerned if they encounter severe weather.

Invertebrate prey was found to be in short supply in April and there is a considerable risk of frost and spells of cold, northerly weather in Scotland at this time. An example of this occurred in April 1981 when a late blizzard covered the study site in snow after several male Willow Warblers had arrived. None of the colour ringed birds died, probably because temperatures soon rose again and the snow melted. Insectivorous migrants have been recorded dying when they encountered unfavourable weather in Morocco in April immediately after crossing the Sahara (Ash 1969).

8:3 The timing of breeding

In a Norwegian study Jarvi (1983) found that older male Willow Warblers did not always arrive earlier than one year olds, but they did tend to breed earlier, since females that had bred before mated with the older males which were identifiable by their more complex songs. Harvey, Greenwood & Campbell (1984) found that in Pied Flycatchers, Ficedula hypoleuca, breeding in England only pairs where both partners had bred in a previous year were able to breed earlier than combinations involving one year old birds. Unfortunately, in this study too few combinations of birds of known age were available to test the effect of age on the date of laying.

When three years data were combined there were significant declines in clutch size the later the clutches were started in all three warbler species; these relationships were not always significant when each year was examined separately and sample sizes necessarily were reduced. In the case of Whitethroats the weights of nestlings from later broods were significantly lower than nestlings from earlier broods. Similar relationships have been found in other studies. Using nest record cards Bibby (1978), Cramp (1955) and Mason (1976) all found that clutch size in Sedge Warblers, Willow Warblers and Whitethroats was reduced in late clutches. Nest record cards are likely to be biased against late nests, as these are likely to be better hidden by growing vegetation than earlier nests (Newton 1964), and it is possible that these late nests are more productive if predators find a lower proportion of them than more exposed, earlier nests. In this study intensive fieldwork meant that the outcome of all breeding attempts in the main study site were known and later nests were not significantly more successful than other nests.

Studies of other insectivorous British passerines, notably

tits, Paridae, over much longer time periods than in this study, have demonstrated that late clutches usually have fewer eggs, produce fewer young, which are often below average weight, and have below average survival rates (Perrins 1970 and 1979). In this study it was not possible to compare survival rates over the winter for warblers from different nests since so few nestlings were recorded in later years.

Perrins (1970) has suggested that scarcity of food early in the breeding season prevents some females in a variety of species from starting their clutches as early as other birds of the same species, since their physical reserves are inadequate for egg production.

Prior to egg laying female warblers must obtain enough food to form up to seven eggs in the case of Willow Warblers and up to six eggs in Whitethroats and Sedge Warblers. Since females do not stop feeding when egg laying starts and eggs are normally laid at 24 hourly intervals, the increase in a hen's body weight during egg formation is never as great as the weight of her full clutch. Even so females in this study weighed when feeding young (and therefore probably near to their lean weights) were around 17% lighter than females weighed during egg laying in the case of Whitethroats, 22% lighter in the case of Sedge Warblers and 21% lighter in the case of Willow Warblers. Clearly the females' food intake must rise during egg formation and the hens that were watched throughout a day prior to egg laying all spent significantly more time feeding than their mates.

Egg formation requires protein, which is probably not a problem for an insectivorous bird provided she can obtain enough invertebrates; in Great Tits the increase in the female's food intake during egg formation has been calculated at 40% (Perrins 1979). In this study

females of all species varied considerably in the time spent between arrival on the site and the commencement of egg laying, suggesting that some hens could not obtain sufficient food to form eggs as well as maintain themselves. Some Whitethroats and Willow Warblers started laying from two to six days after arrival in the main study site. These females had above average weights compared to the arrival weights of other females, indicating that in these hens ovulation had started as soon as they reached the site or even before that. A similar situation has been described in tropical Africa where Red-billed Quelea, Quelea quelea, were able to start laying at most four days after arrival at a breeding colony, indicating that yolk deposition had commenced well before pairing, which took place in the colony (Jones & Ward 1976).

It is not known why some females arrived in the study site apparently in better condition (as evidenced by weights) than others. Such females were not noticeably later than the others which would be the case if they were birds that had spent time feeding at nearby sites before moving into the main study site. It may simply be that some birds were in better condition after spring migration, which is usually more demanding than in autumn due to head winds (Moreau 1961), than others, possibly because they encountered more favourable weather conditions on the journey.

The stimulus to initiate ovulation could be provided by environmental factors, such as changing day length, possibly supplemented by the effect of male birds singing and displaying at sites that the females used as temporary stop-overs on their way north. In at least one species, the Ruff, Philomachus pugnax, mating is thought to take place on migration when some females are over a thousand kilometres from their likely nesting grounds

(van Rhijn 1983). However Ruffs have a very different breeding system compared to warblers and, since fertilization takes place approximately 24 hours before an egg is laid (Follett & Goldsmith 1985), a male that paired with a female that started laying even two days after arrival in his territory could still be the father of her chicks.

Examination of individual territories in relation to the timing and outcome of breeding attempts proved inconclusive although the effects of predation could have masked the influence of territory quality.

8:4 Feeding behaviour, prey selection and nest sites

Willow Warblers, Whitethroats and Sedge Warblers all fed different proportions of prey items to their young than they ate themselves, probably because the energetics of collecting and carrying small items, such as aphids, to the nest are less favourable than for larger items such as caterpillars (Royama 1970). Caterpillars formed around 70% of the prey items given to nestling Willow Warblers in early June and just under 40% of the prey given to nestling Whitethroats at the same time. However caterpillar biomass peaked in late May and early June, when only the earliest Willow Warblers and Whitethroats had young in the nest, and later broods of all species made increasing use of other prey items such as flies, beetles and plant bugs which were usually smaller and may have required more effort to catch.

Although it might seem advantageous for warblers to lay earlier, to ensure that their young were in the nest during the peak in caterpillar abundance, they probably could not do so due to the scarcity of invertebrates in April, when warblers exploited plants such as gorse, which are of minor importance later in the season, but a useful source of spiders and beetles before deciduous species have leafed out. It seems noteworthy that gorse is particularly important to resident Dartford Warblers in early spring in southern England (Bibby 1977).

Caterpillars declined after early June. This was the principal cause of the drop in biomass in trees and tall shrubs since the increase in the numbers of aphids and flies, which occurred in summer, could not compensate for the loss of the larger caterpillars. However biomass increased in nettle and willowherb during the summer. Some of this was due to caterpillars but these were outweighed by beetles, flies and bugs which were more numerous in the herb layer in summer than in trees or bushes. This seasonal pattern in invertebrate

abundance is linked to the growing seasons of the dirferent plant species (Clapham, Tutin & Warburg 1968) since young growth is much more attractive to phytophagous invertebrates than mature foliage, which is less nutritious, and may contain toxic substances (Dixon 1973), though in some plant species senescence is also accompanied by an increase in invertebrates such as aphids. All three species of warblers showed seasonal variation in their use of different vegetation types in parallel with changes in invertebrate biomass. However there were important interspecific differences in feeding methods, prey selection and the proportion of time spent in different vegetation types, which allowed the three species to co-exist in parts of the main study site where their territories overlapped.

Willow Warblers belong to a genus most of whose members show adaptations (in wing and tail shape and proportions and tarsus length) to arboreal feeding (Gaston 1974). In this study Willow Warblers spent a higher proportion of time feeding in trees and tall shrubs than the other species. Some tree species, such as birch, were only used by Willow Warblers. Willow Warbler territories usually contained more trees and tall shrubs than the other species. In all three years there were significant relationships between the size of Willow Warbler territories and the area of trees and tall shrubs within them.

Willow Warblers' most frequent feeding method was stand pecking, which allowed them to pick caterpillars and aphids from leaves, especially their undersides. Willow Warblers spent more time flycatching than the other species; this technique is particularly suited to a bird feeding in the outermost branches of a tree or large bush. Willow Warblers ate more Diptera, Hemiptera and Lepidoptera larvae than the other species. They fed a much higher proportion of Lepidoptera larvae to their young than the others; even when

Whitethroats were in nest at the same time as Willow Warblers they received a lower proportion of caterpillars.

Willow Warblers arrived in the site earlier in spring than the other warblers and usually started nesting before them. Most Willow Warblers' nests were built on the ground, typically in a grassy bank with an open aspect. This meant the birds were not dependent on growing vegetation providing supports for the nest; in the other species nests were built above ground level, either in growing herbs, or in bushes through which herbs grew up. Willow Warblers were also the smallest of the three species and might find it easier to obtain their food requirements early in spring than the larger Whitethroats and Sedge Warblers; Perrins (1979) has described how in the Parus tits the smaller species begin breeding before the larger ones, apparently for this reason.

Sedge Warblers belong to a group of warblers which are adapted (notably in the structure of their legs and feet, and the relative proportions and shape of their wings and tails) to feeding in tall, herbaceous vegetation (Leisler 1975). Many Acrocephalus warblers breed in reed beds. Although Sedge Warblers often breed in habitats where reeds are absent, as in this study, they move into reeds on migration (Bibby & Green 1981) and in Africa in winter (Pearson, Backhurst & Backhurst 1979).

Sedge Warblers used climb pecking more than the other species, typically when taking prey from the stems and leaves of nettle and willowherb. Sedge Warblers spent even more time hop pecking and stand pecking. However climb pecking is an inappropriate technique when feeding in bushes (Sedge Warblers never fed in trees) which Sedge Warblers had to do in spring. Sedge Warblers spent less time hop pecking than Whitethroats and less time stand pecking than

Willow Warblers; they spent little time using such active techniques as flycatching or leap catching. Sedge Warblers spent more time feeding in nettle and willowherb than Willow Warblers. They made slightly more use of these plants than Whitethroats. They took more beetles, but fewer caterpillars and flies, than Whitethroats or Willow Warblers and fewer plant bugs than Whitethroats. Comparison of the rate at which Sedge Warblers and Whitethroats caught prey hop pecking (their most frequently used technique) showed that Sedge Warblers were slower. In general Sedge Warblers used less active techniques than the other species and took a lower proportion of active prey such as flies.

Sedge Warbler territories showed relationships with the area of herbs within each territory in two out of three years. The lack of a stronger relationship could be due to the relatively crude measuring technique, which did not take volume into account, but could also reflect the fact that both Sedge Warblers and Whitethroats made most use of nettle and willowherb later in the season when territorial boundaries broke down as the nestlings fledged.

Sedge Warblers were usually the last species to arrive on the site and started laying significantly later than the other species in all three years. Their nests were usually built higher above ground than Whitethroats. This may have been a factor in the timing of breeding, but it is more likely that Sedge Warblers had to adopt feeding methods and situations in spring to which they were not as well adapted as the other warbler species in the study site.

Whitethroats and the other Sylvia warblers of temperate Europe have been described as "secondarily generalized" insectivorous birds (Voous 1977), able to exploit a variety of scrub habitats. In this study there were some relationships between the territory sizes of Whitethroats and the areas of all three major vegetation groups.

Whitethroats used hop pecking, a fairly active technique which involved snatching prey as the bird moved through vegetation, more than the other species, but made less use of more specialized techniques such as flycatching or climb pecking. Whitethroats took fewer Lepidoptera, Diptera and Hemiptera than Willow Warblers and fewer Coleoptera than Sedge Warblers. Whitethroat territories contained similar areas of herbs and low shrubs to Sedge Warbler territories but significantly larger areas of herbs and low shrubs than Willow Warbler territories. In one year Whitethroat territories contained more tall shrubs than Sedge Warblers.

The timing of breeding in Whitethroats was significantly later than Willow Warblers in two years and significantly earlier than Sedge Warblers in all three years. Whitethroats required stands of herbs or herb/shrub mixtures for their nest sites. Like Sedge Warblers Whitethroats made increasing use of the herb layer for feeding as the season progressed. They appeared to be more efficient than Sedge Warblers when feeding in bushes, which may explain why they were able to start breeding earlier.

If relationships exist between territory size and the areas of vegetation known to be used by feeding birds, then it would be reasonable to expect that large territories would be particularly sought after, and produce more young, either due to a better food supply or because older and more experienced males held such territories. Such links were not established in this study. No territories consistently produced more young than others though the effect of predation may have masked the influence of territory quality. Returning adults did not always return to the same territory, although changes in boundaries from year to year meant that it was often difficult to decide what constituted a change in territory as opposed to a readjustment.

The high density of breeding birds in the main study site, and the fact that adults were known to have been recruited into the breeding population, suggest that the site as a whole (with the exception of some grazed areas) was particularly attractive to breeding warblers. Comparisons of territory size and structure between the main study site and other sites might have been more revealing if time had allowed them to be made.

It should also be stressed that the principal function of territory in songbirds may not be to provide a feeding area, although in this study birds fed almost exclusively within their territories during incubation and when young were in the nest. Other studies of Sedge Warblers have shown that they sometimes feed extensively outwith territorial boundaries, although these data were obtained from a waterside habitat with an abundant food supply in a narrow strip of vegetation along the waters edge (Catchpole 1972). The main function of territory appears to be to space out breeding pairs, which may reduce the risk of predation and interference by other birds (Perrins 1979), although the fact that insectivorous species tend to defend individual territories, whereas seed eaters often form loose colonies, indicate that food supply has some relationship with territory formation (Newton 1972).

8:5 The number of breeding attempts in a season

Few birds in this study were involved in second broods and those that were changed mates. One advantage of such a strategy over conventional double brooding is a saving in time since second broods could be started while the first brood young were still being fed by one of the original pair. The polygamous male Willow Warbler in this study was involved in five breeding attempts in two years. The first egg dates of the females involved ranged from three to 25 days apart; even the highest of these figures is around five days less than the minimum likely interval between first egg dates for a hen involved in conventional double brooding.

It has been suggested that polygamy in Willow Warblers occurs when the male can "deceive" the second female into thinking he is unmated, either by holding two territories which are not adjacent, or by mating with a second hen once the first is committed to breeding (Lawn 1982). In this study no warbler held more than one territory, probably because competition was too intense. Two of the female Willow Warblers that mated with a polygamous male built nests eight metres apart, and began laying within three days of each other, suggesting they were aware of each other's presence early in the breeding cycle. The male concerned was the largest Willow Warbler in the study area and there is some evidence from Finland that larger males hold better quality territories than smaller birds (Tiainen 1983). The extent and causes of polygamy in Phylloscopus warblers seems to vary considerably with habitat and the density of the birds. Temrin, Mallner & Winden (1984) found that up to 40% of Wood Warblers were polygamous in a study area where the birds occurred at relatively low densities and the males were able to defend more than one territory.

This study suggests that references to double brooding by c.25% of

Willow Warbler populations (Brock 1910, May 1949) may have included instances where birds changed mates, although in many cases polygamy would be more likely to be confused with the nesting attempts of different pairs depending on the time interval between the laying dates of the hens and the positions of their nests. Possible bigamy by Willow Warblers was suspected by Howard (1907-14) and Hartley (1934) and the lack of records of this behaviour may simply reflect the lack of studies on colour marked birds.

In this study the output of fledglings per breeding adult was higher in male Willow Warblers and Whitethroats than in females, though not significantly so. This might not be the case if larger samples could be examined to determine whether males that mated with more than one hen in a breeding season produced more recruits to the breeding population than other males.

British Whitethroats are said to rear two broods frequently (Campbell & Ferguson - Lees 1972), although analysis of B.T.O. nest record cards showed a single egg laying peak in May followed by a steady decline in the number of clutches started later in the season (Mason 1976). In this study five male and three female Whitethroats changed mates and bred for a second time. One of the females took 60 days between starting her two clutches, the other two took 36 days. All successfully fledged young from their first nests. Three of the males had time intervals of less than 36 days between the laying dates of their two hens, but two of those males had lost their first clutches to predators. It seems that only a minority of Whitethroats in the study site were prepared to embark on a second breeding attempt from 1979-1981. Some of these attempts could easily have been confused with genuine double brooding if the birds had been unmarked. MacDonald (1979) thought that c 25% of a small population of Whitethroats in Sutherland reared two

broods per year. As the birds were unmarked it is not known if mate changing occurred. MacDonald's observations included the years 1975 and 1976 when the summers were warmer and drier than average. Smith (1984) recorded nine out of 19 territorial males that were colour ringed in a study area in Aberdeenshire making second nesting attempts. Three males definitely bred again with their first partners and one pair reared three broods. These observations were made in an exceptionally warm, dry summer (although weather until June was wetter) and suggest that the proportion of Whitethroats that attempt to rear more than one brood is influenced by weather conditions, especially around the time that first broods are fledging. Unfortunately none of the years when this study was carried out had a warm, dry summer.

In this study no Sedge Warblers attempted to rear more than one brood. Analysis of nest record cards, most of which were from southern England, showed that most Sedge Warblers started their clutches in May, although the analyst (Bibby 1978) speculated that later breeding attempts might be under recorded. In this study Sedge Warblers did not begin laying until June (apart from one bird on 31st May), and adults began leaving the site in July, which suggests that Sedge Warblers in Scotland are even less likely to rear two broods than further south.

In this study only Sedge Warblers laid replacement clutches following egg predation. Female Willow Warblers and Whitethroats that lost eggs, and females of all three species that lost chicks, abandoned their territories. Such behaviour could have survival value since the chief predators were mammals, especially weasels, which have been shown to prey more heavily on small birds when the latter nest at high densities (Dunn 1977). Elsewhere female Willow Warblers have been known to replace clutches; Nilsson (1983) found

that 11 out of 18 hens that lost clutches to predators relaid after choosing new nest sites, but none of the birds that lost chicks tried to breed again. Lawn (1982) recorded some female Willow Warblers laying replacement clutches in an area where density was much lower than in this study and territory sizes were rather larger. It could be that a bird's decision whether to try to breed again on the same territory, or to move elsewhere, is related to the amount of available habitat nearby and the number of birds that occupy it.

Females that abandoned a territory after predation would be likely candidates for polygamy, since the time available to them for breeding would be reduced and their priority would probably be to mate again as quickly as possible.

8:6 Mortality and return rates

Mortality of the breeding adults was remarkably low. Two female Whitethroats were probably killed on the nest by mammals. Sparrowhawks were an occasional danger to birds in mist nets and on one occasion a Sparrowhawk took a Sedge Warbler from a ringer's hand (da Prato 1977) in the study area in a year prior to this study. Tiainen (1982) has suggested that warblers are relatively free from predation by hawks and owls due to their small body size. However Sparrowhawks' prey varies according to what is available to them and small birds such as tits and warblers are often killed by Sparrowhawks in woodland in south west Scotland (Newton in Brown, 1976). Sparrowhawks did not nest in the main study site and seemed to be at low densities in the surrounding countryside, which was largely devoted to intensive cereal production.

The return rates of adult Willow Warblers found in this study (37-57% for males; 35-54% for females) are as high as found anywhere. Tiainen (1983) found that 41% of males, but only 17% of females, returned on average to his study area in Finland while Lawn (1982) found that around 38% of both sexes returned to a site in Surrey. This suggests that few of the males, at least, had gone elsewhere and the missing birds were probably dead. Analysis of British ringing recoveries of Willow Warblers (Norman in prep.) indicates that adults tend to return to sites at most within a few kilometres of their previous breeding site. The situation with young Willow Warblers is probably different, since the return rate of 5% of birds ringed as juveniles to the larger study area was too low to maintain the population, and there is no evidence of decline in Willow Warbler populations either locally or nationally. A first winter survival rate of around 30% for males and 35% for females would maintain the population. Other

studies of breeding Willow Warblers have produced known return rates for birds ringed in the nest or soon after fledging of under 10% (Lawn 1982, Tiainen 1983). The highest recorded return rate for juvenile warblers of any species in Britain appears to be 24% for Reed Warblers (Long 1975), although this figure is really an estimate rather than the actual percentage of marked birds that definitely returned to a study site, and Reed Warblers are rather different to the species in this study as they tend to live longer and make more than one breeding attempt per year. In Great Tits 22% of the young that fledge survive their first winter (Perrins 1979) although the number of fledglings per pair (4.8) is higher than with any of the three warbler species in this study.

The maximum age recorded for a Willow Warbler ringed in Britain is six years seven months (B.T.O. data). In this study the oldest males were at least five years old and the oldest females at least four years old. Theoretical maximum ages calculated from known return rates were eight for males and seven for females. In this study 58% of all eggs laid produced fledged young, an identical figure to that calculated from nest record cards (Cramp 1955).

In this study the number of young Whitethroats fledged per male over three years ranged from 2.8 to 4.0 and per female from 2.5 to 4.0. Overall 66% of eggs produced young birds that fledged successfully. Nest record card analysis (Mason 1976) gave rather lower figures of 2.7 young fledged per nest and 57% of eggs producing fledged young. However the return rate of adult Whitethroats to the main study site was such that, even if the fledglings had the same return rate as the older birds, the population could not be maintained. In fact only 1.5% of Whitethroats ringed as nestlings or as juveniles returned to the larger study area. The maximum age

recorded for a British ringed Whitethroat is seven years and six months (B.T.O.data) while in this study one male was at least seven years old, although the oldest females were only at least three years old. Theoretical maximum ages calculated from the return rates of adults were five years for males and four years for females. This suggests that the return rates, especially for males, may be lower than the true survival rate. Output of young per adult may be higher in some summers than in 1979-81 if different weather conditions encourage a higher proportion of birds to try to rear more than one brood. Analysis of the recoveries of Whitethroats ringed in Britain and recovered in a later year between April and September showed that over 60% were found within 5 km. of their ringing sites and a further 22% within 25 km. of the original ringing site (da Prato & da Prato 1983). Some of these recoveries could refer to birds that were still on migration. These data do not suggest that Whitethroats make large scale changes of breeding sites from year to year, although if some birds move distances of several kilometres they could have returned, unnoticed, to sites outwith the larger study area that was censused each spring. Whitethroats are known to have declined throughout western Europe since 1969 due to the effects of drought in the Sahel zone in tropical Africa (Winstanley, Spencer & Williamson, 1974), although the period when this study was carried out was not one when the national Common Bird Census recorded large decreases in the British population. The decline has continued into the 1980's (B.T.O. data).

Sedge Warblers have been found to have low return rates to breeding sites in several studies (Catchpole 1972, Bibby 1978). Bibby (1978) suggested that most pairs of Sedge Warblers must make a second breeding attempt if their first nest failed and that a

higher proportion reared two broods than he actually found in his analysis of nest record cards. These assumptions led to an estimate of 4.8 young reared per pair in England, which is well above the 3.2 per pair found over three years in this study. The overall success rate of eggs in this study was 56% which is the same as that found from nest record cards and similar to the 54% found by Catchpole (1972) in a study of colour ringed birds in the English midlands. The maximum age recorded for a British ringed Sedge Warbler is six years one month (B.T.O. data). In this study two males were at least six years old and one female was at least three years old. Theoretical maximum ages calculated from return rates were four years, which does suggest that the known return rates were below the true survival rates. One female ringed as a transient in the main study site was found breeding 26 km. away in a later summer. As with Whitethroats the known return rates of adults and juveniles to the larger study area were inadequate to maintain the population. Since Sedge Warblers have also been affected by droughts in West Africa (Winstanley, Spencer & Williamson, 1974 and Common Bird Census data) the evidence for decline found in this study may genuinely reflect what is happening in the population as a whole.

8:7 Moult and the timing of departures

The fact that so few warblers tried to rear more than one brood strongly suggests that time is a limiting factor for these birds in south east Scotland. Further evidence for this comes from the fact that late broods of all three species spent less time in the study site after leaving the nest than young from earlier broods. Adult Whitethroats and Sedge Warblers also showed relationships between the fledging dates of their young and the time the adults remained in the site once their young could fly. This relationship only applied to male Willow Warblers in one year.

Some Willow Warblers started to moult before their young had fledged and some left the study area before moult was complete. Overlap between breeding and moulting has also been recorded in Willow Warblers in Finland (Tiainen 1981). The duration of Willow Warbler moult found in this study (38-45 days) was similar to estimates made in southern Finland (Lehikoinen and Niemela 1977) and Lapland (Evans 1971) but shorter than captive birds in central Europe which took around 50 days to moult(Gwinner 1973). All the breeding Whitethroats left the main study site well before moult completion. Some Willow Warblers and Whitethroats migrating through Crete in autumn were found to be in arrested moult, especially of the secondaries (Swann & Baillie 1979). These authors suggested this was due to the shorter season available to warblers breeding in eastern Europe and the U.S.S.R. causing them to commence migration when only some wing feathers had been replaced. Up to 40% of Whitethroats, and a few Willow Warblers, have been found with a mixture of old and new remiges in different parts of the Iberian peninsula in autumn (Pimm 1973 , Mead & Watmough 1976) suggesting that some birds from north west Europe start migration

before they have completed moult. Adult Sedge Warblers do not moult until they reach tropical Africa. It seems superficially surprising that Whitethroats and Willow Warblers do not delay moulting until they reach the tropics, where Palearctic warblers can moult much more slowly than in summer in Europe (Pearson 1973). This would mean that their plumage would be in better condition for the flight north in spring, when the prevailing winds tend to be unfavourable (Moreau 1961). Willow Warblers moult again in Africa (Williamson 1974) but this two moult per year strategy is exceptional among passerines and there is evidence that some British birds do not moult in their first winter in the tropics (Ginn & Melville 1983). The timing of moult seems to be linked to the birds' destinations in Africa with those species, or populations, that move furthest south most likely to delay moult until they reach the tropics (Pearson 1973).

Some juveniles of all three species had left the main study site before they could have completed post juvenile moult. There was evidence for local movements of up to 3.5 km. for young Willow Warblers and c.1 km. for the other species. Many juvenile warblers visited the main study site although they had not been reared there. Colour marking samples of these birds indicated a rapid turnover among them. Such movements probably serve to acquaint young birds with potential breeding sites to which they can return in later years (Lohrl 1959, Catchpole 1974). In all three species birds ringed as wandering juveniles in the main study site returned to breed there in a later year. Four Willow Warblers and one Sedge Warbler ringed as nestlings in the main study site were found at sites up to 3.5 kms. away in later years. Norman (1981) found that juvenile Willow Warblers in

north east England were involved in local movements before post juvenile moult was complete. In this study young warblers were often seen with other species in loose, mixed flocks. In 1980 14 such flocks were recorded with Willow Warblers and Blue Tits, Parus caeruleus, the most frequent constituents; this flocking habit may help the birds detect predators (da Prato 1981). With Willow Warblers there is evidence from ringing recoveries that young birds do not initiate long distance migration, as opposed to local, wandering movements, until post juvenile moult is complete at around 55-60 days old (Norman & Norman 1985).

Birds prepare for long distance migration by laying down energy reserves in the form of fat (see Berthold 1975 for a review). Although the weight of a live bird in late summer is not an absolute guide to the presence or absence of fat due to physiological changes connected with moult (Newton 1968, Baggott 1975) the amount of fat needed for a warbler to fly directly from a breeding area in NW Europe to tropical Africa would be very obvious when the bird was examined.

In this study all the Willow Warblers, Whitethroats and Sedge Warblers that bred in the main study site left it before the end of August, as did their progeny. Relatively few warblers were recorded in late August and only a very few juvenile Willow Warblers and Whitethroats (and occasional Chiffchaffs and Blackcaps) of unknown origin were recorded in the first week of September. None of these birds showed any evidence of significant weight gains. A few Sedge Warblers caught in reed beds on the river Tay between July and September showed evidence of weight gains (McMillan, 1978) but to a considerably smaller extent than birds caught on the south coast of England (Bibby,

Green, Pepler & Pepler 1976). Evans (1966), who compared radar evidence with observations of migrants on the Northumberland coast in autumn, considered that local breeding populations of Sedge Warblers and Willow Warblers probably left NE England in August, but that some Sylvia warblers did not leave until September. However in this study no colour ringed Whitethroats were still present in September. The same was true of Blackcaps and Garden Warblers, although the numbers of these were small, and it is possible that some Scottish birds do leave later. Evans could find no evidence of weight gains in the small samples of local birds he weighed while examination of the fat levels of migrants killed at a lighthouse in north Wales (Evans & Baggott 1969) indicated that the birds concerned, which presumably originated in the northern half of the British Isles, were unlikely to have flown much further than the English Channel.

It is possible that unringed birds which visited the study site in August and September could have included migrants from Scandinavia. Ringing evidence indicates that Scandinavian Willow Warblers are unlikely to reach the east coast of Britain until mid August (Norman & Norman 1985). To date there is no firm evidence to show that Scandinavian Whitethroats pass through Scotland (da Prato & da Prato 1983). The very low numbers of warblers seen in the study site after mid August mean that, even if Scandinavian birds do pass through Scotland, the numbers that alight are very small.

Some Sedge Warblers have been found in August and September in reed beds in southern England with enough fat to allow a non stop flight to west Africa (Gladwin 1963, Bibby, Green, Pepler & Pepler, 1976) although it seems that more birds probably use western France as a final, fattening area (Bibby & Green 1981).

Boddy (1983) found that some juvenile Whitethroats on the Lincolnshire coast in early September showed weight gains, although probably only sufficient to allow them to fly to SW Europe; all these birds had departed by mid September. There is no published evidence to show that Willow Warblers acquire large fat reserves anywhere in Britain in autumn, but in Iberia both Willow Warblers and Whitethroats have been found increasing in weight in August and September, despite the apparent harshness of the environment at the end of the hot, dry summer. Whitethroats were seen taking berries (Ferns 1975). Although several species of plants produced numerous berries in the main study site they were ignored by most warblers, probably because birds left before the fruit (bramble, hawthorn and rose) was fully ripe. British ringing recoveries also indicate that both these species move into Spain and Portugal between August and October (Norman & Norman 1985, da Prato & da Prato 1983).

Sedge Warblers seem to be unusual in putting on so much weight so far north; however migrating Sedge Warblers rely heavily on a rather patchy food resource, reed aphids, Hyalopterus prunei, which are less numerous in SW Europe by late summer (Bibby & Green 1981). By moving gradually towards SW Europe other species of warbler do not need to carry large reserves of fat until the last stage of their migration to west Africa; heavy birds may be more vulnerable to predators due to impaired flying ability (Fry, Ash & Ferguson-Lees 1970).

Early departure from northern breeding grounds avoids the increasing risk from bad weather depressing food supplies, or even blowing the birds off course if they are caught up in a front when on migration. Atlantic depressions increasingly affect NW Europe

in August and, as their centres usually lie to the north of the British Isles, their associated fronts tend to be more vigorous in Scotland than further south (Manley 1962).

Wind and rain tend to depress the numbers of invertebrates on foliage (Dixon 1973) and also damage some of the vegetation, such as stands of nettle, known to be used by feeding warblers in late summer. Although superficially the vegetation in the main study site still appeared luxuriant, the sampling programme indicated a considerable reduction in potential prey by late August or early September, even in the herb layer which had a higher invertebrate biomass in late summer than other vegetation groups.

Another factor likely to influence the timing of autumn migration is that on the southern edge of the Sahara food supplies are at their maximum in October after the summer rains (Morel in Moreau 1972) and it could be advantageous for migrants to arrive in time to establish territories (eg. Whitethroat) or to acquire further reserves for onward migration (eg. Willow Warbler).

The few ringing recoveries from this study, together with others from the files of the Edinburgh Ringing Group, support the theory that warblers from SE Scotland move south to prepare for migration. Four Sedge Warblers handled in the breeding season in the Lothians were caught in reed beds in Dorset in August. Of special interest are a nestling ringed on 6th July which had reached Dorset by 18th August and an adult female caught in Dorset on 15th August when she weighed 16.5 gms, over 20% higher than her weight in May. A juvenile Sedge Warbler ringed on 5th July was killed by a cat near Oxford on 4th August.

A juvenile Whitethroat ringed on 18th July was found in

Warwickshire on 17th August and another ringed on the late date of 2nd September was present in Dorset between 18th and 20th September; both birds were ringed as juveniles of unknown origin. Two juvenile Willow Warblers ringed in July were controlled near Nottingham on 13th August and near Oxford on 19th August respectively while a third juvenile ringed on 8th August had reached Spain by 1st September.

8:8 Warbler numbers in different habitats

Using data from Common Bird Census plots Williamson (1967) suggested that, on average, farmland in England held from 100-400 songbird territories per km^2. It was not possible to census all songbird species over the large area covered for warblers in 1982 but in 1984 a follow up study covering most of the same ground (da Prato 1985) established that songbirds occurred at a density of under 100 territories per km^2 although the presence or absence of woods, shelterbelts, or other areas of diverse habitat considerably affected songbird numbers on particular farms. It seems noteworthy that the English farms often contained such features. For example a farm with the high density of 700 territories per km^2 contained several woods and areas of scrub (Benson & Williamson 1972). Since most CBC plots are chosen by observers concerned for fieldwork in their spare time it is likely that they chose relatively interesting sites, which may give an unrepresentative picture of British farmland.

Since most British songbirds evolved in woodland, farm hedges are often considered to be refuges for species that would otherwise be absent from farmland (Moore, Hooper & Davies, 1967, Pollard, Hooper & Moore 1974). However there is evidence that hedges are sub-optimal habitats for many species. Wrens, Troglodytes troglodytes, colonize hedges when other habitats are crowded (Williamson 1969) and Great Tits, Parus major, left hedges when territories became available in a nearby wood (Krebs 1971). Censuses carried out on a farm before and after hedgerow removal did not show a parallel decrease in bird numbers, although there were changes in species composition (Bull, Mead & Williamson 1976), suggesting that some hedges were of limited value to birds.

In this study few hedges held warbler territories. Those that did were taller and/or wider than the average; even so they often held only one or two species of warbler. Willow Warblers occurred in tree lines with a well developed shrub layer whereas Whitethroats and Sedge Warblers were found along tracks, where the hedges were associated with stands of nettle or other herbs. This distribution follows the pattern found in the main study site and suggests that feeding opportunities were limited in many hedges although time did not permit this to be investigated.

Hedges or tree lines that supported warblers also supported more thrushes, finches, Wrens and Dunnocks, Prunella modularis, than most field hedges (da Prato 1985). Detailed study of the hedges on a Dorset farm (Osborne 1984) has shown that bird rich hedges were those with large basal areas and a complex vegetation structure. Some of Osborne's study hedges were up to 7.5 metres wide, with a double row of trees and shrubs and adjacent ditches. In this study only a few tree lines provided similar habitat. The majority of hedges were much smaller and narrower and composed almost entirely of hawthorn. Such hedges seem to be the predominant type over large areas of farmland in SE Scotland (Tozer & Taylor 1979). The pattern of small enclosed fields, typical of southern England, was not at all common further north. Here field enclosures came relatively late and were largely carried out in the late 18th and early 19th centuries by land owners who planned larger and more regular field patterns than had developed earlier in the south (Millman 1975, Parry & Slater 1980). Modern hedge management may also have reduced the numbers and variety of birds. Arnold (1983) found that hedges in Cambridgeshire held no warblers or tits and many fewer species compared to the hedges surveyed earlier by

Moore, Hooper & Davies (1967).

Although this study has cast doubt on the ornithological value of farm hedges in SE Scotland it has also shown that many songbirds still exist alongside intensively cultivated arable land. All the woods examined held at least four species of warblers (and 19 or more other passerines). None of these woods could be described as conifer monocultures. Even when a wood had been planted with exotic species native shrubs colonized, especially along the edges, and a varied habitat resulted.

The finding that former industrial land often held many warblers and other songbirds is particularly interesting since considerable areas of such land exist in many regions of Britain. Such land is rarely considered to have conservation value although increasing interest in its potential as a "countryside substitute" has developed in urban areas especially for educational purposes. Recently a botanical survey of railway lines found that they were of value in their own right (Sargent 1984). This study suggests that old railways are also potentially valuable for small birds, especially species such as Whitethroats, which naturally occur on wood edges, but for which many hedgerows now seem inadequate.

Unlike many lowland woods old railways are difficult to convert into arable land. They seem to be a particularly valuable resource since they readily lend themselves to public recreation if the line is made a public path (Parham 1972) which can be done while conserving wildlife interest along the sides and banks.

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Appendix A1

The biomass of different invertebrate groups in Hawthorn 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass sample in mgs.
April	0.6	-	29.9	6.0	51.7	1.5	3.0	7.3	-	10.3
May 1-15	0.8	-	24.2	17.5	45.4	2.2	7.6	2.3	-	17.6
16-31	0.8	-	21.4	41.2	26.7	0.9	5.5	3.5	-	31.3
June1-15	0.2	-	19.7	38.6	28.4	2.4	5.6	5.1	-	32.1
16-30	0.1	-	29.7	22.5	39.1	2.8	4.0	1.8	-	21.6
July1-15	0.2	-	35.3	9.8	49.5	1.6	2.6	1.0	-	13.7
16-31	0.3	-	36.1	7.5	41.3	3.3	7.4	4.1	-	11.8
Aug 1-15	0.1	0.8	36.8	5.0	43.7	3.6	4.1	5.9	-	7.8
16-31	-	-	30.8	4.1	46.9	3.5	6.1	8.6	-	4.5
Sept1-15	0.2	-	30.5	2.4	46.6	2.4	8.2	9.7	-	2.4
16-30	0.3	-	30.8	1.3	48.0	2.7	7.6	9.3	-	1.5

Figures are percentages of the mean biomass per sample.

Appendix A2

The biomass of different invertebrate groups in Birch 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass sample in mgs
April	0.2	-	5.2	-	74.5	-	11.9	8.2	-	7.8
May 1-15	0.1	-	16.4	0.6	62.3	0.7	12.2	7.7	-	18.2
16-31	0.7	-	23.9	5.9	43.4	0.8	14.4	10.9	-	20.8
June1-15	-	-	20.9	26.0	30.4	2.2	11.9	8.6	-	18.0
16-30	-	-	43.5	11.5	33.8	3.2	4.8	3.2	-	7.5
July1-15	-	-	51.8	6.5	36.9	1.0	1.9	1.9	-	6.3
16-31	0.3	-	40.4	2.1	48.3	0.6	6.2	2.1	-	6.6
Aug 1-15	0.6	-	41.2	1.0	43.1	2.0	5.2	6.9	-	5.5
16-31	-	3.1	37.1	-	39.4	0.4	10.6	9.4	-	4.9
Sept1-15	0.2	-	38.2	-	47.7	0.6	7.4	5.9	-	3.4
16-30	0.1	2.3	34.6	-	47.9	1.1	8.2	5.8	-	2.9

Figures are percentages of the mean biomass per sample.

Appendix A3

The biomass of different invertebrate groups in Willow 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass /sample in mgs.
April	1.7	-	13.0	2.9	57.4	-	20.3	4.7	-	7.3
May 1-15	1.1	-	18.3	3.3	46.1	-	24.7	6.5	-	13.1
16-31	0.3	-	22.5	4.9	46.0	2.8	15.9	7.6	-	9.4
June1-15	0.8	-	25.0	5.0	40.0	10.0	12.0	7.2	-	8.0
16-30	0.6	-	29.0	3.7	35.1	11.0	15.0	5.6	-	6.5
July1-15	0.5	-	37.5	2.3	31.3	12.5	8.3	7.6	-	6.0
16-31	0.3	-	38.6	4.1	31.4	9.7	9.4	6.5	-	4.5
Aug 1-15	-	-	31.2	3.1	43.0	9.4	6.2	7.1	-	4.7
16-31	-	-	43.7	-	40.6	6.1	6.2	3.4	-	4.1
Sept1-15	0.1	-	40.4	-	37.9	3.8	12.0	5.8	-	3.0
16-30	-	-	41.6	-	41.9	2.7	9.7	4.1	-	2.3

Figures are percentages of the mean biomass per sample.

Appendix A4

The biomass of different invertebrate groups in Elder 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass/ sample in mgs.
April	5.3	1.6	21.7	-	57.7	-	5.1	8.6	-	5.5
May 1-15	6.1	-	29.3	-	52.2	1.6	6.2	4.6	-	10.9
16-31	3.5	-	28.5	4.6	48.9	-	8.1	6.4	-	6.6
June1-15	2.6	2.1	30.8	3.7	50.0	2.7	5.4	2.7	-	8.8
16-30	3.4	-	31.4	2.9	44.4	8.6	5.7	2.8	0.8	8.8
July1-15	2.8	1.3	38.2	-	44.6	2.6	7.9	2.6	-	7.7
16-31	3.1	-	47.4	1.7	34.7	1.7	5.4	6.0	-	6.9
Aug 1-15	3.0	-	45.7	-	37.1	5.6	3.8	4.8	-	5.0
16-31	2.0	-	42.3	-	35.0	4.7	6.0	10.0	-	3.0
Sept1-15	1.0	-	35.2	-	44.0	2.9	4.9	12.0	-	1.9
16-30	1.6	-	39.4	-	37.3	3.1	5.4	13.2	-	2.7

Figures are percentages of the mean biomass per sample.

Appendix A5

The biomass of different invertebrate groups in Gorse 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass /sample in mgs
April	0.3	-	26.9	-	17.6	-	28.1	27.1	-	10.7
May 1-15	0.4	-	20.0	4.0	19.0	-	28.6	28.0	-	14.6
16-31	0.3	1.9	19.2	3.8	28.9	-	24.5	21.4	-	12.6
June1-15	0.9	-	19.6	4.1	22.4	-	28.0	25.0	-	10.9
16-30	0.3	-	17.0	2.2	22.5	-	29.2	28.8	-	11.9
July1-15	0.2	-	19.1	1.3	23.7	1.6	26.1	28.0	-	9.1
16-31	0.2	-	21.0	1.9	25.4	3.6	25.4	22.5	-	6.5
Aug 1-15	0.1	-	19.3	1.0	22.1	6.1	24.3	27.1	-	5.1
16-31	-	-	21.3	-	22.7	9.0	27.0	20.0	-	3.7
Sept1-15	0.3	-	22.2	-	20.1	12.0	22.3	23.1	-	2.4
16-30	-	2.0	21.6	-	27.2	10.3	20.2	18.7	-	2.8

Figures are percentages of the mean biomass per sample.

Appendix A6

The biomass of different invertebrate groups in Bramble 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass /sample in mgs.
April	1.4	-	16.3	-	31.5	0.8	21.0	29.0	-	3.1
May 1-15	2.7	-	18.4	-	29.8	1.3	18.1	29.7	-	4.6
16-31	0.8	-	19.1	1.9	27.0	4.6	18.8	27.8	-	7.7
June1-15	1.1	-	23.7	2.3	30.7	8.7	12.8	20.7	-	7.8
16-30	1.2	-	30.4	1.7	35.4	3.2	12.9	15.2	-	10.9
July1-15	0.8	-	25.5	2.5	39.6	4.3	10.5	16.8	-	12.9
16-31	0.4	-	20.4	1.0	38.0	3.4	16.9	19.9	-	11.3
Aug 1-15	1.5	-	19.3	2.8	36.6	7.9	14.3	17.6	-	9.4
16-31	0.4	-	22.5	-	32.9	6.4	18.5	17.6	1.7	8.2
Sept1-15	-	1.0	24.4	1.0	33.3	4.9	14.7	20.7	-	4.3
16-30	0.8	-	25.4	-	30.8	5.1	15.6	21.0	1.3	4.7

Figures are percentages of the mean biomass per sample.

Appendix A7

The biomass of different invertebrate groups in Rose 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass sample in mgs.
April	1.5	-	14.8	-	43.5	2.1	21.6	16.5	-	3.1
May 1-15	0.8	-	21.2	-	44.7	-	20.0	13.3	-	3.6
16-31	1.6	-	25.9	-	35.8	2.3	18.8	15.6	-	4.6
June1-15	0.3	-	25.7	-	36.0	2.6	16.2	19.2	-	7.0
16-30	0.9	1.8	29.4	-	39.6	6.1	11.9	10.3	-	10.0
July1-15	0.5	-	28.0	2.5	43.0	5.0	14.0	7.0	-	10.9
16-31	-	-	22.8	2.1	37.9	6.3	18.3	12.6	-	11.2
Aug 1-15	0.6	1.3	24.5	3.8	38.6	4.3	17.7	8.4	0.8	6.1
16-31	0.1	-	30.8	1.2	32.2	7.1	14.3	14.3	-	5.1
Sept1-15	0.5	4.7	25.2	-	37.3	6.0	15.1	11.2	-	2.5
16-30	0.3	-	25.3	-	39.3	4.9	15.3	13.2	1.7	2.0

Figures are percentages of the mean biomass per sample.

Appendix A8

The biomass of different invertebrate groups in Nettle 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass sample in mgs.
April	1.0	-	18.5	-	35.7	-	19.0	23.8	2.0	5.2
May 1-15	1.4	-	30.3	1.4	31.3	-	18.7	16.9	-	8.9
16-31	-	-	32.3	3.2	28.0	1.1	25.0	9.8	0.6	20.9
June1-15	0.4	1.9	27.1	1.7	31.1	0.6	26.9	8.8	1.5	23.1
16-30	0.2	-	23.5	2.9	33.0	9.8	23.7	6.9	-	20.9
July1-15	0.7	3.0	35.7	5.8	32.9	1.4	12.8	5.7	2.0	20.2
16-31	-	1.3	40.6	6.0	34.3	0.7	12.0	5.1	-	29.8
Aug 1-15	0.4	-	40.7	3.6	33.1	0.9	12.8	6.9	1.6	24.1
16-31	-	-	40.3	2.7	38.3	3.7	10.4	4.6	-	16.2
Sept1-15	-	1.0	34.3	1.1	45.4	3.4	9.1	5.7	-	10.1
16-30	0.1	-	36.8	-	42.2	2,9	11.3	5.9	0.8	6.2

Figures are percentages of the mean biomass per sample.

Appendix A9

The biomass of different invertebrate groups in Nettle/Bishopweed mixture 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass /sample in mgs.
April	0.7	-	21.4	-	43.8	1.2	13.5	19.4	-	3.3
May 1-15	2.3	-	26.8	-	41.4	-	13.6	15.9	-	7.5
16-31	1.1	-	35.3	2.0	30.1	2.9	14.7	12.9	1.0	18.8
June1-15	2.1	-	33.7	1.1	28.3	4.2	20.2	9.3	1.1	16.4
16-30	2.0	-	28.0	5.0	32.0	4.0	18.0	11.0	-	16.5
July1-15	0.3	-	37.8	6.2	30.8	3.1	13.2	8.6	-	19.6
16-31	-	-	37.8	7.7	34.3	1.6	12.8	5.1	0.7	26.2
Aug 1-15	1.0	1.7	43.4	4.4	31.2	2.7	8.6	6.5	0.5	25.4
16-31	-	-	40.5	3.4	38.8	2.8	7.3	7.2	-	16.1
Sept1-15	0.4	-	37.5	1.3	44.1	4.2	8.3	4.2	-	9.8
16-30	-	-	38.2	-	42.1	3.2	9.4	6.3	0.8	4.7

Figures are percentages of the mean biomass per sample.

Appendix A10

The biomass of different invertebrate groups in Willowherb 1979-81

	Collembola	Dermaptera	Hemiptera	Lepidoptera	Diptera	Hymenoptera	Coleoptera	Araneae	Mollusca	Mean biomass /sample in mgs.
April	2.4	-	22.9	-	41.0	-	17.7	14.7	1.3	3.3
May 1-15	1.7	-	25.9	-	39.1	2.9	17.6	12.8	-	4.3
16-31	0.2	-	37.9	0.8	41.3	0.6	11.6	7.6	-	11.1
June1-15	0.6	1.4	36.9	4.7	32.7	5.1	10.2	8.4	-	11.7
16-30	-	-	37.7	4.7	32.0	9.0	8.3	7.0	1.3	19.6
July1-15	-	1.2	30.6	6.8	35.0	10.0	10.6	3.7	2.1	23.2
16.31	-	-	35.0	7.1	34.2	8.3	9.2	6.2	-	15.6
Aug 1-15	0.3	-	32.5	2.0	47.3	4.1	8.0	4.1	1.7	9.4
16-31	-	-	36.1	-	45.4	2.3	11.6	4.6	-	7.8
Sept1-15	-	-	36.7	0.6	44.5	1.2	13.3	3.7	-	3.9
16-30	-	-	38.2	-	40.0	2.0	14.2	4.0	1.6	4.6

Figures are percentages of the mean biomass per sample.

Appendix B1

Invertebrate prey eaten by adult Willow Warblers 1979-81

	APRIL				MAY		JUNE		JULY				AUGUST				
Collembola	10.1	9.4	6.4	2.4	1.0	0.3							0.3				
	7.5	9.4	6.8	2.0													
Dermaptera													0.03	0.1			
															0.6	0.4	
Hemiptera	34.3	25.2	17.4	22.6	15.6	20.3	18.1	17.1	12.0	10.8	14.4	18.9	28.3	31.0	31.9	39.7	38.4
	33.3	30.1	19.3	20.1	19.5	20.1	19.0	16.4	14.2	10.8	16.0	25.4	27.2	31.8	34.6	38.0	42.3
Lepidoptera	1.7	1.5	2.8	12.1	17.9	17.0	19.7	22.1	21.2	22.5	12.3	9.4	4.1	2.6	2.6	1.3	1.1
	-	1.2	2.8	11.9	15.9	17.2	18.7	20.9	20.4	19.5	11.1	7.9	4.2	2.3	1.2	1.1	1.2
Diptera	40.7	53.8	61.3	52.8	56.1	53.8	49.2	45.8	47.4	56.0	61.3	60.7	56.0	53.5	55.2	54.2	54.7
	47.3	49.4	59.9	55.9	55.3	54.2	49.2	46.1	50.1	57.3	62.8	58.9	56.5	55.0	53.6	53.1	48.5
Hymenoptera	1.4	1.5	3.9	5.0	6.1	5.4	8.3	11.1	12.8	7.2	7.0	6.8	7.0	8.4	5.6	3.1	2.5
	1.1	1.8	3.8	4.8	5.9	5.5	9.3	11.8	10.8	9.8	6.7	5.0	6.9	7.8	5.5	4.4	3.1
Coleoptera	3.3	3.4	1.4	0.8	0.5	0.4	1.1	1.7	2.6	1.7	2.4	2.0	2.5	2.9	2.6	1.5	3.0
	4.3	3.5	2.2	0.6	0.8	0.7	0.4	3.0	1.5	1.2	1.6	0.7	3.3	2.7	1.7	2.2	3.7
Araneae	8.5	5.2	6.8	4.3	2.8	2.8	3.6	2.2	3.7	1.8	2.6	2.2	2.1	1.2	2.1	0.2	0.2
	6.5	4.6	5.2	4.7	2.6	2.3	3.4	1.8	3.0	1.4	1.8	2.1	1.9	0.4	2.3	0.8	1.2
Mollusca									0.3					0.03			0.1
															0.5		
Total prey items	1899	2424	4305	5220	5024	4605	4441	2544	2131	2471	2073	2250	3044	4379	3719	4474	1344
	93	215	230	319	294	346	230	243	264	229	300	301	275	267	304	234	68
	(8)	(16)	(20)	(29)	(29)	(33)	(24)	(23)	(26)	(25)	(27)	(28)	(25)	(23)	(25)	(18)	(5)

For each invertebrate group the upper line shows the percentage of the total prey items seen to be eaten per week contributed by that group. The lower line shows the percentage of each invertebrate group found in faeces each week. The number of faecal samples is shown in parentheses.

Appendix B2

Invertebrate prey eaten by adult Whitethroats 1979-81

	APRIL		MAY			JUNE			JULY			AUGUST					
Collembola												0.1	0.03			0.03	
Dermaptera														0.4			4.2
Hemiptera	5.5	9.8	12.6	12.2	19.5	16.1	11.7	9.7	8.0	4.7	3.6	7.3	4.7	6.3	5.8	6.0	5.5
		11.8	13.1	9.8	18.0	13.6	9.8	12.1	8.1	8.2	5.2	8.4	6.5	5.6	4.7	1.5	4.2
Lepidoptera	-	-	5.9	6.2	8.9	15.5	21.4	18.0	12.5	7.1	6.4	3.3	2.5	2.5	2.5	1.9	0.9
	-	-	4.3	8.0	8.6	16.8	17.8	16.2	11.1	6.4	4.5	2.4	1.3	0.4	1.9	-	4.2
Diptera	25.5	28.3	25.5	46.6	46.1	44.1	41.3	52.6	59.2	65.0	62.8	50.9	66.5	60.8	68.4	64.3	72.0
	-	23.5	23.8	42.7	44.4	41.6	46.5	52.9	56.7	60.6	61.0	53.8	68.0	65.5	66.6	77.1	62.5
Hymenoptera	-	-	-	0.5	1.1	0.3	1.3	2.1	4.4	0.8	3.1	3.6	4.6	3.5	3.6	1.6	1.5
	-	-	1.2	1.7	1.3	2.1	2.5	1.1	4.9	3.8	3.6	3.0	1.8	2.8	6.1	1.5	-
Coleoptera	16.3	30.3	36.3	26.5	18.9	17.3	16.6	12.2	12.1	14.9	16.8	27.2	16.3	17.0	11.3	15.3	15.0
	-	35.3	35.7	26.9	21.0	18.9	16.6	11.6	14.8	16.0	19.2	24.8	16.2	15.8	10.7	15.7	16.7
Araneae	52.7	31.6	19.7	8.0	5.5	6.7	7.7	5.4	3.8	7.5	7.3	7.5	5.4	9.9	8.4	10.9	5.1
	-	29.4	21.9	10.9	6.7	7.0	6.8	6.1	4.4	5.0	6.5	7.6	6.2	9.1	9.5	4.2	8.2
Mollusca												0.1					
														0.4	0.5		
Total prey	55	307	960	3751	4711	4394	3495	2919	1885	1923	2831	3065	1955	2458	1956	1385	776
items	-	17	70	136	233	233	220	223	197	157	174	144	138	124	111	42	24
	-	(2)	(8)	(16)	(24)	(24)	(29)	(29)	(25)	(23)	(23)	(19)	(18)	(16)	(13)	(5)	(3)

For each invertebrate group the upper line shows the percentage of the total prey items seen to be eaten per week contributed by that group. The lower line shows the percentage of each invertebrate group found in faeces each week. The number of faecal samples is shown in parentheses.

Appendix B3

Invertebrate prey eaten by adult Sedge Warblers 1979-81

	MAY	JUNE							JULY				AUGUST		
Collembola															
Dermaptera													0.03		
Hemiptera	26.6	30.5	28.1	25.8	13.8	9.8	19.2	10.9	18.0	21.8	7.3	8.0	9.9	13.3	16.6
	-	29.4	26.9	25.0	16.1	13.8	15.7	13.6	16.5	18.4	7.9	9.2	10.9	13.0	12.9
Lepidoptera	3.8	12.1	8.3	7.0	16.7	11.7	10.0	5.1	5.6	4.1	3.1	1.5	0.4	0.4	0.5
	-	8.3	8.5	7.4	15.1	11.5	7.8	5.2	4.2	2.7	3.2	-	1.9	-	-
Diptera	26.6	28.0	37.0	44.9	32.5	48.6	50.4	65.3	46.0	52.8	53.2	57.9	49.4	54.2	38.1
	-	29.9	37.8	42.1	36.0	44.6	55.9	60.1	54.2	53.7	55.1	54.1	49.4	48.8	39.3
Hymenoptera															
Coleoptera	30.3	21.6	18.0	11.0	26.1	25.4	17.8	14.9	21.8	15.3	26.9	22.3	30.9	24.4	32.4
	-	23.6	17.7	15.0	24.0	24.6	17.8	16.7	18.8	18.9	25.2	26.1	27.6	28.4	34.9
Araneae	12.7	7.8	8.6	11.3	10.9	4.5	2.6	3.8	8.6	6.0	9.5	10.3	9.4	7.7	12.4
	-	8.8	9.1	10.5	8.8	5.5	2.8	4.4	6.3	6.3	8.6	10.6	10.2	9.8	12.9
Mollusca															
Total prey	79	1419	4396	5161	4494	4875	1849	1656	1386	1828	2395	2508	2678	2577	848
items	-	130	195	211	206	231	185	219	183	147	127	146	109	122	17
	-	(15)	(21)	(22)	(25)	(25)	(21)	(23)	(20)	(17)	(18)	(21)	(15)	(15)	(3)

For each invertebrate group the upper line shows the percentage of the total prey items seen to be eaten per week contributed by that group. The lower line shows the percentage of each invertebrate group found in faeces each week. The number of faecal samples is shown in parentheses.

Appendix C1

Invertebrate prey fed to young Willow Warblers 1979-81

	JUNE			JULY					
Collembola									
Dermaptera									
Hemiptera	1.8	7.0	11.9	17.6	21.8	23.6	26.9	20.0	30.3
	2.7	5.4	13.6	18.8	21.8	24.5	23.7		
		2.9	12.3	21.7	21.4		19.1		
Lepidoptera	69.8	65.3	59.4	49.3	39.6	33.8	25.0	21.9	16.0
	70.3	65.5	60.2	49.3	40.6	31.4	27.3		
		71.0	61.4	47.8	42.9		29.8		
Diptera	24.8	25.8	24.1	29.2	32.0	34.7	38.7	50.8	46.0
	24.3	26.7	22.9	26.2	31.6	34.6	41.8		
		24.7	26.3	26.2	35.7		36.2		
Hymenoptera	2.5		1.1		0.8	1.4	3.6	2.4	
		1.0	0.7		0.4	3.5	1.8		
							2.1		
Coleoptera	0.7	1.6	2.7	3.2	4.1	3.7	4.6	4.9	5.4
	2.7	0.9	1.7	3.8	3.5	3.5	3.6		
				4.3			6.4		
Araneae	0.4	0.3	0.6	0.5	1.4	2.4	0.5		1.8
		0.5	0.9	1.6	1.4	1.9	1.8		
		1.4					4.3		
Mollusca			0.2	0.2	0.3	0.4	0.7		0.5
				0.3	0.7	0.6			
							2.1		
Total prey items	282	1761	2628	2191	2732	2691	1707	830	930
	37	226	475	380	296	181	55		
	(3)	(15)	(32)	(28)	(24)	(10)	(5)	Number of faecal samples	
		69	57	23	14		47		
		(3)	(3)	(1)	(1)		(2)	Number of broods	

For each invertebrate group the upper line shows the percentage of the total prey items seen to be collected per week contributed by that group. The middle line shows the percentage of each invertebrate group found in faeces each week. The lower line shows the percentage of each invertebrate group found in food parcels each week obtained by collaring nestlings.

Appendix C2

Invertebrate prey fed to young Whitethroats 1979-81

	MAY		JUNE					JULY				AUGUST	
Collembola													
Dermaptera													
Hemiptera	2.3	2.6	5.3	13.1	11.9	10.6	11.2	9.3	10.7	8.9	12.1	11.1	
	1.9	2.1	5.1	10.6	13.4	11.7	11.2	10.4	8.0	11.1	13.3	11.1	
			5.2					10.3					
Lepidoptera	28.1	36.8	37.4	22.8	16.8	13.2	12.3	10.9	8.2	6.9	5.4	4.6	
	30.9	38.7	38.6	23.1	14.2	13.5	13.0	12.3	7.6	5.6	6.8	5.6	
		40.8	36.4					12.8					
Diptera	55.9	49.2	43.4	41.1	44.1	45.4	42.0	47.2	52.4	52.7	55.7	62.7	
	60.0	49.1	42.5	42.7	42.9	44.7	43.8	48.3	53.1	52.7	53.3	55.5	
		50.0	46.7					51.3					
Hymenoptera													
Coleoptera	8.4	9.5	10.8	19.3	23.2	27.3	29.9	27.2	23.1	27.7	21.6	21.6	
	3.6	7.7	11.7	16.9	24.8	26.5	27.1	23.8	25.1	25.0	23.3	22.2	
		5.1	10.4					15.4					
Araneae	5.3	1.9	3.1	3.3	3.5	3.5	4.6	4.6	4.5	3.1	5.2		
	3.6	2.4	2.1	6.2	3.7	2.8	3.7	3.4	4.6	5.6	3.3	2.8	
		4.1	1.3					7.7					
Mollusca				0.4	0.5			0.8	1.1	0.7			
				0.5	1.0	0.8	1.2	1.8	1.6			2.8	
								2.5					
Total prey items	728	1247	1912	2926	2727	2205	1371	1946	1205	552	371	153	
	55	103	142	162	105	102	106	58	47	36	30	36	
	(6)	(11)	(16)	(17)	(12)	(11)	(13)	(6)	(5)	(4)	(3)	(3)	Number of faecal samples
		98	77					39					
		(3)	(3)					(2)					Number of broods

For each invertebrate group the upper line shows the percentage of the total prey items seen to be collected per week contributed by that group. The middle line shows the percentage of each invertebrate group found in faeces each week. The lower line shows the percentage of each invertebrate group found in food parcels each week obtained by collaring nestlings.

Appendix C3

Invertebrate prey fed to young Sedge Warblers 1979-81

	JUNE			JULY		AUGUST				
Collembola										
Dermaptera										
Hemiptera	14.9	13.6	14.8	17.0	16.6	15.7	14.5	18.2	21.0	
	15.3	14.9	15.8	18.0	16.2	16.2	15.8	17.7	21.8	
		10.6		16.7		13.3	15.4	23.5		
Lepidoptera	15.1	12.3	9.8	9.3	6.2	3.7	3.7	2.8	2.6	
	15.0	11.9	9.1	8.1	5.2	3.3	2.5	3.0		
		15.2		10.0			3.8			
Diptera	40.2	46.0	38.7	40.7	38.5	41.6	45.4	43.8	40.5	
	40.9	42.7	40.9	40.4	41.2	41.3	45.2	42.3	39.2	
		50.0		40.0		40.0	42.3	47.1		
Hymenoptera										
Coleoptera	27.4	24.3	33.0	30.2	33.5	34.3	32.1	30.0	32.4	
	26.6	26.8	31.6	29.5	32.1	33.4	31.8	33.4	34.7	
		22.7		33.3		40.0	34.7	29.4		
Araneae	2.4	3.3	3.7	2.8	5.2	4.7	4.3	5.2	3.5	
	2.2	3.7	2.6	4.0	5.3	5.8	4.7	3.6	4.3	
		1.5				6.7	3.8			
Mollusca		0.5								
Total prey	3031	3311	3746	3435	2750	2587	2217	1292	193	
	108	171	141	100	174	174	160	107	23	
	(11)	(15)	(13)	(9)	(15)	(16)	(14)	(9)	(2)	Number of faecal samples
		66		30		15	26	17		
		(3)		(1)		(1)	(1)	(1)		Number of broods

For each invertebrate group the upper line shows the percentage of the total prey items seen to be collected per week contributed by that group. The middle line shows the percentage of each invertebrate group found in faeces each week. The lower line shows the percentage of each invertebrate group found in food parcels each week obtained by collaring nestlings.

Appendix D1

Time allocation by a pair of Willow Warblers watched throughout one day before egg laying

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time nest building*		percentage time singing	
	male	female	male	female	male	female	male	female	male	female	male	female
0500-0700	62	55	32	40	9	5	4	39	10	16	45	-
0700-0900	53	59	59	82	1	3	-	15	-	-	40	-
0900-1100	49	56	50	69	8	2	9	9	6	20	27	-
1100-1300	58	42	29	37	13	10	16	12	16	41	26	-
1300-1500	53	49	21	28	19	8	40	28	10	36	10	-
1500-1700	60	55	26	41	12	16	18	12	18	31	26	-
1700-1900	57	59	60	75	4	3	13	10	17	12	6	-
1900-2100	49	60	49	67	5	9	11	20	-	4	35	-

* In this category the male did not help in nest building but chivied the female, followed her and courted her.

Appendix D2

Time allocation by a pair of Whitethroats watched throughout one day before egg laying

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time nest building *		percentage time singing	
	male	female	male	female	male	female	male	female	male	female	male	female
0500-0700	60	50	43	61	6	9	-	15	12	15	39	-
0700-0900	54	55	59	80	-	3	4	9	7	8	30	-
0900-1100	51	63	41	68	4	5	10	8	13	19	32	-
1100-1300	62	50	33	49	14	11	2	12	10	28	41	-
1300-1500	50	61	28	46	20	15	20	20	5	19	27	-
1500-1700	56	50	39	48	5	21	19	14	13	17	24	-
1700-1900	47	60	56	89	1	2	2	-	21	9	20	-
1900-2100	62	47	71	91	4	7	6	2	-	-	19	-

* In this category the male did not help in nest building but chivied the female, followed her and courted her.

Appendix D3

Time allocation by a pair of Sedge Warblers watched throughout one day before egg laying

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time nest building*		percentage time singing	
	male	female	male	female	male	female	male	female	male	female	male	female
0500-0700	52	57	59	70	3	12	-	6	8	12	30	-
0700-0900	61	49	64	77	6	5	1	7	9	11	20	-
0900-1100	61	49	56	68	6	9	1	9	13	14	24	-
1100-1300	48	58	54	58	8	11	6	21	12	10	20	-
1300-1500	63	49	44	52	14	17	29	28	-	3	13	-
1500-1700	53	55	46	61	13	4	20	24	4	11	17	-
1700-1900	58	48	70	73	9	18	-	6	5	3	16	-
1900-2100	53	57	72	85	12	11	10	4	3	-	3	-

* In this category the male did not help in nest building but chivied the female, followed her and courted her.

Appendix D4

Time allocation by a pair of Willow Warblers watched throughout one day during incubation

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time incubating		percentage time singing	
	male	female	male	female	male	female	male	female	male	female	male	female
0500-0700	55	54	39	-	19	-	5	-	-	100	37	-
0700-0900	60	53	60	31	2	12	2	-	-	57	36	-
0900-1100	58	42	59	44	6	19	6	-	-	37	29	-
1100-1300	65	50	32	49	20	17	31	6	-	28	17	-
1300-1500	58	60	30	-	9	-	55	-	-	100	6	-
1500-1700	49	54	37	49	27	2	19	-	-	49	17	-
1700-1900	53	63	78	59	11	8	2	4	-	29	9	-
1900-2100	44	64	63	-	18	-	-	-	-	100	19	-

Appendix D5

Time allocation by a pair of Whitethroats watched throughout one day during incubation

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time incubating		percentage time singing	
	male	female	male	female	male	female	male	female	male	female	male	female
0500-0700	65	50	43	-	8	-	14	-	-	100	35	-
0700-0900	65	49	56	43	11	5	7	-	-	52	26	-
0900-1100	64	46	50	53	8	14	12	4	-	29	30	-
1100-1300	53	62	36	40	14	11	13	3	-	46	37	-
1300-1500	58	51	31	6	8	3	36	-	-	91	25	-
1500-1700	50	62	42	47	11	7	17	-	-	46	30	-
1700-1900	49	53	68	65	9	12	3	3	-	20	20	-
1900-2100	44	61	71	14	6	-	2	-	-	86	21	-

Appendix D6

Time allocation by a pair of Sedge Warblers watched throughout one day during incubation

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time incubating		percentage time singing	
	male	female	male	female	male	female	male	female	male	female	male	female
0500-0700	55	49	41	-	14	-	9	-	-	100	36	-
0700-0900	63	56	59	44	9	5	4	-	-	51	28	-
0900-1100	58	61	57	50	8	9	10	-	-	41	25	-
1100-1300	58	52	30	47	28	16	27	5	-	32	15	-
1300-1500	56	61	29	4	14	1	54	-	-	95	3	-
1500-1700	62	44	36	51	20	2	25	-	-	47	19	-
1700-1900	53	62	71	67	9	2	2	-	-	31	18	-
1900-2100	60	54	68	-	7	-	-	-	-	100	25	-

Appendix D7

Time allocation by Willow Warblers watched throughout one day when feeding young in the nest

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time singing	
	male	female	male	female	male	female	male	female	male	female
0500-0700	50	55	89	96	3	2	1	2	7	-
0700-0900	54	57	94	97	3	3	-	-	3	-
0900-1100	60	58	80	86	9	7	5	7	6	0
1100-1300	57	51	68	76	13	11	10	13	9	-
1300-1500	51	59	62	71	13	10	15	19	10	-
1500-1700	49	59	70	80	12	11	5	9	13	-
1700-1900	56	60	87	94	2	4	4	2	7	-
1900-2100	62	54	93	98	7	2	-	-	-	-

Appendix D8

Time allocation by Whitethroats watched throughout one day when feeding young in the nest

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time singing	
	male	female	male	female	male	female	male	female	male	female
0500-0700	54	56	76	95	3	4	-	1	21	-
0700-0900	53	62	83	93	2	4	5	3	10	-
0900-1100	59	55	78	86	5	10	5	4	12	-
1100-1300	62	51	65	78	12	11	9	11	14	-
1300-1500	52	54	60	70	11	10	8	20	21	-
1500-1700	53	59	70	82	7	7	2	11	21	-
1700-1900	47	57	88	97	-	-	-	3	12	-
1900-2100	57	52	94	98	6	2	-	-	-	-

Appendix D9

Time allocation by Sedge Warblers watched throughout the day when feeding young in the nest

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time singing	
	male	female	male	female	male	female	male	female	male	female
0500-0700	46	55	86	90	8	6	4	4	2	-
0700-0900	53	51	93	96	5	2	-	2	2	-
0900-1100	58	59	81	82	11	6	5	12	3	-
1100-1300	54	51	80	80	9	8	11	12	-	-
1300-1500	49	62	70	77	11	9	16	14	3	-
1500-1700	66	46	85	88	9	9	4	3	2	-
1700-1900	59	53	90	98	7	2	3	-	-	-
1900-2100	54	52	80	90	11	1	9	9	-	-

Appendix D10

Time allocation by a pair of Willow Warblers watched throughout one day when feeding fledged young

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time singing	
	male	female	male	female	male	female	male	female	male	female
0500-0700	60	54	55	65	29	26	6	9	10	-
0700-0900	58	57	67	84	14	13	7	3	12	-
0900-1100	48	57	59	66	22	18	9	16	10	-
1100-1300	49	55	50	50	28	33	20	17	2	-
1300-1500	56	59	52	61	30	27	18	12	-	-
1500-1700	54	60	71	74	11	17	14	9	4	-
1700-1900	49	58	82	86	15	12	-	2	3	-
1900-2100	54	60	79	86	15	14	-	-	6	-

Appendix D11

Time allocation by a pair of Whitethroats watched throughout one day when feeding fledged young

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time singing	
	male	female	male	female	male	female	male	female	male	female
0500-0700	53	60	68	88	6	4	8	8	18	-
0700-0900	58	59	71	74	6	11	4	15	19	-
0900-1100	48	53	62	79	7	8	9	13	22	-
1100-1300	60	49	60	63	14	16	9	21	17	-
1300-1500	65	47	58	69	14	13	6	18	22	-
1500-1700	56	59	52	71	8	14	15	15	25	-
1700-1900	62	53	72	80	4	12	2	8	22	-
1900-2100	62	49	70	81	1	13	-	6	29	-

Appendix D12

Time allocation by a pair of Sedge Warblers watched throughout one day when feeding fledged young

Time of day	Total time watched in minutes		percentage time feeding		percentage time preening		percentage time resting		percentage time singing	
	male	female	male	female	male	female	male	female	male	female
0500-0700	56	50	80	80	13	15	7	5	-	-
0700-0900	57	53	80	82	16	15	4	3	-	-
0900-1100	57	60	69	72	18	19	13	9	-	-
1100-1300	61	49	50	51	19	19	31	30	-	-
1300-1500	54	54	53	59	29	19	18	22	-	-
1500-1700	60	47	75	80	12	8	13	12	-	-
1700-1900	47	61	70	73	22	17	8	10	-	-
1900-2100	50	61	69	69	17	19	14	12	-	-