

AN EXPERIMENTAL AND OBSERVATIONAL STUDY
OF INTERSPECIFIC TERRITORIALITY BETWEEN
THE BLACKCAP *Sylvia atricapilla* (LINNAEUS)
AND THE GARDEN WARBLER *Sylvia borin* (BODDAERT).

BY

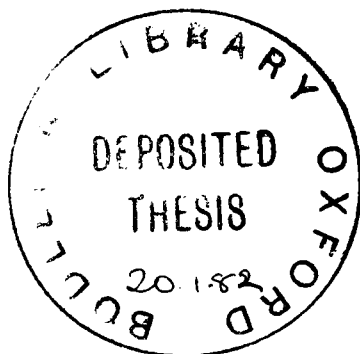
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A thesis submitted
for the degree of
Doctor of Philosophy
at the University of
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ABSTRACT

Ecological divergence between Blackcaps and Garden Warblers appears to be incomplete. They resemble each other closely in morphology and their foraging behaviour and food (in the breeding season) are at least broadly similar. Nevertheless, they are sympatric and occur together in a wide range of habitats, although Garden Warblers are proportionately commoner in lower, denser vegetation.

The two species are strongly interspecifically territorial where they occur together. However, Blackcaps are more interspecifically aggressive than Garden Warblers and are clearly dominant to them in interactions. Blackcaps respond just as strongly to playback of Garden Warbler song as they do to that of Blackcap song. They sometimes intrude into Garden Warbler territories and seek-out and chase the territory holders. In contrast, with rare exceptions, any Garden Warblers which intrude into Blackcap territories are attacked and chased until they leave the area. Also, during song playback experiments, Garden Warblers approach the loudspeaker less closely in response to Blackcap song than they do to Garden Warbler song.

Many Blackcaps arrive on the breeding grounds before the earliest Garden Warblers do. A removal experiment, in which such established Blackcaps were systematically removed, showed that some of them had been keeping-out potential Garden Warbler settlers, since the latter then readily established territories and bred in a large part of the Blackcap-free zone. Normally, Garden Warblers have their territories outside Blackcap-occupied habitat, partly because they are prevented by the aggressiveness of the Blackcaps from settling elsewhere. However, observation and song playback experiments have shown that, once established, Garden Warblers do defend their territories against both conspecifics and Blackcaps.

Blackcaps have recently increased dramatically in Britain and Garden Warblers have decreased simultaneously. However, although Blackcaps can limit the local breeding densities of Garden Warblers in any one year, it is not yet clear whether Blackcap numbers are a significant factor in determining the total sizes of Garden Warbler populations.



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PROLOGUE

The principle of competitive exclusion (Hardin 1960), which states that any two species must occupy different niches to coexist because otherwise one will exclude the other competitively, has come to be regarded as a cornerstone of modern ecology and numerous studies have been undertaken which demonstrate its validity. In particular, work has centred on the converse of the principle, namely that if two or more species are coexistent they must be occupying distinct niches.

The niche concept precludes rigid definition but it is useful to regard the niche as the totality of the resources which a species uses, where it finds them and the strategies by which it harvests them (Diamond 1978). The inclusion of resource location and utilisation methods in this definition stems from the work of MacArthur (1958) on the niche characteristics of *Dendroica* warblers. He showed that different species have different foraging heights, substrates and strategies, which apparently enable them to coexist. His results were the outcome of meticulous fieldwork, and were one of the earlier illustrations that niche differences between closely-related sympatric species may be relatively subtle. At first glance, the five species which he considered seemed to be taking the same food in the same way in the same trees.

It has been suggested that niche differences between coexisting species result from interspecific competition (Diamond 1978); they are the means by which those species minimise competing with each other in nature. It is seldom possible to observe such competition directly because the status quo of sympatric species is frequently a reflection of past competition which has been resolved (Lack 1944). Interspecific competition can chiefly be detected by observing niche shifts and the outcome of experimental

manipulations of natural populations. Niche shifts are the changes in the niches of species which may occur in localities where competitors which are normally present alongside them are absent, for natural reasons. Many examples are known, especially among birds (Diamond 1978). Experimental approaches have involved observing what happens when a species is introduced to, or removed from, a locality occupied by a close relative. In general it has been found possible to demonstrate that by varying the levels of competition with one species, changes can be produced in the abundance of other species, or at least alterations in the niches which they occupy (Connell 1975).

The phenomenon of interspecific territoriality in birds can be seen as an additional opportunity to record interspecific competition in action, largely because the segregation of the participant species is more a behavioural than an ecological process. Here the mechanisms of segregation are rehearsed, and are observable, each time the territorial system is set-up, this occurring during the breeding season in most temperate-zone songbirds.

The significance of the phenomenon of interspecific territoriality is a controversial subject, as later discussed, but its understanding will be assisted by having as many detailed examples of it available as possible. The present study, which examines the interspecific relationship between the Blackcap and the Garden Warbler, is intended to be such an example. These two species were chosen because there already existed anecdotal accounts by Howard (1907-1914) and Raines (1945) that they interact strongly, although little was known in detail about such behaviour. The work was conducted at Wytham woods, near Oxford, during the springs and summers of 1978, 1979 and 1980.

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E.F.J.G.

GIBRALTAR

August 1981

NOTE. The scientific names of the bird and plant species mentioned in the text are given in Appendices A and B respectively.

CHAPTER ONE

THE COMPARATIVE ECOLOGY
OF
THE BLACKCAP AND THE GARDEN WARBLER
IN
BRITAIN

CHAPTER ONE

THE COMPARATIVE ECOLOGY OF THE BLACKCAP AND THE GARDEN WARBLER IN BRITAIN

1-1. INTRODUCTION

As many as 60 % of all bird species are wholly or partly insectivorous (Morse 1971) but it is often unclear how the same general food resource (insects) is partitioned among an often large number of sympatric exploiters. Ecological segregation may be achieved in a number of ways. Congeners are often separated because they occupy distinct habitats. If they share the same habitat they may use different parts of it, or they may use the same parts in different ways; for example, they may differ in foraging behaviour. Differences in modes of exploitation of the same general resources may also be achieved or enhanced by morphological differences between the species. Finally the same resource can be exploited by different species if they use it at separate seasons i.e. segregation may be temporal.

This chapter contrasts the ecology of Blackcaps and Garden Warblers, attempting initially to assess whether conditions exist which might be expected to promote interspecific territoriality between them. It presents results of some field investigations and reviews relevant information from the literature. Overlap in the types of habitat used by the two species is discussed in Chapter 2.

1-2. THE GEOGRAPHICAL DISTRIBUTION OF BLACKCAPS AND GARDEN WARBLERS

The two species are widely sympatric in the breeding season (Figure 1-1). However the Garden Warbler extends further north than the Blackcap, into the subarctic birch zone. The northern limit of its range approximates to that of the 53°F July isotherm whereas the Blackcap's range is chiefly south of the 57°F isotherm (Voous 1960), although the latter has been spreading its range northwards recently (Chapter 7). The ranges are quite different in the Mediterranean area where the Garden Warbler is largely absent, or restricted to mountain forests, and the Blackcap is widespread and

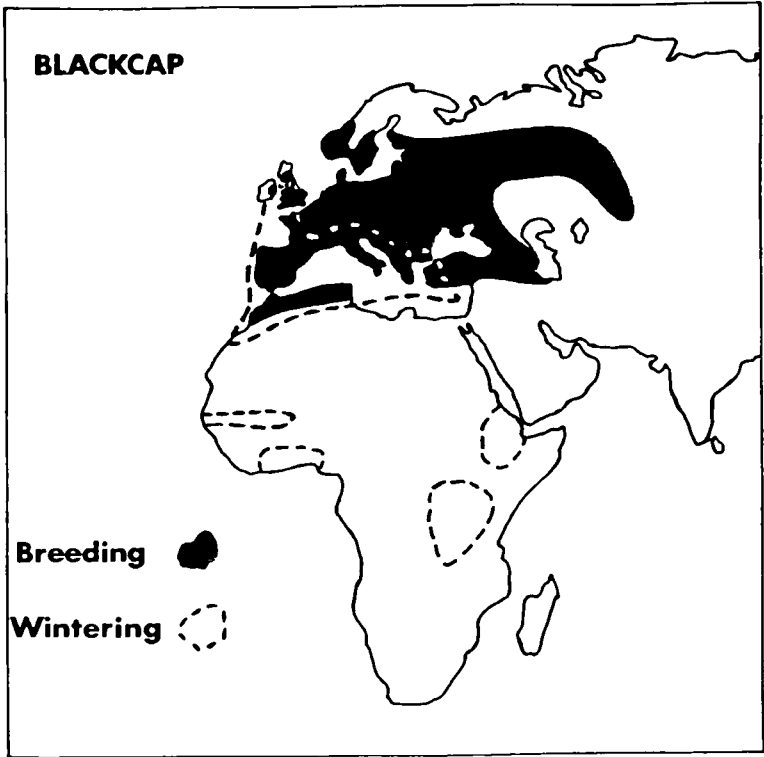
locally common. The southern limits of the breeding ranges of the Blackcap and Garden Warbler respectively are approximately the 87°F and 82°F July isotherms.

Both are migratory but have largely-separate winter quarters (Figure 1-1). The Garden Warbler is entirely a trans-Saharan migrant; winter records in the Palearctic are rarities. In winter it is found in a range of deciduous and evergreen forest communities, being one of the few Palearctic migrants which regularly inhabits montane evergreen forest (Moreau 1972, pers. obs.). In Africa the Blackcap also inhabits humid, often montane evergreen forest and Moreau suggests that the two species appear to be in competition where their winter ranges overlap. The Garden Warbler however extends much further south, being common in South Africa, whereas the Blackcap has wintering populations in Eritrea and also in the belt of acacia steppe across sub-Saharan west Africa (Moreau 1972). More strikingly, very large numbers of Blackcaps, perhaps most west-European breeding birds, winter in the Mediterranean area (Etchécopar & Hüb 1967, Leach 1981). The Blackcap appears to be adapted to wintering in colder climates than the Garden Warbler since it has a denser, heavier (by about 21%) winter plumage than the latter (Berthold & Berthold 1971).

The differences in the breeding and wintering ranges may itself indicate that the ecological requirements of the two species do not overlap completely, but this is uncertain. The greater extension northwards of the Garden Warbler's breeding range may be partly due to its later arrival in Europe in spring (Chapter 3), many Blackcaps arriving when the subarctic fringe would still be inhospitable to either species. An analogous situation occurs in Phylloscopus, where the later-arriving Willow Warbler extends well north of the more precocious Chiffchaff (Voous 1960). Perhaps the absence of the Garden Warbler from the Mediterranean in summer, and its association with humid mountain vegetation in winter, reflects an avoidance of arid woodlands. However it may be that competition between both species, other Sylvia warblers, and

FIGURE 1-1. THE GEOGRAPHICAL RANGES OF THE BLACKCAP AND THE
GARDEN WARBLER

Adapted from Moreau (1972) and Peterson et al. (1974).



perhaps other bird species as well, has been and is important too in determining the positions of their summer and winter ranges.

1-3. THE MORPHOLOGY OF BLACKCAPS AND GARDEN WARBLERS

1.3.1. Introduction

Difference in size, particularly of the bill and other structures associated with food capture, has frequently been proposed as a method of resource-partitioning between bird species (Schoener 1965, Murray 1971, Diamond 1973, 1975, Hespenheide 1975). Accordingly, the suggestion is that where such differences are small or absent the species concerned may also resemble each other in the types or sizes of food which they are best equipped to obtain, in the foraging techniques used in locating and capturing the food and/or in the habitats which they are most suited to exploit. This section compares the morphology of Blackcaps and Garden Warblers, using other Sylvia warblers as a yardstick for assessing the degree of structural resemblance between them.

1.3.2. Methods

All warblers mist-netted were weighed to the nearest 0.1g using a 50g Pesola balance, and their wing lengths were recorded (maximum chord method, Svensson 1975). Those netted by myself were mostly males attracted by conspecific-song playback. A second source of weights and wing measurements came from permanent mist nets operated by N.J. Phillips at Rough Common (see Figure 3-1) chiefly late in the season, in July, August and September. Bill measurements were taken from skins examined during this study at the British Museum (Natural History) at Tring. Tarsus measurements are from Williamson (1976).

1.3.3. Results

A. The weights of Blackcaps and Garden Warblers at Wytham.

The weights of a total of 94 Garden Warblers and 196 Blackcaps are summarised in Table 1-1. Morning weights of both adults and fledged

TABLE 1-1. WEIGHTS OF BLACKCAPS AND GARDEN WARBLERS AT WYTHAM COMPARED INTRASPECIFICALLY AND INTERSPECIFICALLY BETWEEN DIFFERENT TIMES OF DAY AND DIFFERENT STAGES OF THE SPRING AND SUMMER

Mean weights in grammes. Standard deviations in parentheses. Pairwise comparisons made by Students t-test (2-tailed). A.M. and P.M. refer to birds weighed before 10.00 hrs and after 17.00 hrs (BST) respectively.

A. Blackcap weights.			Intraspecific comparisons.		B. Garden Warbler weights.			Intraspecific comparisons.	
Adults A.M. Apr-Jul	Adults P.M. Apr-Jul				Adults A.M. May-Jun	Adults P.M. May-Jun			
16.99 (1.01), n=40	17.39 (1.17), n=37		n.s.		16.96 (0.99), n=33	18.38 (0.71), n=15		p<0.001	
Ad.males A.M. Apr-Jul	Ad.females A.M. Apr-Jul				Juveniles A.M. Jul-15 Aug	Juveniles A.M. 16-31 Aug			
16.83 (1.11), n=23	17.21 (0.84), n=17		n.s.		16.72 (0.69), n=13	17.20 (1.28), n=6		n.s.	
Ad.males P.M. Apr-Jul	Ad.females P.M. Apr-Jul								
16.80 (0.82), n=34	18.05 (1.39), n=6		p<0.01		C. Comparisons between Blackcap (BC) and Garden Warbler (GW) weights.				
Adults A.M. Apr-May	Adults A.M. 16 Aug-Sep				BC adults A.M. May-Jun	GW adults A.M. May-Jun			
17.04 (0.96), n=18	18.48 (1.13), n=13		p<0.001		17.20 (0.96), n=21	16.96 (0.99), n=33		n.s.	
Juveniles A.M. Jul-15 Aug	Juveniles A.M. 16 Aug-Sep				BC adults P.M. May-Jun	GW adults P.M. May-Jun			
16.12 (1.01), n=22	17.93 (1.52), n=39		p<0.001		17.49 (1.23), n=28	18.38 (0.71), n=15		p<0.02	
					BC juveniles A.M. Aug	GW juveniles A.M. Aug			
					17.56 (1.17), n=29	16.87 (0.94), n=15		n.s.	

- NOTES**
1. One very heavy male Blackcap (21.9g at 09.00 on 15/4/80) has been excluded. It was not seen again. The exceptional weight (2.9g more than the next heaviest spring weight recorded for a male Blackcap) suggests that it was on passage.
 2. Weights of three female Blackcaps and three Garden Warblers (not known to be males) each greater than 20g in May-Jun have been excluded. They were probably about to lay.
 3. Too few evening weights were available from late summer for both species, and too few late summer morning weights for Garden Warblers, for inclusion in the table.
 4. The period May-Jun corresponds to the major part of the breeding season for both species. See Chapter Two.
 5. n.s. = $p > 0.05$.

juveniles do not differ significantly between the two species. Adult Garden Warblers were significantly heavier (by about 0.8g on average) than adult Blackcaps in the evenings however. This is because adult Garden Warblers gained weight substantially during the day whereas adult Blackcaps were not significantly heavier in the evenings than they had been in the mornings. This observation requires further investigation with larger samples gathered in the same habitat over shorter periods of time, to control for seasonal or local prey-availability fluctuations, and a series of retrap weights for individuals of both species could prove instructive. However it is possible that a real physiological difference exists between the two species and that Garden Warblers have a tendency to accumulate weight faster than Blackcaps do. Perhaps such an ability would be of greater advantage to a long-distance migrant such as the Garden Warbler than to a short-distance traveller, such as the Blackcap.

The sexes of Blackcaps are readily distinguishable in the field, unlike those of Garden Warblers, which can not be reliably separated even in the hand. The lack of a significant weight difference between morning and evening weights applies to both male and female Blackcaps separately. However female Blackcaps were significantly heavier than males in the evenings, but not in the mornings. This is probably related to the usual pattern of egg formation in which an egg is laid early in the morning after being formed during the previous day, although the difference remains even after three very heavy females (over 20g), presumably about to lay, were excluded from the comparison.

Birds of both species might be expected to become heavier later in the season as they accumulate pre-migration fat deposits. Adult Blackcaps weighed in August and September were significantly heavier than those weighed in April and May but too few adult Garden Warblers were caught in late summer to permit a similar comparison. Juvenile Blackcaps weighed in August and September were not significantly heavier

than adults caught during the same period although three late September juveniles (weights 20.9, 21.5 & 22.4 g) were the heaviest birds caught in that month. Juvenile Garden Warblers caught in August were not significantly different in weight from juvenile Blackcaps caught in the same period. The heaviest Garden Warbler (an adult) caught in late summer was only 19.4g in weight. Migrating birds are often heavier than this; e.g. the mean weight of 23 Garden Warblers handled at Dungeness on the south coast in autumn was 20g (Williamson 1976), and some individuals of both species can attain maximum weights of about 30g when fully laden with fat (J.C.Finlayson, pers.comm., Smith 1966).

B. Bill, tarsus and wing measurements of Blackcaps and Garden Warblers.

Garden Warblers have significantly shorter and wider bills, shorter tarsi and much longer wings than Blackcaps, but bill depth is similar in the two species (Table 1-2).

C. The comparative morphology of the genus Sylvia.

1. Weight Body weight (Table 1-3) is the best comparative measure of overall size, comparisons between linear dimensions often being complicated by factors described below. On this basis the Blackcap and the Garden Warbler are virtually identical, and distinctly larger than the two other Sylvia warblers, the Whitethroat and the Lesser Whitethroat, which are also common in Britain.

2. Wing dimensions, wing shape and the tail/wing ratio

Differences in wing length may reflect differences in the lengths of migrations which different species undertake. Both in Sylvia and in Phylloscopus there is a tendency for the more migrant populations to be longer-winged than the short distance migrants and residents (Gaston 1974). However this phenomenon is most pronounced within species rather than between species in both genera i.e. resident and migratory subspecies show a clear trend towards having short and long wings respectively in intraspecific comparisons. Gaston suggests that at the interspecific level ecological niche

TABLE 1.2. BILL, TARSUS AND WING MEASUREMENTS OF BLACKCAPS AND GARDEN WARBLERS

Measurements are in millimetres. Comparisons between species made by Student's t-test (2-tailed).

	BLACKCAP				GARDEN WARBLER			
	Mean	S.D.	Range	N	Mean	S.D.	Range	N
Bill length	14.64	0.52	(13.7 - 15.7)	33	14.22	0.59	(13.2 - 15.5)	34
Bill width	4.66	0.24	(4.1 - 5.2)	33	4.87	0.28	(4.3 - 5.5)	34
Bill depth	3.89	0.35	(3.4 - 4.9)	33	4.05	0.27	(3.6 - 4.7)	34
Tarsus	21.40	0.81	-	40	20.76	0.66	-	17
Wing length	74.37	1.86	(69 - 79)	120	77.51	1.94	(73 - 81)	71
								p<0.01
								p<0.01
								n.s.
								p<0.01
								p<0.001

NOTES

1. Measuring procedures followed Svensson (1975).

2. Bill and tarsus measurements are of adults and fledged juveniles combined. In the case of the bill measurements the sample contained approximately equal numbers of males and females of both species.

3. Wing lengths are of adults. They did not differ significantly between the sexes in the case of

Blackcaps. Fledged juveniles of both species measured before mid-August had significantly shorter wings than adults but juveniles measured later in the season, nearly all Blackcaps, had achieved adult wing length.

TABLE 1-3. A COMPARISON OF THE WEIGHTS, BILL LENGTHS AND TARSUS LENGTHS
OF SYLVIA WARBLERS

SPECIES	WEIGHT (g.) W	N.	Relative bill length (Bill/ $\sqrt[3]{W}$)	Relative tarsus length (Tarsus/ $\sqrt[3]{W}$)
Blackcap	17.0	40	5.5	8.2
Garden Warbler	17.0	33	5.4	8.0
Whitethroat	14.3	200	5.5	9.0
Lesser Whitethroat	12.5	78	4.9	8.5
Barred Warbler	20.8	50	6.0	8.9
Orphean Warbler	20.0	24	6.0	8.7
Sardinian Warbler	12.1	393	5.5	9.1
Subalpine Warbler	9.5	161	4.8	8.7
Spectacled Warbler	8.1	3	5.8	9.3
Dartford Warbler	9.0	9	5.2	9.4

- NOTES
1. Weights of Blackcaps and Garden Warblers are from the present study and those of Orphean, Sardinian and Spectacled Warblers from Finlayson (1979). The remainder are from Williamson (1976).
 2. Weights are means of the largest available series from breeding birds or spring migrants, i.e. avoiding heavy birds trapped as autumn migrants in Europe.
 3. Bill and tarsus lengths are from Williamson (1976).
 4. The data presented refers to nominate subspecies only.

differences are more important in determining relative wing length than distance of migration. Relative wing length, taking into account interspecific differences in size, can be expressed by plotting the square of mean wing length (W^2) against $\log_{10}$ weight, these two functions being related in an approximately linear fashion for flying birds (Hartman 1961). This relationship is clearly exhibited by Sylvia warblers (Figure 1-2) and the Blackcap and Garden Warbler are in close proximity to each other.

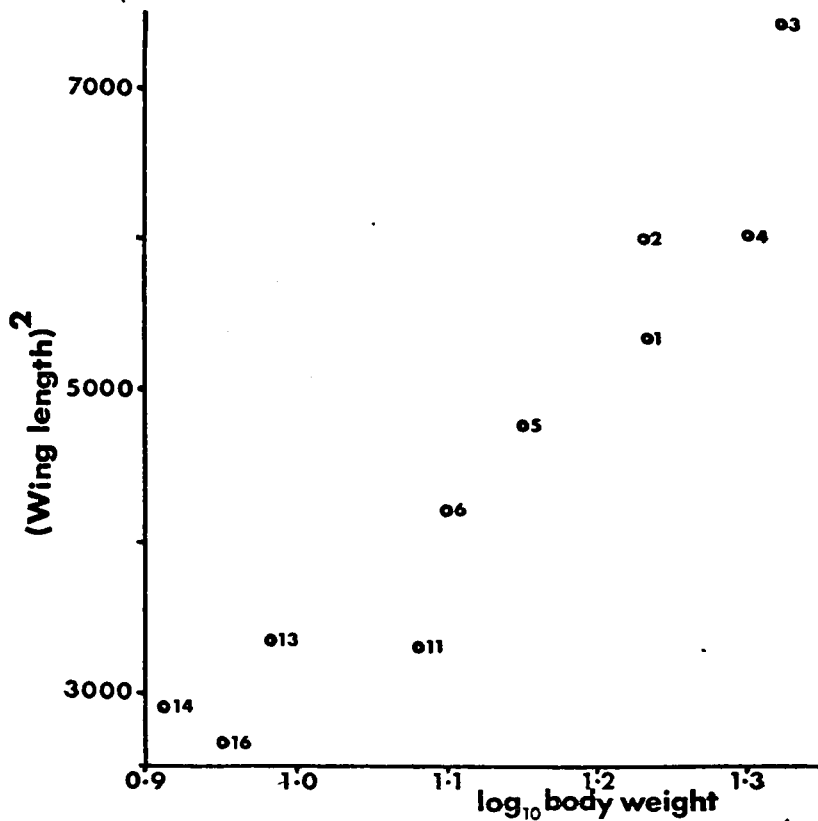
In both Phylloscopus and Sylvia there is a relationship between wing shape and migration distance. Wing shape can be expressed as an index of roundness, based on the length of the first primary (numbered descendantly) in relation to the total wing length (Gaston 1974:433). Indices of roundness may be plotted against tail/wing ratio to obtain an illustration of the relative position of warbler species in respect of weight, wing dimensions and tail length (Figure 1-3). It is seen that there is a clear separation between two groups of Sylvia species. Those with the lowest indices of roundness (most pointed wings), including the Blackcap and the Garden Warbler which are in close proximity in the Figure, are all migratory whereas the largely resident species of the Palearctic deserts and the Mediterranean maquis are comparatively round-winged.

Arboreal species are relatively shorter-tailed (or longer winged) than those inhabiting scrub and other low vegetation. This is believed to show the tendency of species living on the ground or in low dense vegetation to have long tails in order to balance while maintaining a necessarily horizontal stance as they walk or thread their way through dense cover (Gaston 1974). The Garden Warbler is relatively the shortest-tailed (longest-winged) of the genus but the next-closest species to it in this respect is the Blackcap, followed by the other migrant species.

3. Bill and tarsus lengths

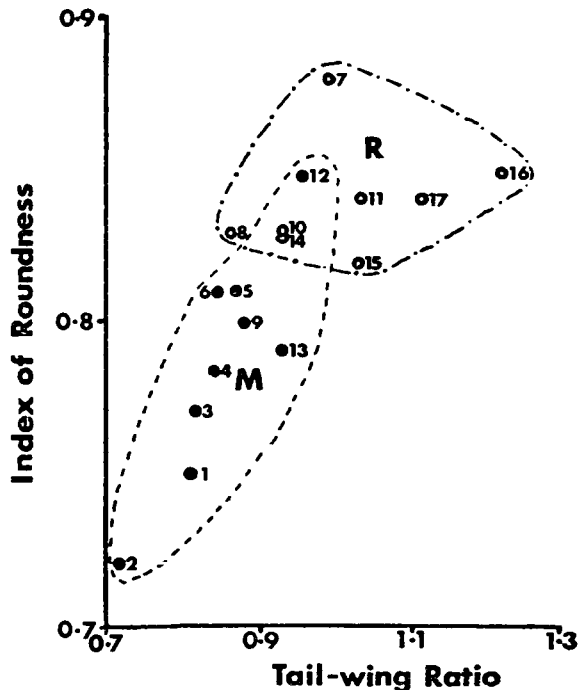
Bill and tarsus lengths can be compared between species by dividing each by the cube root of body weight (Table 1-3). Only

FIGURE 1-2. RELATIVE WING LENGTH IN SYLVIA WARBLERS



NOTES. 1. All wing lengths are means from Williamson (1976).
2. Body weights are as given in Table 1-3.

FIGURE 1-3. THE RELATIONSHIP BETWEEN THE INDEX OF WING ROUNDNESS AND THE TAIL-WING RATIO IN SYLVIA WARBLERS



KEY TO SPECIES (W = warbler)

1 Blackcap	9 Ruppell's W
2 Garden W	10 Cyprus W
3 Barred W	11 Sardinian W
4 Orphean W	12 Menetries's W
5 Whitethroat	13 Subalpine W
6 Lesser Whitethroat	14 Spectacled W
	15 Tristan's W
7 Arabian W	16 Dartford W
8 Desert W	17 Marmora's W

NOTES. 1. M = migrants (●), R = residents or partial migrants (○).
2. Species 1 - 4, and 13 (partly), mainly inhabit woodlands. The remainder are characteristic of scrub.
3. Only nominate subspecies are included. The data used is from Williamson (1976)

ten data points are available since few reliable weights have been published for the genus.

Bill lengths do not show any clear relationship with preferred habitat but the general consensus in the literature is that species of low cover tend to be longer-legged than arboreal congeners (Grant 1966). This pattern is found in Phylloscopus. In Sylvia the two most arboreal species are the Blackcap and the Garden Warbler and they are also the shortest-legged. Next comes the Lesser Whitethroat (ssp. curruca) which although not a woodland bird in Britain does exhibit a preference for vegetation with a tall vertical structure, such as hedgerows. On the continent the Lesser Whitethroat is a forest bird at high altitudes (Voous 1960). Of the remaining species for which data is available the shortest legs are those of the Barred and Orphean Warblers, both woodland species, and also the Subalpine Warbler, a species of open woodland with a tall, dense undergrowth (pers.obs.). All the other species in Table 1-3 inhabit medium to very low scrub.

Bill length differences are generally related to differences in the size of insect prey taken and differences in tarsus length to differences in foraging strategies. The coefficient of variation for mean tarsus length is greater than that for mean bill length ($F_9 = 1.20$, $p > 0.05$) but the difference is not significant, unlike in Phylloscopus (Gaston 1974). Hence in Sylvia, unlike in Phylloscopus, intra-generic adaptation cannot be said to have proceeded mainly by evolution of distinct behavioural strategies between species. Nevertheless, within the genus, the close proximity of the Blackcap and the Garden Warbler in respect of both morphological parameters further suggests that they are similarly equipped to exploit their environment.

4. Plumage

The most striking physical difference between Blackcaps and Garden Warblers is in plumage. Here the two are separated by the span of virtually the entire genus. The Garden Warbler is at one extreme (with the Desert Warbler) in having an identical plumage in both sexes. It is a mousy grey-brown, paler on the underside. The Blackcap shows striking sexual

dimorphism between the black-capped males and the brown-capped females. Other Sylvia warblers tend to be intermediate, females resembling pale versions of males (Subalpine & Barred Warblers) or having dark grey replacing the black head markings of males (Sardinian & Ruppell's Warblers). The reason for the plumage difference between the Blackcap and the Garden Warbler remains unknown but it provides grounds for believing that they can distinguish each other on sight.

1.3.4. Discussion

The selective pressures which have shaped the morphology of both the Blackcap and the Garden Warbler can be divided into three categories. Firstly the physical dimensions of both must be partly a response to the foraging opportunities of their breeding grounds. Secondly, both species must be equipped to perform two migratory journeys each year, these being much longer for Garden Warblers than for many Blackcaps. Thirdly, the morphology of both may be partially moulded by the ecological opportunities of the winter quarters and the competitive regime which they encounter there, which may be very different from that of the breeding grounds. In short, like other migrant birds, the morphology of both warblers is probably a compromise between the requirements of a travelling life during part of the year and a largely sedentary existence during the remainder.

It is unknown whether the morphology of the Blackcap and the Garden Warbler has been formed primarily by ecological selective pressures or by the requirements of migration, let alone whether one type of selection has been more important in its effects on one species than on the other. However the only large size difference to emerge from the data analysed is the difference in wing length and this seems most likely to be due to the difference in length of migration between them. In general it is clear that the two species are closer to each other in morphological similarity than either of them is to any other Sylvia species.

1.4. THE FORAGING BEHAVIOUR OF BLACKCAPS AND GARDEN WARBLERS

1.4.1. Introduction

Qualitative descriptions of the foraging behaviour of both species assert that Garden Warblers forage low down in the vegetation and Blackcaps higher up, in the canopy (Lack 1971, Moreau 1972). Lack suggests this vertical separation as a way in which the two are able to coexist. A quantitative comparison in Sweden (Cody 1978) showed Garden Warblers to be restricted to the lower levels of vegetation and scarcely overlapping with Blackcaps, which foraged higher up. Unfortunately the sample size was very small (two Blackcap and six Garden Warbler territories) and it was not made clear whether the vegetation height distribution in the territories gave both species similar opportunities to forage over the same vertical height range. Horizontal separation (interspecific territoriality) is pronounced between the two species (Chapter 3) so that vertical separation would seem to be unnecessary for interspecific segregation, at least during the breeding season. Nevertheless some observations of foraging birds were made in order to contribute to the general picture of their behaviour in the study areas.

1.4.2. Methods

Preliminary observations showed that Blackcaps and Garden Warblers often forage in the interior of dense vegetation, and hence suggested that a thorough comparison of their foraging behaviour would take too long to be within the scope of the present study. Observations were confined to recording the heights at which foraging birds were first encountered, the substrates on which they foraged and the techniques which they were first seen to employ when capturing food, on as many separate occasions (different days) as possible. Nevertheless the total number of such observations made was small. The height of the woodland canopy was found to average about 20 metres, using the method of Mitchell (1974). Foraging heights below about ten metres were estimated by comparison with the length of a three metre-long mist-net pole. Observations of birds foraging higher up were difficult to estimate with any accuracy and

were simply classified as being between ten and fifteen metres or over fifteen metres above the ground. No observations of Garden Warblers were made before early May and few later than early July so that, for comparative purposes, observations of Blackcaps made outside May and June are not considered here.

Colour-ringed Blackcaps and Garden Warblers were rarely seen outside their territories until their young had fledged, when they wandered widely. Perhaps warblers are harder to observe outside their territories, particularly if they are trying to forage undetected in those of neighbours, but nevertheless the lack of sightings suggests that in both species the territory provides the food and other requirements of adults and young throughout the nesting season.

1.4.3. Results

A. Foraging height.

Foraging heights are compared separately for birds occupying territories dominated by scrub and those in woodland proper, since in general scrub territories offered fewer opportunities for high-level foraging than woodland ones, even though most of the former included one or two tall trees (as described in Chapter 3).

The heights at which foraging adults of both species were first observed are compared in Figure 1-4A. The figure includes only one observation, the first made, per bird, this ensuring that the comparison is free from bias due to over-sampling of a few individuals. Foraging heights did not differ significantly between the species in either woodland or scrub areas (Mann-Whitney U Test, 2-tailed, $p > 0.05$ in both cases). Both foraged mainly at levels of up to six metres, i.e. chiefly in the shrub layer when in woodland, but the vertical extent of foraging activity covered the full span of the available vegetation height. There is no indication in the limited data available that Garden Warblers avoid the canopy or that Blackcaps prefer to forage high up. In support of the former observations, data is presented for two Garden

FIGURE 1-4. THE HEIGHTS AT WHICH FORAGING BLACKCAPS AND GARDEN WARBLERS WERE FIRST OBSERVED

A. The foraging height distributions of Blackcaps (BC) and Garden Warblers (GW) holding territories in areas dominated by woodland or by scrub

Only one observation, the first made, is included for each individual. The Figure comprises pooled observations from all three years of the study.
 n = the number of different birds observed.

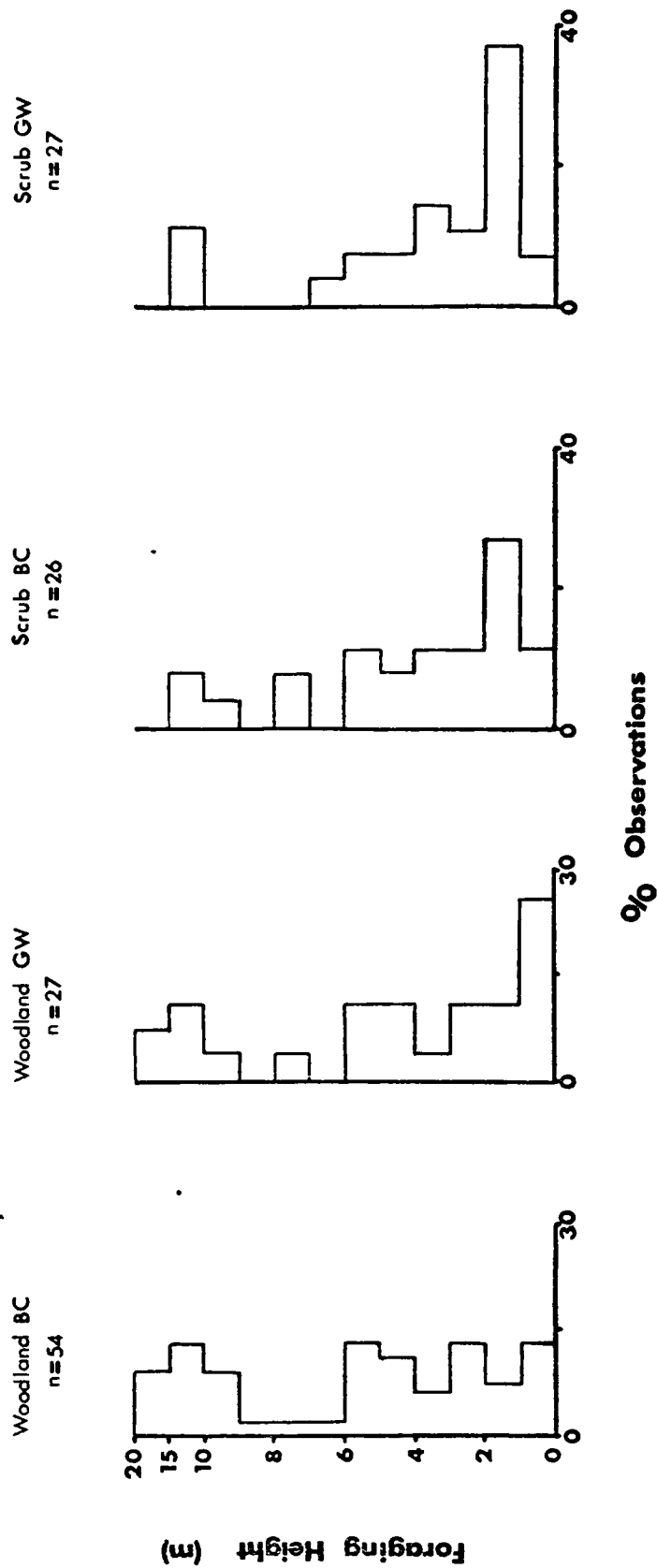
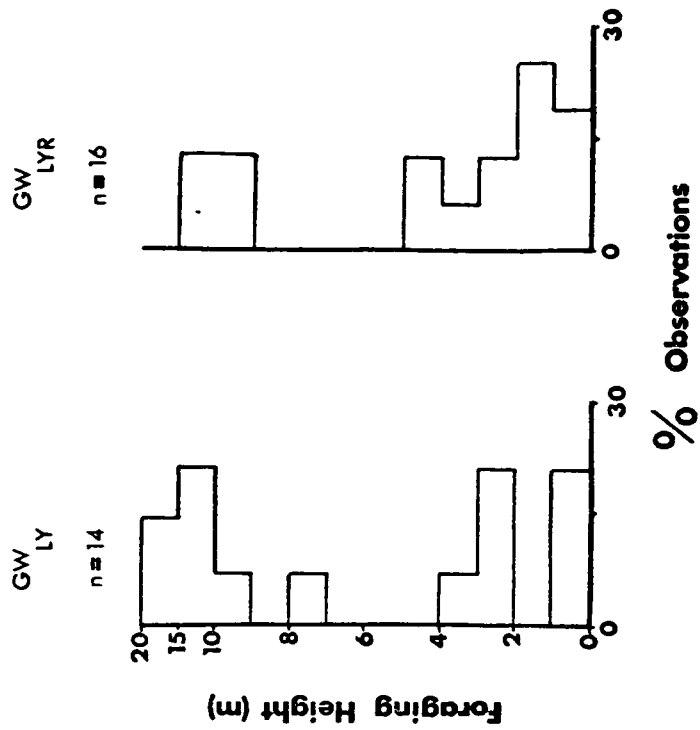


FIGURE 1-4 (continued)

B. The foraging height distributions of two Garden Warblers holding territories in woodland

n = the number of observations made



Warblers, both inhabiting woodland territories, for which a number of separate observations of foraging heights were made (Figure 1-4B); neither bird avoided the canopy.

B. Foraging substrates.

A more intensive study is required to establish whether the two species use different substrates to different extents. However both are primarily foliage-gleaners, taking insects from leaves and twigs from the full range of available trees and shrubs. Although they often forage low down they were not seen to do so in much of the ground vegetation (grasses, Dog's Mercury, nettles), although brambles were searched by both species.

C. Foraging methods.

Both Blackcaps and Garden Warblers are comparatively sluggish when foraging and the great majority of insect captures involved taking settled prey (Table 1-4). The most active (and hence energy-costly) technique is fly-catching and this was rarely seen in either species. All the fly-catches seen to be performed by Blackcaps were aimed at the large, slow-moving Bibionidae which were numerous during early spring. Since these could easily be caught by myself by hand it probably did not require great agility for the birds to capture them. In contrast, the Phylloscopus warblers (which are about half the weight of the large Sylvia species) were often seen fly-catching, especially when attacking swarms of midges (Chironomidae) and mosquitoes (Culicidae). Such insects are probably too small to be an economical food resource for Sylvia warblers to catch in this energetic way.

1.4.4. Discussion

The limited data available has failed to reveal any conspicuous differences in the foraging behaviour of Blackcaps and Garden Warblers. Both take most of their food by foliage-gleaning, searching mainly in the shrub layer but also using canopy vegetation if it is available within their territories. The overall similarity in morphology between both species might

TABLE 1-4. THE COMPARATIVE FREQUENCY OF DIFFERENT FOOD CAPTURE METHODS USED BY BLACKCAPS AND GARDEN WARBLERS

	<u>Number of observations of each food-capture method</u>					TOTAL
	Stand-pick (P)	Leap-pick (LP)	Hover-pick (HP)	Leap-catch (LC)	Fly-catch (FC)	
BLACKCAP	34	3	7	0	2	46
GARDEN WARBLER	24	4	7	0	2	37

The proportion of active (LP,HP,LC & FC) to static (P) food-capture attempts does not differ significantly between the two species;
 $\chi^2 = 0.005$, d.f.=1, $p > 0.05$.

- NOTES
1. Only one observation per individual bird is included.
 2. The method used for the first observed food-capture attempt only is tabulated.
 3. All birds were adults observed in May or June.
 4. The methods tabulated are as defined by Davies & Green (1976).

make the existence of large differences in foraging behaviour seem unlikely. However, the foraging methods employed by different species are only partly a function of morphology. For example, Reed Warblers use more active techniques, such as fly-catching, when they are feeding young and need to gather as much food as they are able to (Davies & Green 1976). Moreover, efficient insectivory probably requires a capacity to adjust foraging behaviour in response to changes in prey behaviour and availability. For example, below certain threshold temperatures flies are sluggish and unable to take off (Taylor 1963), and clearly fly-catching is only employable when flying insects are available. However, both Blackcaps and Garden Warblers are undoubtedly predators of settled insects mainly and so their foraging behaviour is less likely to be affected by external factors than that of the Phylloscopus species and other "flycatchers".

1.5. THE FOOD OF BLACKCAPS AND GARDEN WARBLERS AT WYTHAM

1.5.1. Methods

A comprehensive analysis of the diet of the two species, involving the use of emetics or gut-analyses of killed birds, was incompatible with the need to maintain largely-undisturbed subjects for observation of territorial behaviour. Nevertheless, some indication of the food of insectivorous birds can be obtained by direct observation, by analysis of faeces and by intercepting food brought to pulli by using collars of pipe-cleaner to prevent swallowing of food balls (Davies & Green 1976, Davies 1977).

Direct observation was useful early in the season when available prey-diversity was probably low and birds (Blackcaps) spent much time eating aphids and other obvious foods, such as fruits. Frugivory in autumn was also directly observable. At other times it was often impossible to see what prey was being taken, especially when birds were feeding in the canopy.

Faeces were collected whenever possible. Adults and fledged juveniles were kept in bags to await ringing and they normally left a sample there. This was the main source of faeces of full-grown birds. Pulli readily

voided a faecal sac when they were handled (possibly as a shock-reaction since pulli handled daily from a very early age were less prone to defaecate than those from broods discovered at a later stage). Recently-fledged young of both species are fed by the parents for several days after leaving the nest (Howard 1907-1914). Five such broods of Blackcaps (but not Garden Warblers) were located, the young sitting huddled together in low cover being attended by the adults, and large numbers of faeces were collected from beneath their perches. Individual faeces from all sources were kept as distinct samples in 70% ethanol. Faeces were individually boiled gently in 15% Potassium Hydroxide solution. This dissolved the uric acid and soft organic residues, leaving a clear liquid in which caterpillar jaws, insect wings, other arthropod exoskeletal fragments and seeds were suspended. The liquid was examined under low-power binocular magnification and identifiable remains were sorted and counted.

The pipe-cleaner collars were used once-daily on nestlings aged between two and seven days. Newly-hatched pulli seemed unable to raise their heads when they had collars on and there was a risk that pulli near to fledging might "explode" from the nest still wearing the collars. Collars were left in situ for 20 minutes and the food balls (henceforth called collar-samples) then removed using forceps. They comprised several insects bound together in a mucilaginous mass, which made it unlikely that tiny items could be swallowed so biasing the sample in favour of large items, as suggested by Orians (1966). Collar samples were preserved in alcohol and later examined under the binocular microscope.

Arthropods were identified using standard field guides, notably Chinery (1976), Linssen (1959) and Collyer & Hammond (1968). Specimens were identified to order, and to family where possible in the cases of Diptera and Coleoptera especially. Seeds were compared with those from a reference collection of fruits collected in the wood.

1.5.2. Results

A. A general description of the foods of Blackcaps and Garden Warblers

Both species are primarily insectivorous although both eat many fruits before and during their autumn migration (pers.obs., Kroll 1972). In northern Europe fruit is only a supplement to the diet and arthropods remain an essential component, since both species lose weight rapidly and eventually die if fed exclusively on north-European fruits (Berthold 1976). Blackcaps wintering in the Mediterranean area are predominantly frugivorous but the fruits available there in winter are relatively nutritious, with a high lipid content (Herrera 1981). In Africa both species are reported to eat many fruits (Moreau 1972, Pearson 1972). A few Blackcaps winter in Britain, where they rely heavily on fruits, and on exotic foods (bread, fat, peanuts) available on garden bird-tables (Leach 1981)

The first Blackcaps arrive in British woodlands in April when the main tree species are still in bud and foliage is limited to the bramble ground layer, ivy and certain shrubs, notably hawthorn. Nevertheless insects are probably the main part of the diet at this time, although ivy berries are also eaten if available (Howard 1907-1914, pers.obs.) and nectar-eating may occur (see below). Sycamore buds are among the first to burst in spring and as they do so they become covered in aphids, which were picked-off by many Blackcaps in April and early May at Wytham. The arrival of the first Garden Warblers in early May occurs when the foliage is better-developed and insects are manifestly abundant.

B. The diet of the two species at Wytham

A rigorous comparison of the diet of the two species requires material gathered at the same time of year and in the same habitats in both cases, in order to avoid distortions due to seasonal changes in prey-availability and to local differences in the abundance of certain prey types. Comparisons between data gathered in different years may be complicated by between-year differences in prey-availability and seasonality.

A total of 179 faeces and 18 collar-samples were obtained from Blackcaps and 68 faeces and 19 collar-samples from Garden Warblers, in 1978 and 1979 combined. This total is too small to enable allowances to be made in the analysis for the different times of year and habitats in which the individual samples were collected. Moreover, a substantial number of the faeces from both Garden Warblers (53 %) and Blackcaps (31 %) were collected from pulli. However, warbler nests proved hard to find so that all these faeces, and all the collar-samples, came from just five and six nests respectively. This means that the samples are highly likely to be biased if any pairs had access to localised prey types which just happened to be particularly numerous near their nests but were not uniformly available throughout the wood. This bias probably affected the sample. For example, one of the Blackcap nests yielded 22 faecal sacs and remains of the Scorpion Fly Panorpa communis were found in 17 of them. This order (Mecoptera) was not represented at all in the Garden Warbler sample. Nevertheless it would be premature to take this as an example of an interspecific difference in prey-selection, particularly since Panorpa was only found in three other Blackcap faeces. Instead it seems more likely that only Blackcaps at that particular nest had ready access to Scorpion Flies.

A further bias is that the tendency of certain prey types to occur in clumps (e.g. aphid clusters) can result in their easily being numerically over-represented in the overall sample if faeces from birds feeding on such prey are encountered. This bias has been partly compensated-for in the analysis by considering both the number of samples in which a particular prey type was found and the total number of prey individuals detected.

In the absence of a really representative collection of prey remains, which would require finding large numbers of nests or killing many birds, the material gathered lends itself only to a general, mainly qualitative analysis. The central question of whether Blackcaps and Garden Warblers take different prey species or sizes, or the same foods in different

proportions, (which might enable them to coexist) can not be answered definitively by the present study.

1. Prey diversity.

The range and abundance of prey items identified in the diets of both species are given in Table 1-5. Arthropods, chiefly insects, occurred in all the faeces and collar-samples, even in faeces from birds which were feeding on fruit, showing that frugivory in autumn is not exclusive.

Non-insects were represented by a woodlouse found in a Blackcap collar-sample, by gastropod molluscs and by arachnids. The gastropods were tiny shells (2 mm) found in a few samples from pulli of both species, and in faeces of two adult Blackcaps. Some birds, for example tits (Perrins 1979), bring snail shells and bits of bird egg-shell to their young occasionally, presumably as a calcium supplement to the diet. Adult Blackcaps have also been recorded eating small snails in quantity when on passage through Denmark (Laursen 1978). More arachnids were found in the Blackcap sample than in the material from Garden Warblers but in both cases they accounted for only a very small proportion of the animal prey taken (1.3% and 0.6% of identified items for Blackcaps and Garden Warblers respectively). Arachnids are liable to under-representation in faeces. They lack wings, which tend to pass through birds largely undamaged (Davies 1977), and their exoskeletons are more delicate than those of large insects. Spiders in the collar-samples were barely recognisable whereas insects kept their shape well. Some arachnids were probably overlooked but it remains certain that insects make up the bulk of the diet of both warblers during the breeding season.

2. The representation in the diet of different insect groups

Three insect orders, Diptera, Coleoptera and Lepidoptera, made up over 75% of the diets of pulli of both species, and of fledged Blackcaps. Hemiptera were also important in the diets of adult Blackcaps and Garden Warblers. The remaining orders (excluding Mecoptera) were represented only by a few individual items (Tables 1-5, 1-6).

TABLE 1-5. THE PREY ITEMS IDENTIFIED IN FAECES AND COLLAR SAMPLES FROM BLACKCAPS (BC) AND GARDEN WARBLERS (GW)

The table shows the minimum number of prey items detected. The number of samples in which each taxon was found is given in parentheses. 0 = order, F = family, U.I.D. = unidentified. n = total number of samples.

TAXON	BLACKCAP FAECES			GARDEN WARBLER FAECES			COLLAR SAMPLES		
	PULLI	FLEDGED JUVENILES	ADULTS	TOTAL BC FAECES	PULLI	ADULTS	TOTAL GW FAECES	BC	GW
	n = 56	n = 60	n = 63	n = 179	n = 36	n = 32	n = 68	n = 18	n = 19
A. Class INSECTA									
O. DIPTERA									
f. Bibionidae	11 (8)	-	27 (8)	38 (16)	2 (2)	2 (1)	4 (3)	8 (4)	2 (2)
f. Stratiomyidae	-	-	2 (2)	2 (2)	-	-	-	-	-
f. Tipulidae	26 (25)	43 (37)	17 (14)	86 (76)	9 (8)	3 (3)	12 (11)	7 (4)	8 (4)
f. Scatophagidae	3 (3)	1 (1)	3 (3)	7 (7)	1 (1)	-	1 (1)	-	1 (1)
f. Muscidae	9 (8)	-	3 (3)	12 (11)	3 (3)	-	3 (3)	2 (2)	3 (3)
f. Empididae	2 (2)	3 (3)	1 (1)	6 (6)	-	-	-	1 (1)	-
f. Cecidomyiidae	-	2 (2)	1 (1)	3 (3)	-	-	-	-	-
f. Syrphidae	1 (1)	1 (1)	-	2 (2)	2 (2)	1 (1)	3 (3)	-	7 (4)
f. Rhagionidae	-	-	-	-	-	-	-	1 (1)	-
f. Culicidae	-	-	-	-	-	-	-	1 (1)	3 (2)
f. Otitidae	-	-	-	-	1 (1)	-	1 (1)	-	-
f. Milichidae	-	-	-	-	2 (2)	-	2 (2)	-	-
f. Chironomidae	-	-	-	-	-	-	-	-	-
U.I.D. Diptera	31 (27)	24 (21)	1 (1) 69 (42)	1 (1) 124 (90)	35 (23)	20 (18)	55 (41)	1 (1)	16 (9) ⁱⁱ
O. COLEOPTERA									
f. Coccinellidae	14 (9)	30 (26)	20 (17)	64 (52)	13 (12)	3 (3)	16 (15)	1 (1)	3 (2)
f. Cantharidae	-	11 (8)	-	11 (8)	-	-	-	4 (1)	-
f. Cerambycidae	-	-	-	-	-	-	-	-	3 (2)
f. Curculionidae	4 (4)	1 (1)	2 (2)	7 (7)	7 (4)	3 (2)	10 (6)	-	-
U.I.D. Coleoptera ⁱⁱⁱ	39 (21)	88 (52)	81 (39)	208 (112)	51 (30)	23 (16)	75 (46)	8 (5)	7 (4)
O. LEPIDOPTERAⁱⁱⁱ									
	112 (40)	36 (33)	16 (11)	164 (84)	69 (30)	24 (8)	93 (38)	13 (9)	15 (12)

i. includes Calliphoridae, ii. includes 13 larvae, all other Diptera are imagos, iii. caterpillars

(Continued)

TABLE 1-5. (continued)

TABLE 1-6. (continued)

B. THE PERCENTAGE CONTRIBUTION MADE BY EACH ORDER TO THE TOTAL NUMBER (n) OF INDIVIDUAL ANIMAL PREY ITEMS IDENTIFIED

ORDER	FAECES						COLLAR SAMPLES	
	Pulli			Adults ⁱ			TOTAL GW ⁱ	
	BC n = 276	GW n = 202	Fledged BC juveniles n = 256	BC n = 1100	GW n = 364	FAECES n = 1632	FAECES n = 566	BC n = 51
DIPTERA	30.1	27.2	28.9	11.3(46.1)	7.1(30.6)	17.2(35.4)	14.3(28.2)	41.2
COLEOPTERA	20.6	35.1	50.8	9.4(38.3)	8.0(34.1)	17.8(36.5)	17.8(35.2)	27.5
LEPIDOPTERA	40.6	34.2	14.1	1.5 (6.0)	6.6(27.1)	10.1(20.6)	16.4(32.4)	25.5
HEMIPTERA	0.4	1.0	5.1	75.9	77.5	52.0	50.1	1.9
MECOPTERA	7.6	0	0.8	0.1	0	1.4	0	1.9
NEUROPTERA	0	1.0	0	0.8	0.3	0.6	0.5	1.9
HYMENOPTERA	0.7	0	0	0.7	0	0.6	0	0
DERMAPTERA	0	0	0.4	0.3	0	0.2	0	0
ODONATA	0	1.5	0	0	0	0	0.5	0
PSOCOPTERA	0	0	0	0.1	0.5	0.1	0.4	0
ORTHOPTERA	0	0	0	0	0	0	0	0
EPHEMEROPTERA	0	0	0	0	0	0	0	0
								1.2
								1.2

i. Numbers in parentheses are the percentage contributions made to the total sample by Diptera, Coleoptera and Lepidoptera after excluding the large number of aphids found in the faeces of adult warblers.

a) Diptera The commonest family identified in the diet of both species was the Tipulidae (crane flies), which includes large, slow-moving insects which are probably easily captured (since I could do so myself by hand). Ease of capturability is also a characteristic of the Bibionidae, the next-commonest family in the Blackcap sample but one less apparent in the Garden Warbler sample. A relatively obvious family at Wytham, the Syrphidae (hover flies), was better represented in the Garden Warbler sample than in the Blackcap sample. Syrphids are very fast fliers and this could be taken to suggest that Garden Warblers are more adept at capturing elusive prey. Some of them may have been gleaned from the foliage, perhaps early in the morning when they were still inactive. However the seven syrphids from Garden Warbler collar samples were all taken around 13.00 hours on warm June days. The Muscidae and Calliphoridae were abundant in the wood in summer 1978 but they were not particularly numerous in the warbler diet samples. Like syrphids, they would be comparatively difficult to catch.

b) Coleoptera Coleoptera were abundant in the sample but few could be identified even to family. A surprising discovery was the prominence of the Coccinellidae (ladybird beetles), which occurred in 29% of the Blackcap faeces samples and 22% of the Garden Warbler faeces samples, comprising 22% and 16% respectively of the total number of individual beetles detected. They were also found in collar-samples from the two species (Table 1-5). In addition, two pellets regurgitated by members of a recently-fledged Blackcap brood contained elytra of a total of five 7-spot Ladybirds Coccinella septempunctata (as well as of 5 Cantharid beetles and 2 caterpillars).

Ladybirds (and also cantharid beetles) are reputedly highly distasteful and their bright patterns have been widely described as an example of aposematic coloration. There are few records of their consumption by birds (Imms 1947). For example in a recent study of the diet of the Dartford Warbler only one ladybird was found among 3544 prey items identified, although ladybirds were abundant in the study area (Bibby 1978). Similarly only one ladybird was identified among 4621 prey items brought to nestling

Spotted Flycatchers (N.B.Davies, pers.comm.). Bibby found ladybirds and ants (also generally avoided by birds) in the stomachs of a Whitethroat and three Pied Flycatchers obtained as road casualties in France in September. He suggests that the birds were probably hungry migrants which had been driven to eat prey which they would normally avoid. This could also explain the presence of a total of 16 ladybirds in 12 stomachs (out of 80 examined) of Garden Warblers captured on Heligoland during their autumn migration (Kroll 1972). It is unknown whether aposematically-coloured insects were only being consumed at a time when other prey types were scarce. Virtually all ladybirds taken by adult warblers were eaten either early or late in the season, in April and early May and in July and August. Similarly most of the ladybirds and cantharids brought to pulli and recently-fledged young were collected in late June and in July, after the peak period of caterpillar availability, suggesting that they were being taken at a time of food shortage. Information on the relative availability of distasteful insects and other potential prey in the wood at different times of the season is required to clarify whether ladybirds and cantharids are normally eaten by warblers.

c) Lepidoptera Caterpillars were prominent in the diet of both species in May and June but they were rarely found later or earlier and were probably unavailable then. The larvae of several species are abundant on oak foliage at Wytham in early spring (Varley et al. 1973), descending to pupate underground in June. Many insectivorous birds, notably tits (Perrins 1979) and warblers have young in the nest in late May and early June when the caterpillar density on the oaks is highest. Later in the season this food resource is absent and this may contribute to the fact that late broods of tits (Perrins 1979) and warblers (Chapter 2) are smaller than those started early in the season.

Clearly caterpillars are an important component of the diet of young warblers. They may even be the most important prey when they are available since they were eaten to the almost total exclusion of Coleoptera by pulli in early June, this otherwise important taxon appearing

in the diet of pulli only from mid-June onwards. Both Blackcap and Garden Warbler broods fit into a pattern in which a progressive decline in the frequency of caterpillars is matched by a compensatory increase in the numbers of Coleoptera and, to a lesser extent Diptera, brought to them (Figure 1-5). Other taxa have a variable but minor representation in the diet of pulli throughout the breeding season.

d) Hemiptera The great majority of the hemipterans detected were aphids, which were eaten in quantity by adult Blackcaps and Garden Warblers in April and the first half of May. Many faeces collected at this time contained remains of several dozen aphids, with maxima of about 200 found in two Blackcap faeces in April. Aphid remains were rarely found later, although the insects were abundant on sycamore leaves especially throughout the summer. Only five individuals figured in the diet of pulli. The fact that aphids were eaten commonly only early in the season suggests that they were being taken mainly at a time of food scarcity for both species.

3. Consumption of plant material

Fruit seeds and skins were found in faeces of both species from late July onwards, although few faeces were examined from this period (Table 1-7). Little or no fruit was available earlier in the breeding season and none was known to have been brought to pulli.

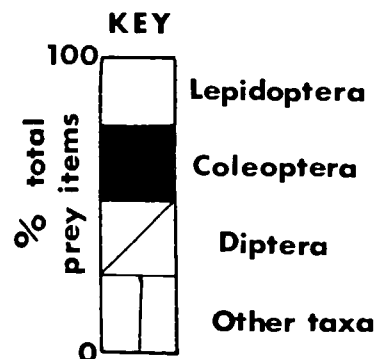
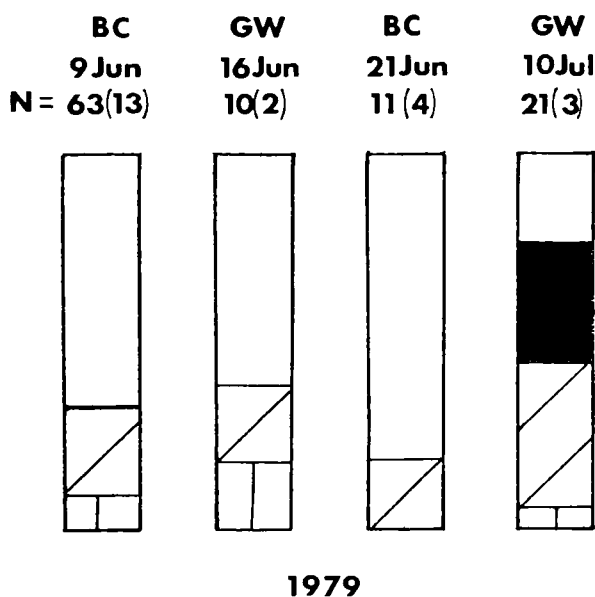
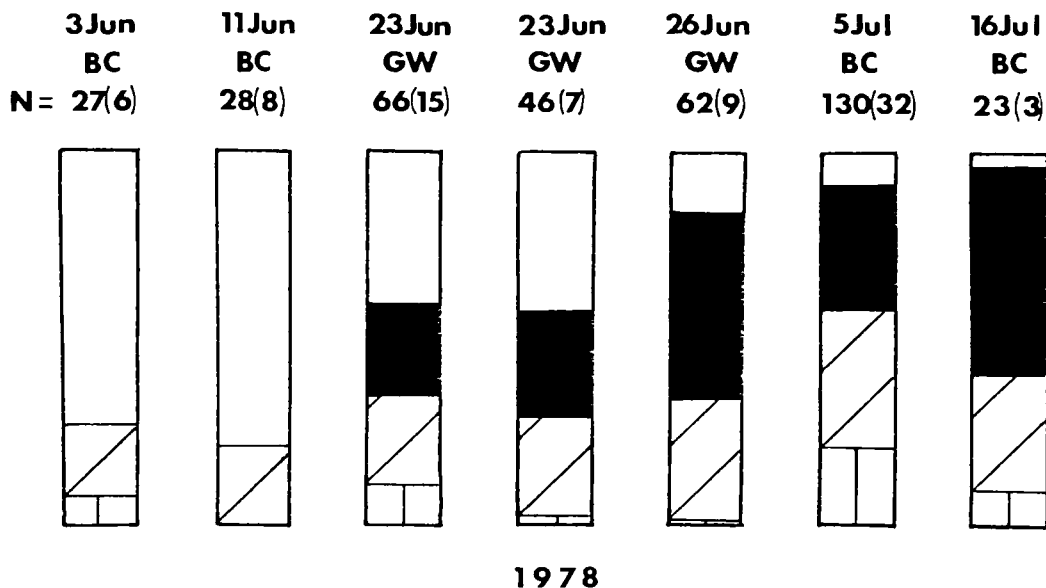
Tiny leaf fragments, too small to be likely to have had any nutritional significance, were found in the faeces of both species at all ages. Most or all of these were probably actually eaten originally by caterpillars and other herbivorous insects captured.

Tiny anthers, probably of hawthorn, were found in several faeces. Most samples in which they occurred contained between one and three anthers and probably they had been ingested accidentally. However, the faeces of an adult Blackcap handled on 22 July 1978 contained over 300 anthers. This is comparable with a single Garden Warbler, out of 166 examined by Laursen (1978), which contained 86 hawthorn stamens in its stomach. None of the 170 Blackcaps

FIGURE 1-5. THE CHANGE IN THE RELATIVE PROPORTIONS OF THE MAJOR PREY TAXA FOUND IN THE DIET OF BLACKCAP (BC) AND GARDEN WARBLER (GW) FULLI AS THE BREEDING SEASON PROGRESSES, AS SHOWN BY FAECAL SAC AND COLLAR SAMPLE CONTENTS

Each column summarises all the material obtained from one brood. n = the total number of prey items obtained. The total number of samples examined is given in parentheses. Dates are medians for the samples obtained from each brood and columns are in order of date from left to right.

A. FAECAL SACS



continued

FIGURE 1-5. (continued)

B. COLLAR SAMPLES

The first sample on the left was collected in 1979. The others in 1978.

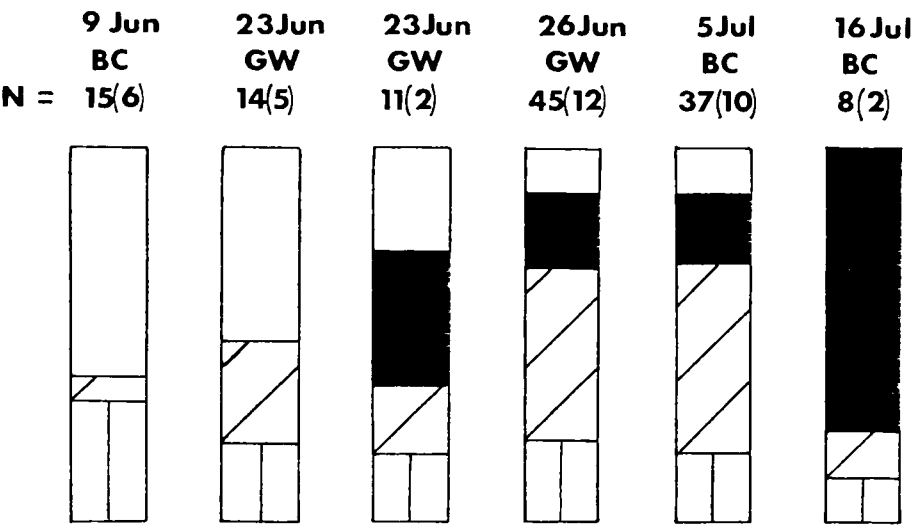


TABLE 1-7. THE VEGETABLE MATERIAL IDENTIFIED IN FAECES OF BLACKCAPS (BC) AND GARDEN WARBLERS (GW)¹

The table shows the number of samples in which each kind of item was found. n = the total number of samples.

ITEM	Pulli		Fledged BC juveniles n = 60	Adults		TOTAL BC		TOTAL GW	
	BC n = 56	GW n = 36		BC n = 63	GW n = 32	FAECES n = 179	FAECES n = 68		
A. FRUIT									
Elder	-	-	-	3	-	3	-	-	-
Wayfaring Tree	-	-	-	-	1	-	-	1	-
Woody Nightshade	-	-	-	1	-	1	-	-	-
Unidentified	-	-	-	2	3	2	3	-	-
B. LEAF FRAGMENTS	18	2	3	17	5	38	7	-	-
C. ANTHERS	4	1	2	12	1	18	2	-	-
D. BRACTS	2	-	-	1	-	3	-	-	-

i. No plant material was found in any of the collar samples.

in Laursen's sample contained a large number of stamens. Neither species has been observed eating stamens but the two observations above suggest that both do so deliberately occasionally.

4. Nectar-eating

Four male Blackcaps were observed in separate parts of the study area in April 1979 taking nectar from female flowers of Goat Willow. Similar behaviour at these flowers was also observed in Chiffchaffs. In winter both species take nectar from flowers of Aloe arborescens at Gibraltar (pers.obs.) and from Eucalyptus flowers in France (Yeatman 1978). Possibly nectar is important to warblers only when other food is scarce since nectar-eating was not seen in summer although many flowers were available then.

5. The sizes of prey items consumed by pulli

The lengths of prey items in the collar samples ranged from 2 - 20 mm in the Blackcap sample and from 1 - 30 mm in the Garden Warbler sample. The mean prey lengths were 10 mm in both cases and the two samples do not differ significantly ($t_{127} = 0.049$, $p > 0.05$). It would have been more meaningful to compare prey sizes within a taxon, such as caterpillars, where variation in size is substantial. Otherwise it is easy to confuse prey-preferences for size-preferences. Moreover the diversity of insect shapes means that length comparisons between taxa may bear little relation to the size (weight) of prey taken.

1.5.3. Discussion

The analysis has shown a high degree of general similarity between the diets of Blackcaps and Garden Warblers, although there remains room for a more comprehensive and detailed investigation.

At least one study has shown that the two species overlap closely in diet. Laursen (1978) analysed stomach contents obtained by flushing live birds with physiological saline. The birds were spring migrants captured on a small island in Denmark, where different warbler species were confronted

with the same insects in the same restricted habitat. Percentage overlaps in diet composition and prey size distributions (the latter calculated from caterpillars only) were determined for Blackcaps, Garden Warblers, Lesser Whitethroats, Whitethroats, Willow Warblers and Chiffchaffs. The diets of Blackcaps and Garden Warblers did not differ significantly in either respect except in the second half of May in one of the two years studied, when they took different sizes of caterpillars. By contrast, significant differences between them and other species were frequent. Another study, based on gut analyses of Blackcaps, Lesser Whitethroats and Sardinian Warblers in Israel (Boren & Safriel 1978) showed only low to moderate overlaps between the Blackcaps and their smaller congeners in the species-composition of their diets.

In the first study the pattern of diet overlap between species differed between the two years and also within different periods of each season. This was interpreted as being due to differences in the intensity of interspecific competition. For example, Willow Warblers and Lesser Whitethroats showed a large overlap in diet when Willow Warblers were relatively scarce (interspecific competition low) but on days when Willow Warblers were numerous (interspecific competition high) the diets were significantly different in composition. A similar example is the discovery that the diets of nestling Reed Warblers and Great Reed Warblers differ to a greater extent where the two species are sympatric than where they are allopatric (Dyrce 1979). These findings may have relevance to Blackcaps and Garden Warblers in the breeding season. They suggest that two or more species may overlap closely in diet but that differences between them (in foraging techniques, choice of foraging substrates or prey-selection) only become apparent when the intensity of interspecific competition becomes high. This could result from a variety of causes, notably poor weather affecting prey-availability or accessibility, seasonal or other variations in prey abundance, or (as above) an increase in the density of exploiters of the supply. Interspecific territoriality between Blackcaps and Garden Warblers

would be one way in which they could be sheltered from these eventualities.

1.6. THE POSITIONS OF SONG POSTS OF BLACKCAPS AND GARDEN WARBLERS AT WYTHAM

Garden Warblers have been described as singing from the undergrowth (Peterson et al. 1974) and it has been suggested that high song perches are a requirement of Blackcap territories (Lack & Venables 1939). Some observations were made of the positions of song perches of the two species, by noting the heights at which birds were singing when they were first encountered, in order to investigate whether or not Blackcaps habitually use higher song perches than Garden Warblers do.

RESULTS Only males sing and although they sometimes do so for prolonged periods from particular perches they were also often observed to sing as they foraged. Song post heights both in woodland and in scrub were not found to differ significantly between the two species (Mann-Whitney U test, 2-tailed, $p > 0.05$; Figure 1-⁶~~7~~A). Figure 1-⁶~~7~~B shows the song post heights of two woodland Garden Warblers of which multiple observations were made. Neither bird confined itself to the undergrowth. The limited data obtained suggests that, as with foraging, both species sing at a wide range of heights.

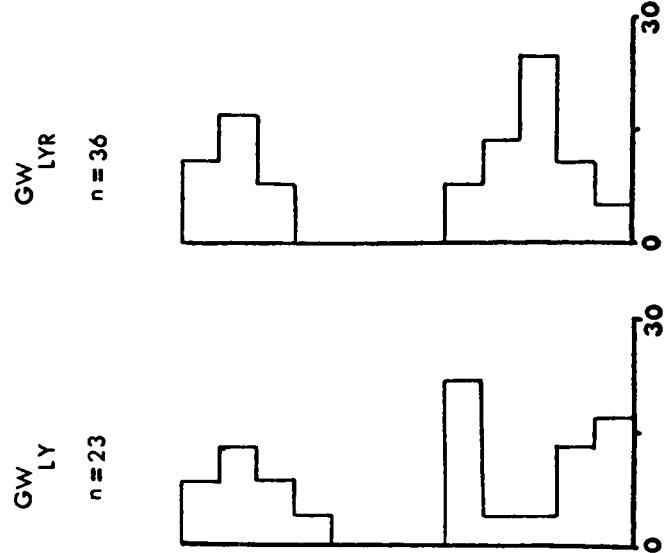
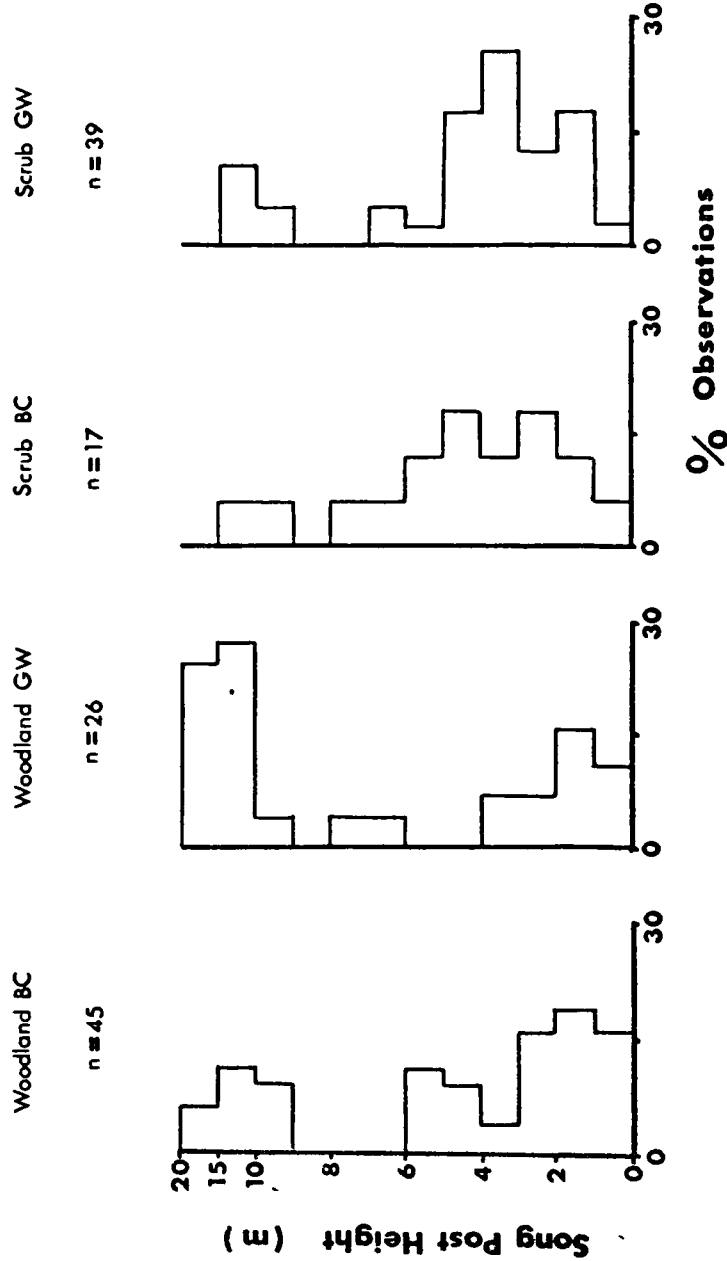
1.7. GENERAL DISCUSSION

Blackcaps and Garden Warblers are widely sympatric over much of their species' ranges. Within Britain they are only partly segregated by habitat (Chapter 2). Both chiefly occupy tall vegetation which apparently offers opportunities for stratification of foraging behaviour but the two species have not been observed to specialise in foraging at different levels. Rather, both concentrate their foraging in the undergrowth but both also search for food in taller vegetation where this is available. The two species are not obviously segregated by foraging techniques. Both are primarily foliage-gleaners and they capture very few insects in flight. Preliminary observations do not suggest any clear-cut differences between them in the foods which they eat. Such a difference would in any case be unlikely, given that they forage in similar ways in the same habitats, and so presumably

FIGURE 1-6. THE HEIGHTS AT WHICH SINGING BLACKCAPS AND GARDEN WARBLERS WERE FIRST OBSERVED

A. The song post height distributions of Blackcaps (BC) and Garden Warblers (GW) holding territories in areas dominated by woodland or by scrub. Only one observation, the first made, is included for each individual. The Figure comprises pooled observations from all three years of the study. n = the number of different birds observed.

B. The song post height distributions of two Garden Warblers holding territories in woodland
n = the number of observations made.



encounter a similar range of prey.

Adaptive radiation in the genus Sylvia has proceeded mainly by differentiation of body size rather than by the evolution of differences between the species in bill, foot and tarsus morphology (Leisler 1977). However, Blackcaps and Garden Warblers are practically identical in body weight and they are closer to each other in structural similarity than either is to any other congener. The significance of this is not obvious to evaluate since similar size is not a precondition of interspecific territoriality (Orians & Willson 1964, Murray 1971). The Red-eyed and Philadelphia Vireos provide a good example of how two interspecifically-territorial species may be substantially different in size (Rice 1978); in these two species, which resemble Blackcaps and Garden Warblers in being foliage-gleaning insectivores inhabiting woodlands, the former is one and a half times the size of the latter. Moreover the relationship between predator size and prey size and type has been found to be "chaotic" for foliage-gleaning insectivores (Hespenheide 1975), although this conclusion, which is based on observations in Californian oak woodlands by Root (1967), need not necessarily be applicable to Sylvia warblers. It remains to be shown that morphological similarity is correlated with interspecific competition in Sylvia warblers but the fact that Blackcaps and Garden Warblers are so similar makes it at least more likely that they do compete than would be the case if they were very different in size.

Ultimately, competition (if any) between these two species is likely to be over food. Competition for nest-sites, the only other unsharable resource needed by both, seems improbable. Both nest low down in dense undergrowth and, at Wytham, extensive bramble thickets and clumps of hawthorn, blackthorn and elder provided an abundant supply of apparently-suitable nest-sites in all parts of the area studied. Indeed, the high number of potentially-usable sites was the main reason why nests of both were so hard to find. Abundance of nest-sites is very probably generally characteristic of the habitats occupied by the two species.

Evidence of competition for food between bird species is hard to obtain. Even if it were possible to show that Blackcaps and Garden Warblers take exactly the same types of prey from the same parts of the same habitats it would still be possible that they are exploiting superabundant food resources, so that the presence of one species has no effect on the foraging efficiency of the other. Moreover, should further fieldwork show that there are differences in food and foraging behaviour between them, the problem of assessing "how different is different enough to permit sympatry" (Orlans & Willson 1964) will still remain.

The data presented in this chapter suggests that the two species are very similar ecologically. It is interesting therefore to note that the fledging success of Great Tit broods at Wytham has been shown to be negatively correlated with the local densities of Blue Tits (Minot 1981). As with the two warblers, the nestling diets of the two tits are broadly similar, even though Great Tits are nearly twice the weight of Blue Tits (Perrins 1979). The fact that competition for food during the nesting season has been shown to have a significant effect even on two species as different in size as the two tits (which are not interspecifically-territorial) reinforces the possibility that competition for food is important in the case of the two warblers. Hogstad (1975) found a significant negative correlation between the combined densities of hole-nesting species (4 tit species & Pied Flycatchers), which he manipulated, and the combined densities of open-nesters (Chaffinches, Chiffchaffs & Willow Warblers), in a Norwegian coniferous forest. This suggests that competitive interactions between relatively-dissimilar species can have noticeable effects and further implies that coexistence could be difficult for ecologically-similar species, which are most likely to compete strongly for food.

Conflicting explanations of interspecific territoriality exist, and are considered in Chapter 8. However, if the territorial behaviour of Blackcaps and Garden Warblers is seen as a way in which individuals secure

adequate food supplies for themselves and their offspring, then the conclusion is that the ecological similarity of the two species might be expected to lead to interspecific territoriality between them.

CHAPTER TWO

THE OCCURRENCE AND BREEDING OF BLACKCAPS AND GARDEN WARBLERS IN DIFFERENT HABITATS IN BRITAIN

CHAPTER TWO

THE OCCURRENCE AND BREEDING OF BLACKCAPS AND GARDEN WARBLERS IN DIFFERENT HABITATS IN BRITAIN

2.1. INTRODUCTION

The Sylvia warblers are known collectively as scrub warblers and indeed most species are characteristic of scrubby habitats and disrupted or sub-climax vegetation generally. In this respect they form a continuum with the Spectacled Warbler and the Desert Warbler at one extreme, inhabiting extremely sparse, short vegetation, and the Blackcap and the Garden Warbler towards the other extreme, in deciduous woodland. Previous descriptions of habitat-selection by the two species comment that Garden Warblers favour lower, denser vegetation (Moreau 1972) and hence occur at an earlier stage than Blackcaps in the vegetational succession which climaxes in deciduous woodland (Yapp 1955, Ferry & Frochot 1970, Williamson 1970). However, the large degree of overlap in the habitats used by Blackcaps and Garden Warblers has also been stressed (Mason 1976, Cody 1978).

It is particularly important to assess the habitat-characteristics of two or more species before deciding that they exhibit interspecific territoriality. If they differ in the habitats which they occupy and if those habitats are discontinuously distributed in any localities, with clumps of one type scattered among clumps of another, then a map will show non-overlapping "territories" between the species which are nothing more than the locations of different habitat patches. Interspecific territoriality can only occur where the habitat occupied by one species is acceptable (not necessarily optimal) to others but where territorial overlap is restricted or prevented by interspecific interactions.

This chapter considers the extent to which Blackcaps and Garden Warblers in Britain use distinct habitats. The values of the major habitats which they occupy are assessed by examining the reproductive outputs of the two species in each of them.

2.2. THE NESTING HABITATS OF BLACKCAPS AND GARDEN WARBLERS IN BRITAIN

2.2.1. METHODS

Information on warbler habitats in Britain as a whole was extracted from the results of two national surveys, the Common Birds Census scheme and the Nest Record Card scheme, run by the British Trust for Ornithology. Observations on the habitats occupied in Wytham wood were also made during 1978, 1979 and 1980.

A. The Nest Record Card scheme (N.R.C.)

The scheme, which commenced in 1939, is described by Mayer-Gross (1970) in a guide incorporating definitions of different habitat types and other instructions to participants. All the cards submitted up to 1978 inclusive were examined but because very few were submitted during the early years of the scheme the analyses were confined to the period 1949 - 1978. For this period the cards totalled 1,336 for Blackcaps and 772 for Garden Warblers. Mason (1976) has similarly analysed the cards for all Sylvia warblers but his study considered only the 935 Blackcap cards and 585 Garden Warbler cards submitted up to 1970.

A total of 1,180 Blackcap cards and 661 Garden Warbler cards gave the nest habitat in adequate detail and these nests were assigned to the following habitat categories (modified from Mayer-Gross 1970 and Mason 1976); the remaining cards were omitted from the analysis.

- a) Broad-leaved woodland; including copses, shelter-belts and other large stands of mature trees.
- b) Coniferous woodland; including mature plantations.
- c) Scrub; areas moderately or densely covered with bushes and young trees. Two kinds were distinguishable:-
 - Woodland scrub; tall shrubs or low bushes with scattered big trees, thorn thickets adjoining woodland.
 - Other scrub; young plantations (trees up to 6 metres high), thorn thickets, gorse, bushy commons, downland,

heathland, birch scrub, bramble patches and other dense low vegetation, all away from woodland or hedgerows.

d) Hedgerows

e) Gardens; including parks and orchards.

f) Miscellaneous; other habitats, distinct from those above

Nests in mixed broadleaf/conifer woodland were assigned to the habitat type of the actual nest location. Disused, overgrown railway lines, used by Garden Warblers especially, were included in category f. They could have been assigned to scrub but structurally they also have much in common with hedgerows.

The cards together show the proportions of Blackcap and Garden Warbler nests found in each habitat type and are probably a good guide to the habitats used by each species. However, they do not enable the detection of birds which nested in one habitat but whose territory mainly included another, e.g. a warbler nesting in scrub, bordering woodland in which it mainly foraged. Such birds probably made up a small minority of cases, unless observers have a disproportionate tendency to search for nests along habitat interfaces. Certain habitat types are perhaps particularly favoured by searchers for nests at the expense of others, conifer monocultures and other areas with low bird densities probably being avoided. It is likely too that nests in scrub (especially thorn) are harder to find than those in more open habitats. These biases would not affect the relative numbers of warbler nests found in each habitat, although they would cause underestimation of the overall amount of use by warblers of difficult or observer-avoided habitats.

B. The Common Birds Census scheme (C.B.C.)

The functions and methods of this scheme are described by Williamson & Homes (1964). A feature of the C.B.C. which was useful to the present study is that workers are requested to supply a detailed habitat map of their census plots. It was possible to overlay the species maps (which are drawn on tracing paper) on such habitat maps and so to record the

habitat in which each territory was located. The C.B.C. material was examined to determine which habitats are used by Blackcaps and Garden Warblers during the breeding season, and also to see whether there is any relationship between the numbers of Blackcaps and Garden Warblers occupying particular census plots in successive years. The latter question is considered in Chapter 7. Not all the C.B.C. material is useful for these purposes. Inevitably for a scheme involving the general public, the quality of the data recorded varies considerably from plot to plot. The censuses used (Appendix 2-1) were selected on the following criteria;

- i. a detailed habitat map, distinguishing open and closed-canopy deciduous woodland, conifers and scrub, had to be available.
- ii. the census plot had to contain both warbler species. Only woodland census results were considered because most farmland plots supported only low densities of both species.
- iii. censuses which were carried on for several successive years were preferred. They contributed data to the investigation of a possible numerical interrelationship between the two species. Moreover they testified to the diligence and experience of the observers and so were perhaps more reliable as data sources.

C.B.C. material is inadequate for identifying interspecific territoriality. Changes in territory positions over the entire breeding season may be considerable (Chapter 3) so that a map summarising registrations taken over a long period of time is likely to show a large degree of overlap between neighbouring territories. C.B.C. maps cover a whole season and so are subject to this difficulty. Moreover, no colour-marked birds are available to C.B.C. observers and so delimitation of one set of registrations from another is often arbitrary and influenced by what the map-plotter thinks is the "correct" size for a warbler territory. Hence some of the C.B.C. maps show clusters of registrations enclosed by a large circular "boundary" orbiting well clear of any of the actual points where birds were seen but

bringing an otherwise "too small" territory up to the species area "norm". For these reasons too, the C.B.C. data was found to be unsatisfactory for detecting changes in the occupancy of specific sites between the two species in different years.

To minimise the above shortcomings, territory boundaries were redrawn using the convex polygon method (Odum & Kuenzler 1955), i.e. by drawing the line which touches all outer registrations with no inward angles. An example of such an adjustment is shown in Figure 2-1. Some of the adjusted territory boundaries enclose areas which are almost certainly smaller than the actual territory sizes. They can be regarded instead as minimum areas of use and, as such, can be assigned to the habitats in which they fell with a high degree of confidence that they were used by the species concerned. Where a territory straddled two habitat types it was found practicable to assign it to the one in which most of the registrations were situated.

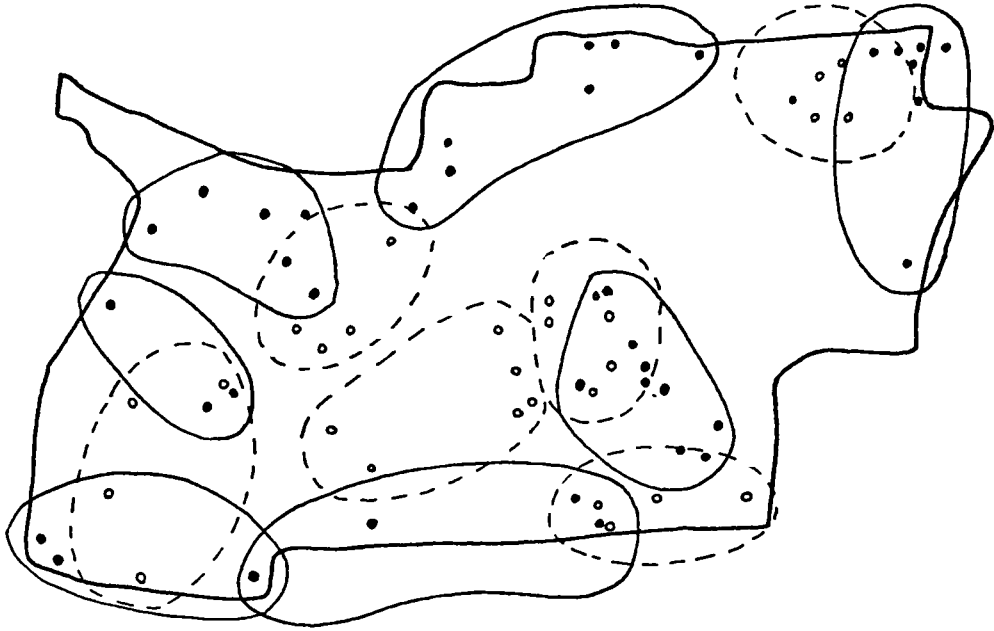
One likely source of error in the data, for which no compensation can be made, is the chance of singing Blackcaps being mistaken for Garden Warblers, and vice-versa, the two species being notorious for the similarity of their songs (Chapter 6). The instructions to participants in the C.B.C. scheme urge them to follow up singing birds and make certain of their identifications. Nevertheless many registrations were probably of birds heard but not seen, and some of these are likely to have been incorrectly identified. This was a further reason why results from experienced observers were selected from the material available at the B.T.O.

C. Observations on habitat use in Wytham wood

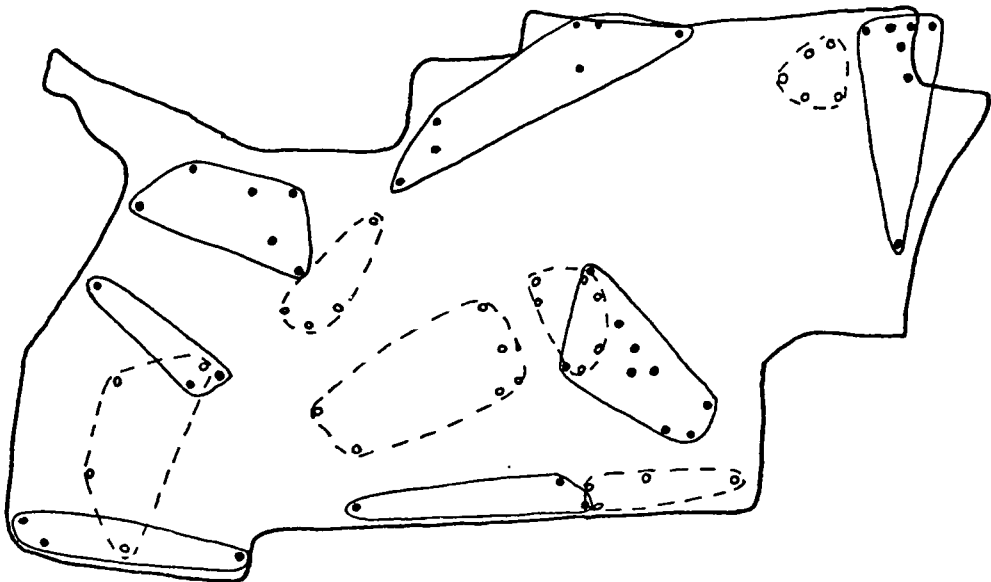
Wytham wood is an expanse of mainly deciduous woodland dominated in different parts by oak, sycamore and ash, with smaller stands of beech. The understorey includes dense thickets of blackthorn and hawthorn which, together with elder, tend to form areas of scrub in the more open parts. Neglected hazel coppice is characteristic of the lower reaches bordering the

FIGURE 2-1.

A. A TYPICAL WOODLAND C.B.C. MAP SHOWING THE ORIGINAL "TERRITORY" BOUNDARIES.



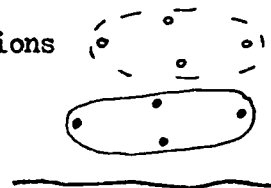
B. THE SAME, REDRAWN BY THE CONVEX POLYGON METHOD TO GIVE MINIMUM AREAS OF USE.



KEY Garden Warbler territory and registrations

Blackcap territory and registrations

Plot boundary



river Thames. Large stands of larch and Norway spruce are scattered within the woodland. Like virtually all surviving woodland in Britain, Wytham wood is a plantation, and this has to be considered when interpreting the data obtained there. However, it is well established; the older trees, mainly oaks, date from the eighteenth century (Lack 1966).

All the territories of Blackcaps and Garden Warblers were mapped each year in parts of the wood. The mapping method and the vegetation of the areas studied are described in Chapter 3. Each territory was assigned to one of the following habitat categories; scrub (including conifer scrub), larch plantations and deciduous (broad-leaved) woodland. Territories found in deciduous woodland were separated according to whether the canopy cover within their boundaries amounted to less than 50% (open woodland) or more than 50% (closed-canopy woodland) of their areas. No territories were found in conifer plantations, other than larch, except when these were at the scrub stage.

2.2.2. RESULTS

A. Nest location in different habitats.

The nest record cards show Blackcaps and Garden Warblers to be distinct from the three other British Sylvia species in that most of their nests are in deciduous woodland (Table 2-1). More Blackcap than Garden Warbler nests were found in every habitat (except "other scrub") reflecting the numerical preponderance of Blackcaps over Garden Warblers in Britain described in Chapter 7. However, between the two species a significantly higher proportion of Blackcap nests were found in gardens and a significantly higher proportion of Garden Warbler nests were found in scrub. The latter difference is due to a much higher proportion of Garden Warbler nests being located in scrub away from woodland; woodland scrub contained a similar proportion of nests of both species, as did the other habitat categories.

B. Territory location in different habitats within woodland C.B.C. plots.

Blackcaps outnumbered Garden Warblers in deciduous woodland

TABLE 2-1. THE DISTRIBUTION OF NESTS OF SYLVIA WARBLERS IN DIFFERENT HABITATS ; DATA FROM NEST RECORD CARDS

HABITAT	BLACKCAP NESTS (N = 1180) %	GARDEN WARBLER NESTS (N = 661) %	WHITETHROAT NESTS (N = 3040) %	LESSER WHITETHROAT NESTS (N = 292) %	DARTFORD WARBLER NESTS (N = 62) %
Deciduous woodland	63.7 (752)	61.6 (407)	18.8	17.1	0
Coniferous woodland	2.3 (27)	2.1 (14)	3.1	0.3	0
Scrub (all types)	12.5 (147)	18.3 (121)	55.7	33.9	100
[Woodland scrub]	[5.1 (60)]	[4.7 (31)]			
[Other scrub]	[7.4 (87)]	[13.6 (90)]			
Hedgerows	6.0 (71)	7.4 (49)	17.7	39.7	0
Gardens	12.0 (141)	7.3 (48)	4.7	6.5	0
Other habitats	3.6 (42)	3.3 (22)	0	2.4	0

NOTES

1. The distributions of nests by habitat are significantly different between Blackcaps and Garden Warblers ($\chi^2 = 20.75$, 5 d.f., $p < 0.001$).
2. Pairwise comparisons of the numbers of Blackcap and Garden Warbler nests found in each habitat with the numbers found in all the other habitats combined show that a significantly higher proportion of Blackcap nests were in gardens ($\chi^2 = 9.60$, 1 d.f., $p < 0.01$) and significantly more Garden Warbler nests were in scrub ($\chi^2 = 11.18$, 1 d.f., $p < 0.001$). Significantly more Garden Warblers nested in "other scrub" ($\chi^2 = 18.29$, 1 d.f., $p < 0.001$) but the proportions of the two species nesting in woodland scrub are similar ($\chi^2 = 0.07$, 1 d.f., $p > 0.5$). No other comparisons give significant differences.
3. The Blackcap and Garden Warbler data is from the present study. It covers the nest record cards for 1949 - 1978. The data for the three other species is from Mason (1976).

but were outnumbered by Garden Warblers in woodland scrub, within the census plots examined (Table 2-2). The scrub contained a significantly higher proportion of Garden Warbler than of Blackcap territories but the opposite was the case in closed-canopy deciduous woodland, where a significantly higher proportion of Blackcap territories were located. Open deciduous woodland was used by a similar proportion of the two species. Territories of both were similarly scarce in coniferous woodland.

C. Territory location in different habitats at Wytham.

Within the study areas Blackcaps outnumbered Garden Warblers in closed-canopy deciduous woodland and the reverse occurred in scrub. These differences between the two species are significant when the proportions of the total number of territories found in both habitats are compared (Table 2-3). The two species occurred in similar numbers in the more open areas of deciduous woodland. The few territories situated in larch plantations represented a similar proportion of the total for both species.

2.2.3. DISCUSSION

The results from the three data sources are not strictly comparable. The N.R.C. scheme is probably a random nationwide sample but the C.B.C. results examined and the study areas used at Wytham were both woodland-based and selected because they held the two species, and so the data from them is clearly biased in favour of habitats where both occur. Also direct comparison of the C.B.C. and Wytham data would require at least that the relative quantities of different habitats in the two samples were similar.

The N.R.C. results show that there is no habitat where only one species occurs and not the other (at least within the broad classification of different habitat types used). Both mainly occur in deciduous woodland but here Garden Warblers are relatively abundant in woodland scrub and Blackcaps in the closed-canopy vegetation. Open deciduous woodland appears

TABLE 2-2. THE DISTRIBUTION OF BLACKCAP AND GARDEN WARBLER TERRITORIES
IN DIFFERENT HABITATS ON WOODLAND COMMON BIRDS CENSUS PLOTS

<u>HABITAT</u>	BLACKCAP TERRITORIES (N = 176)		GARDEN WARBLER TERRITORIES (N = 109)		COMPARISONS ¹ .
	%	(n)	%	(n)	
Closed canopy deciduous woodland	52.8	(93)	28.4	(31)	$\chi^2 = 15.33, p < 0.001$
Open canopy deciduous woodland	36.4	(64)	34.9	(38)	$\chi^2 = 0.02, n.s.$
Scrub	9.7	(17)	35.8	(39)	$\chi^2 = 27.46, p < 0.001$
Mature conifers	1.1	(2)	0.9	(1)	-

The distributions of territories by habitat are significantly different between the two species ($\chi^2 = 32.54, 2 \text{ d.f.}, p < 0.001$, omitting territories in conifers).

NOTES

1. Statistical comparisons are of the proportions of territories found in each habitat type with those in all other habitats combined.
2. The table presents data from 17 C.B.C. plots. The results of two censuses of each plot were selected at random from the total of 81 censuses available. This was the maximum number possible if the sample was to be drawn from the full number of plots examined but without being weighted in favour of those plots for which the longest series of censuses were available.
3. The censuses used are listed in Appendix 2-1. 13 of the plots were in southern England, 1 in Wales and 3 in northern England (Yorkshire, Staffordshire, Cumbria).
4. Scrub areas were mainly hawthorn, blackthorn and/or elder. A very few territories in conifer scrub have also been included in this habitat category.

TABLE 2-3. THE DISTRIBUTION OF BLACKCAP AND GARDEN WARBLER TERRITORIES
IN DIFFERENT HABITATS IN WYTHAM WOOD

<u>HABITAT</u>	BLACKCAP TERRITORIES (N = 64)		GARDEN WARBLER TERRITORIES (N = 51)		COMPARISONS ^{1.}
	%	(n)	%	(n)	
Closed canopy deciduous woodland	57.8	(37)	7.9	(4)	$\chi^2 = 28.75, p < 0.001$
Open canopy deciduous woodland	21.9	(14)	23.5	(12)	$\chi^2 = 0.002, n.s.$
Scrub	12.5	(8)	64.7	(33)	$\chi^2 = 31.48, p < 0.001$
Larch plantations	7.8	(5)	3.9	(2)	-

The distributions of territories by habitat are significantly different between the two species ($\chi^2 = 41.39, 2 \text{ d.f.}, p < 0.001$, omitting territories in larches).

- NOTES
1. Statistical comparisons are of the proportions of territories found in each habitat type with those in all other habitats combined.
 2. The table pools observations from 1978, 1979 and 1980. Only observations made within the principal study areas are included since other areas were probably incompletely censused.
 3. Observations made in the Central study area in 1979 are excluded since populations were artificially-manipulated there in that year (Chapter 4).
 4. The larch plantations used by warblers were mature and had a tall (4 m.) understorey of elder.

to be used by a similar proportion of both species and both avoid conifers. On a national scale, however, Blackcaps outnumber Garden Warblers in all these habitats.

The finding from the N.R.C. analysis that a similar proportion of the two species occur in woodland scrub contradicts that of the C.B.C. and Wytham analyses, which found Garden Warblers to be both relatively and numerically more abundant than Blackcaps in the scrub. This anomaly may simply be a consequence of the difficulty of defining habitats precisely. Scrub and woodland, in particular, are successional stages and there is no obvious point at which "scrub" becomes "woodland". It is also unclear how far away from woodland "woodland scrub" has to be before it can be classified as "other scrub". Quite possibly, therefore, some of the habitat at Wytham assigned to (for example) "woodland scrub", and identified as such (by me) on the C.B.C. maps, would have been classified as (for example) "other scrub" by some of the contributors to the N.R.C. scheme. The lack of objective definitions of habitat types is another reason why comparisons between the three data sources are difficult to make. However, it is clear that scrub (sensu latu) is the breeding habitat of a higher proportion of Garden Warblers than of Blackcaps.

2.3. A COMPARISON OF THE BREEDING BIOLOGY OF BLACKCAPS AND GARDEN WARBLERS NESTING IN DIFFERENT HABITATS

2.3.1. INTRODUCTION

Blackcaps and Garden Warblers establish nesting territories in a variety of different habitats but both are most abundant in deciduous woodland, as described above. This may imply that those birds which occur outside deciduous woodland are disadvantaged individuals compelled to occupy sub-optimal habitats because others have filled all the available woodland locations. This need not be the case. As suggested by ideal-free theory (Fretwell & Lucas 1970), an individual may achieve as great reproductive

success by settling in a thinly-populated area of (for example) scrub as by establishing a poor territory in an already-crowded wood. The best habitat for one individual may accordingly be determined not only by the structural qualities of a location, and its associated capacity to provide food and secure nest sites, but also by the competitive regime which the potential settler finds there.

Superior habitats (if these exist) would be expected to provide some or all of the following advantages, when compared with other habitats;

- a) more young would be raised. Double broods would be relatively frequent.
- b) birds would fledge young earlier. Early fledging has been shown to enhance the survival to breeding age of tits (Perrins 1979) and seems likely to be at least as important to migrant species such as warblers. Early fledglings would have longer to perfect foraging techniques and to lay down fat reserves, before facing their first migration.
- c) early survival of fledglings would be high.

The data from the N.R.C. scheme enables the breeding seasons and pre-fledging histories of birds hatched in different habitats to be compared. The cards cannot provide information on fledgling survival to first-breeding. This factor is essential in the definitive assessment of habitat quality since it is possible that some habitats may provide some of the above advantages but not others. Early breeding or large clutch or brood sizes may be offset by high post-fledging mortality, so that a habitat which appears to produce many young is not in fact superior to another where fewer fledge but a higher proportion survive to breed. In practice the situation is likely to be complicated since juvenile birds are mobile and those fledged in "inferior" habitats can probably move to better localities in order to prepare for migration.

The general breeding biology of British Sylvia warblers as revealed by Nest Record Cards has been described and discussed by Mason (1976). Since a large proportion of the cards are assignable to different habitats, Mason's study can be extended to consider whether different

habitats are equally productive for either species.

2.3.2. METHODS

The cards were assigned to habitats as described above. Where sufficient data was available, information on laying dates, clutch and brood sizes and fledging success was extracted from the cards. Only a minority of the cards provided all this information directly. In many other cases it was possible to derive the necessary data by applying the criteria used by Newton (1964) and Mason (1976) for estimating laying dates and accepting clutch sizes as complete. Mason took survival to an age of seven days as evidence of fledging success although the fledging period averaged ten days for Garden Warblers and eleven for Blackcaps. This was because many warblers will "explode" from the nest if disturbed at this age and many nests were not revisited when the young were near to fledging to avoid this. The same criterion for successful fledging has been used here, although it probably means that overall fledging success is over-estimated for both species. Where nests were discovered only after the young had hatched, brood sizes were not assumed to indicate the original clutch sizes since eggs which fail to hatch may break and be removed from the nests (by the birds), as may pulli which die at an early age. For these reasons, and because many nests fail at the egg stage, many cards only provided information on some aspects of the breeding biology, and hence sample sizes are smaller than those in Table 2-1.

The data examined is first used to make a general comparison of the breeding biology of Blackcaps and Garden Warblers. The reproduction of the two species is then compared between the two major habitats which they occupy, deciduous woodland and scrub (all types combined). The other habitats are omitted since the sample sizes are mainly small. Moreover, hedges and gardens especially are too diverse to be treated meaningfully as discrete habitats; some hedges and gardens have many tall trees and resemble woodland and others are dominated by dense low vegetation and resemble scrub.

Comparisons of breeding success in different habitats may be confounded by two major biases, latitude and season, if these affect the data from the separate habitats to different extents. In general, for many passerines, clutches are larger at the beginning of the breeding season and clutch-size also increases with latitude (Perrins 1979). It will be shown below that the timing of breeding in scrub and woodland habitats is similar. The timing of breeding, clutch-sizes and productivity do not differ significantly between birds nesting in southern or northern Britain (as defined in Chapter 7), for either species (Appendix 2-2).

2.3.3. RESULTS

A. Some general features of the breeding biology of Blackcaps and Garden Warblers.

These are summarised in Table 2-4. The breeding seasons of the two species can be compared by examining the dates on which clutches were started (Figure 2-2). The breeding season of Garden Warblers is significantly later than that of Blackcaps. However, although many Blackcaps establish territories during April (Chapter 3), very few begin nesting in that month and the peak Blackcap laying period only begins 20 - 25 days after the first nests are started. In Garden Warblers, in contrast, the peak laying period occurs comparatively rapidly (10 - 15 days) after the first nests are started. As a result, the temporal separation of the breeding seasons of the two species is not as large as might be expected.

There has been a trend recently towards an even greater overlap in the timing of the breeding activity of the two species. The mean laying date for Blackcaps was four days earlier during the first half of the period examined (1949 - 1963) than during the second half (1964 - 1978), and the two laying date distributions are significantly different. The Garden Warbler laying date distributions are similar for the two halves of the period. The trend is also emphasised by the recent scarcity of Blackcap nests started in April. During 1949 - 1963 April nests made up 10.8% of the total of Blackcap

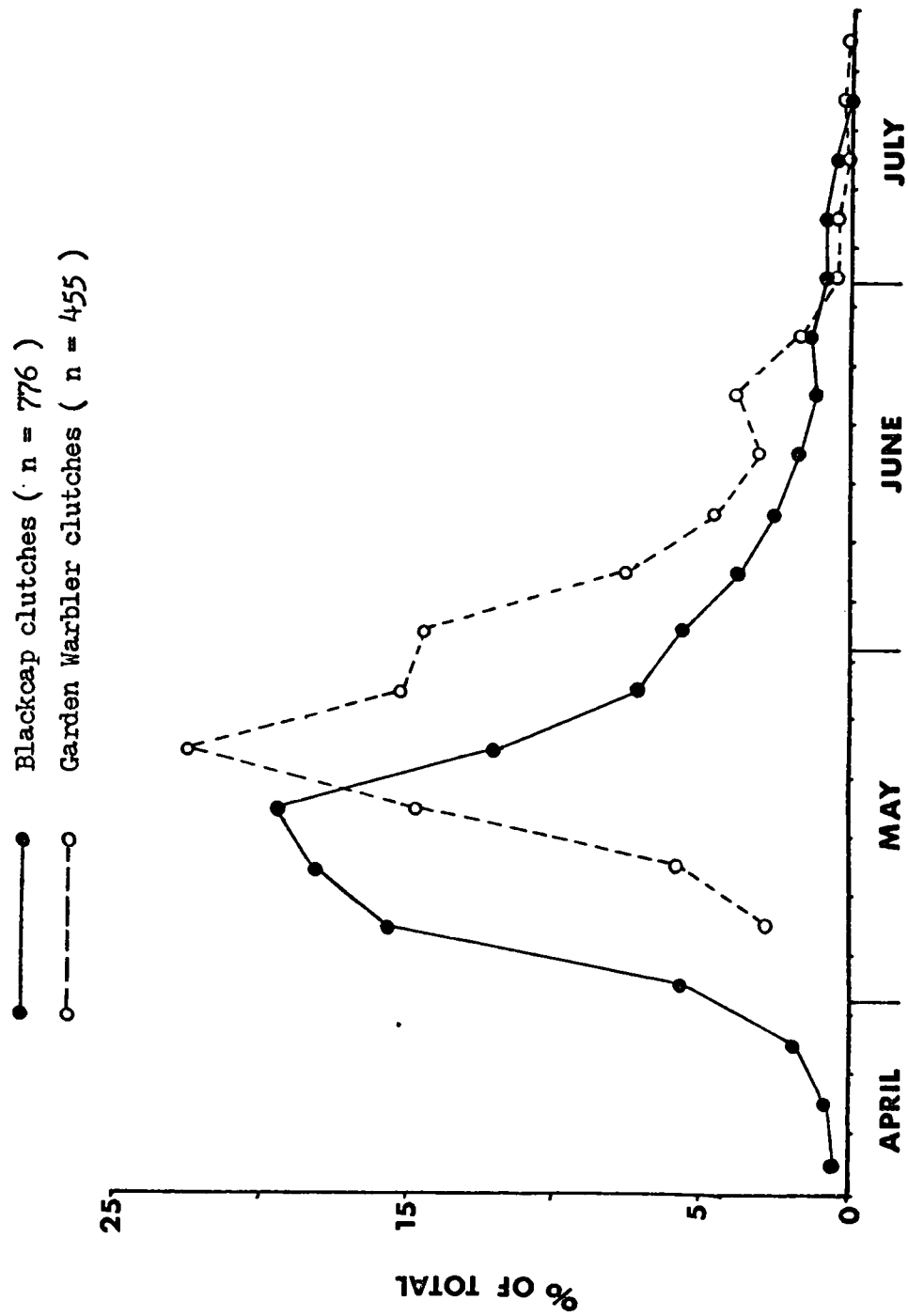
TABLE 2-4. A GENERAL COMPARISON OF THE BREEDING BIOLOGY OF BLACKCAPS AND GARDEN WARBLERS

Data based on the nest record cards examined during the present study.

MEAN DATE OF FIRST EGG (S.D.)		BLACKCAP		GARDEN WARBLER		BETWEEN-SPECIES COMPARISON
	(All nests)	May 19 (15 days), n = 776		May 27 (13 days), n = 455		d = 9.77, p < 0.001
"	" (1949 - 1963)	May 16 (14 days), n = 185		May 27 (13 days), n = 163		
"	" (1964 - 1978)	May 20 (15 days), n = 591		May 27 (13 days), n = 292		
	Between-period comparison	d = 3.18, p < 0.002		d = 0.23, n.s.		
MEAN CLUTCH-SIZE (± 1 S.E.)		4.59 (± 0.03), n = 798		4.41 (± 0.04), n = 375		d = 3.99, p < 0.001
PRODUCTIVITY Mean number of young leaving all nests (± 1 S.E.)		2.40 (± 0.07), n = 837		2.47 (± 0.10), n = 385		d = 0.57, n.s.

FIGURE 2-2. THE BREEDING SEASONS OF BLACKCAPS AND GARDEN WARBLERS

The percentage of clutches started in each five-day period.



nests ($n = 185$) for which the laying date was known. This proportion declined to 1.4% ($n = 591$) during the period 1964 - 1978, and the difference is highly significant ($\chi^2 = 33.56$, $p < 0.001$, 1 d.f.). The trend seems likely to be due to a general tendency of later-arrival among the summer migrants which breed in Britain (Hudson 1973, Lawn 1980).

The mean clutch-size of Blackcaps is significantly larger than that of Garden Warblers. As noted by Mason (1976), most Blackcap clutches are of five eggs but in Garden Warbler nests clutches of four are almost as common as those of five (Figure 2-3). Clutches of other than four or five eggs are uncommon for both species, those of three or fewer usually, but not always, being replacement or second clutches. As with many species (Perrins 1970), clutch-sizes decline as the season progresses, following a similar pattern in the two species (Figure 2-4).

In general, once clutches have been completed, hatching success is over 70% for both species. Once hatched, survival to fledging is very high, about 80%, and about 60% of eggs result in fledged young in both species (Mason 1976). The productivity of Blackcap and Garden Warbler nests, expressed as a mean for all the nests whose final outcome was known, is not significantly different between the two species. However, since Blackcaps generally lay slightly larger clutches, it appears that Garden Warblers fledge as many young from fewer eggs laid.

Both species have been recorded as raising second broods but the proportion of the populations which do this is apparently small (Mason 1976, Bairlein 1978, Solonen 1979). The cards only recorded second broods for Blackcaps, but such records are of doubtful value since the birds were presumably unmarked. Nevertheless, it seems likely that second broods are more frequent among Blackcaps than among Garden Warblers since many of the former arrive earlier and so have more time in which to repeat the breeding cycle than do most Garden Warblers.

FIGURE 2-3. THE FREQUENCY DISTRIBUTIONS OF DIFFERENT CLUTCH-SIZES OF BLACKCAPS AND GARDEN WARBLERS SHOWN AS A PERCENTAGE OF THE SPECIES TOTALS

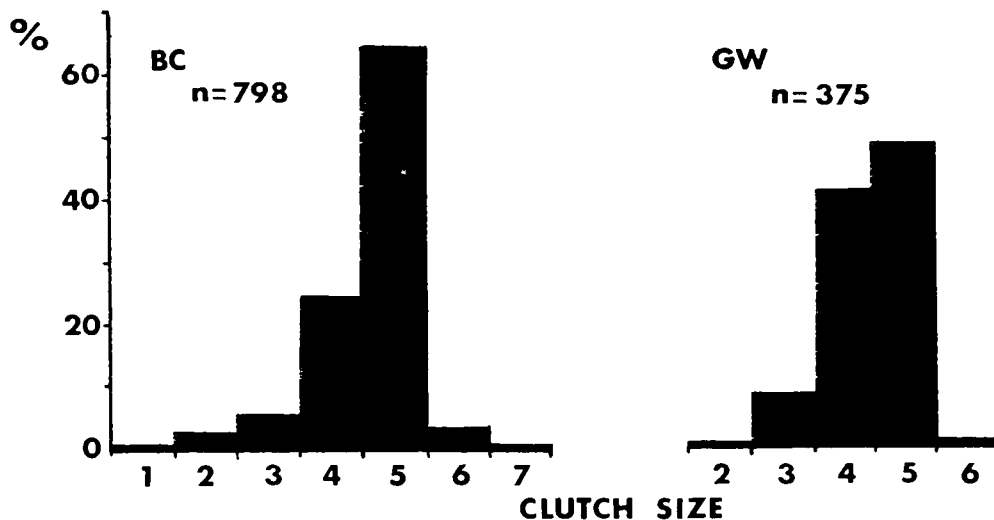
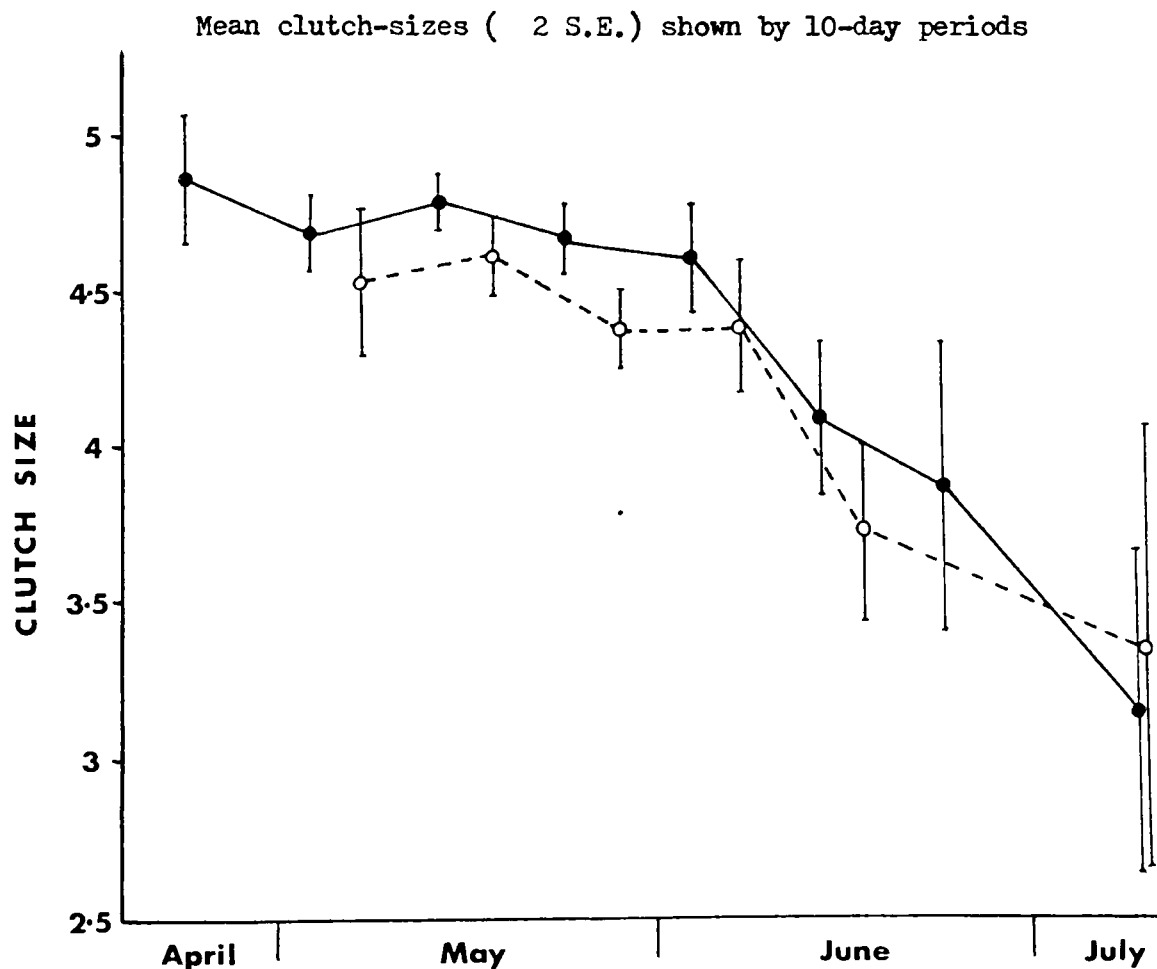


FIGURE 2-4. SEASONAL DECLINE IN THE CLUTCH-SIZES OF BLACKCAPS AND GARDEN WARBLERS



Blackcap clutches, n = 602.

Garden Warbler clutches, n = 301

The courtship and other general breeding behaviour of the two species has been described in detail (Howard 1907-1914). Nests are placed low down in dense undergrowth, brambles being especially favoured and holding about half the nests of both species (Mason 1976).

B. A comparison of the breeding biology of Blackcaps and Garden Warblers nesting in deciduous woodland with that of those nesting in scrub.

This comparison is summarised in Table 2-5.

i. Breeding seasons.

Blackcaps breed significantly earlier than Garden Warblers in both scrub and woodland. However, within species, the timing of breeding in scrub and in woodland is almost identical.

ii. Clutch-sizes.

These do not differ significantly between the two habitats for either species. In deciduous woodland the general tendency for Blackcap clutches to be larger than Garden Warbler clutches remains but in scrub no significant difference was found between the two species.

iii. Productivity.

The mean brood sizes at fledging, derived from all nests whose final outcome was known, does not differ significantly between the two habitats for either species. Productivity is similarly not significantly different between the two species compared within the same habitats.

2.3.4. DISCUSSION

The breeding biology and behaviour of Blackcaps and Garden Warblers is similar, as might be expected of congeners. Some temporal separation of nesting activity exists between them because Blackcaps start nesting earlier than Garden Warblers. However, the overlap is considerable and tending to become greater since early nesting by Blackcaps has recently been less frequent than formerly.

The breeding success of both species does not appear to differ

TABLE 2-5. A COMPARISON OF THE BREEDING BIOLOGY OF BLACKCAPS AND GARDEN WARBLERS NESTING IN DECIDUOUS WOODLAND WITH THAT OF THOSE NESTING IN SCRUB

Data based on the nest record cards examined during the present study.

	<u>BLACKCAP</u>		<u>GARDEN WARBLER</u>	
	1. WOODLAND NESTS	2. SCRUB NESTS	3. WOODLAND NESTS	4. SCRUB NESTS
MEAN DATE OF FIRST EGG (S.D.)	May 20 (15 days), n = 486	May 19 (16 days), n = 101	May 28 (13 days), n = 286	May 28 (13 days), n = 79
Comparisons	1 v 2 d = 0.75, n.s.	3 v 4 d = 0.30, n.s.	1 v 3 d = 7.51, p < 0.001	.2 v 4 d = 3.84, p < 0.001
MEAN CLUTCH-SIZE (± 1 S.E.)	4.61 (± 0.04), n = 507	4.47 (± 0.09), n = 100	4.43 (± 0.04), n = 225	4.54 (± 0.10), n = 52
Comparisons	1 v 2 d = 1.48, n.s.	3 v 4 d = 1.00, n.s.	1 v 3 d = 3.21, p < 0.01	2 v 4 d = 0.52, n.s.
PRODUCTIVITY	2.41 (± 0.10) n = 513	2.28 (± 0.20) n = 121	2.43 (± 0.14) n = 235	2.42 (± 0.24) n = 74
Mean number of young leaving all nests (± 1 S.E.)	1 v 2 d = 0.60, n.s.	3 v 4 d = 0.04, n.s.	1 v 3 d = 0.12, n.s.	2 v 4 d = 0.46, n.s.
Comparisons				

NOTE. Comparisons are between-species within-habitats and between-habitats within-species.

between woodland and scrub, the two major habitats which they occupy. The data thus supports the density-assessment model of the effect of territorial behaviour (Brown 1969, Fretwell & Lucas 1970). This finding is discussed, after the presentation of further relevant data, in Chapter 8.

This chapter considered two further possible ways in which Blackcaps and Garden Warblers could be ecologically segregated; temporally or by habitat. The general finding is that the two overlap to a large extent in the habitats which they use and in the timing of their breeding activity within those habitats. Together with the data presented in Chapter 1, it is seen that in Britain the overall ecological similarity of the two species is high.

CHAPTER THREE

INTERSPECIFIC
TERRITORIALITY
BETWEEN
BLACKCAPS
AND
GARDEN WARBLERS

CHAPTER THREEINTERSPECIFIC TERRITORIALITY BETWEEN BLACKCAPS AND GARDEN WARBLERS3.1. INTRODUCTION

Interspecific aggressiveness between Blackcaps and Garden Warblers has long been known (Chapter 5) but only three studies mention that the two species defend mutually-exclusive breeding season territories. Raines (1945) simply "noticed that Blackcaps would not allow Garden-Warblers in their territory and vice-versa, although other small warblers were tolerated". Solonen (1979), in a study of Finnish Garden Warblers, also mentions briefly that their territories are at least partly mutually-exclusive with those of Blackcaps. Cody (1978) observed sylviid warblers in England and Sweden and concluded that Blackcaps and Garden Warblers interact over habitat. By this he means that much of the habitat classified on grounds of vegetation-height and vegetation-density characteristics (alone) as being suitable for Blackcaps is in fact occupied by Garden Warblers, and vice-versa. The suitability of habitats was gauged by assessing the vegetation-characteristics typical of the territories which the two species did occupy, using discriminant function analyses. However both this, and his resulting references to "atricapilla-preferred" and "borin-preferred" habitat, have the disadvantage that it is probably impossible to be certain that particular habitat patches are or are not suitable for any species. The habitat variables observed or measured to assess suitability may not be those which the species themselves use in selecting habitats. Moreover, where species are interspecifically-territorial, some or many individuals may be prevented, by interspecific interactions, from settling where they would actually have preferred to establish their territories.

Cody also concluded that Garden Warblers are dominant to Blackcaps in interactions. This was supported by an observation of two pairs of Blackcaps which disappeared when one Garden Warbler settled in the area which they had previously occupied. Also, in a case where the territory of one Blackcap pair overlapped extensively with that of a pair of Garden Warblers, the male Blackcap was never heard to sing loudly, although

the male Garden Warbler did so frequently, this implying that the Blackcap was keeping a low profile to avoid conflict with the Garden Warbler. These observations are too few to warrant any generalisations. Alternative explanations (e.g. predation) can always be found to explain the disappearance of a few individuals and several Blackcaps at Wytham had low vocal outputs even though they were not coexisting with any Garden Warblers.

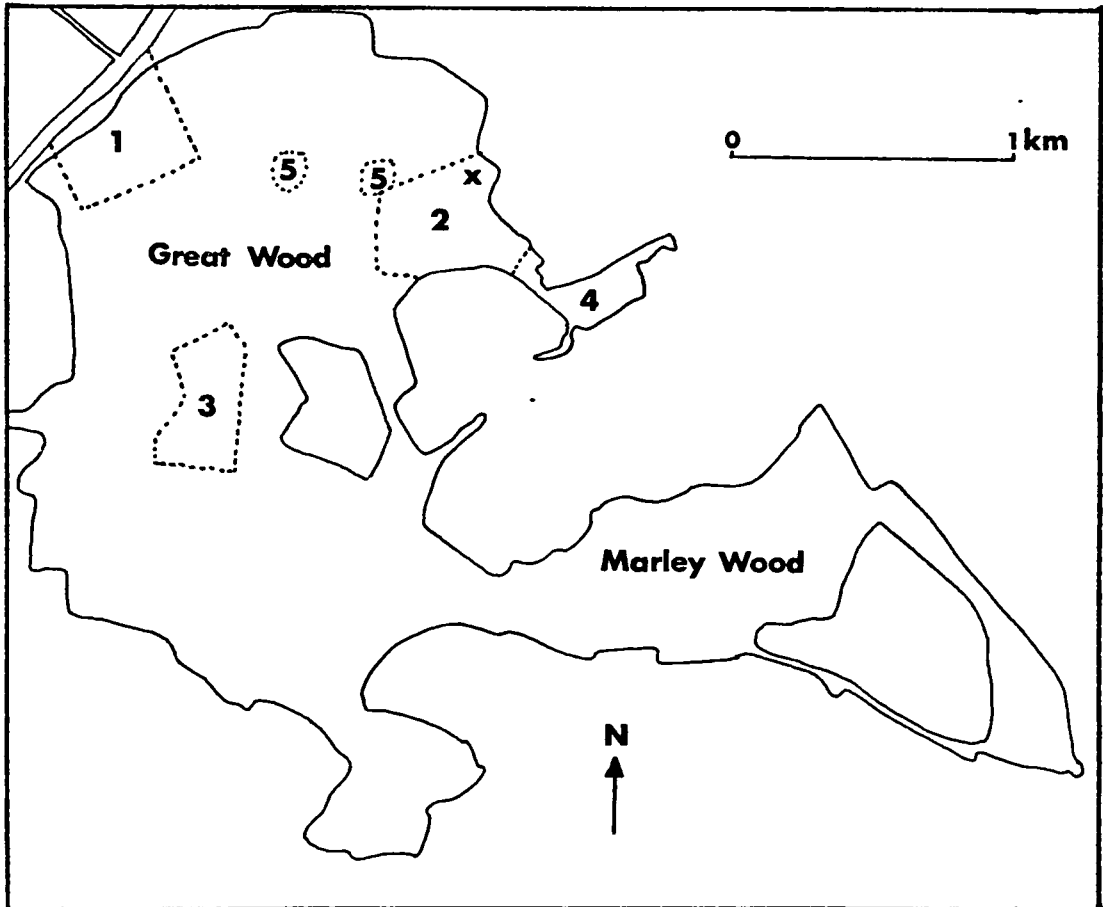
This chapter describes an investigation into the territorial behaviour of the two species and assesses the degree of interspecific territoriality between them in so far as this can be done by observation alone. Chapter 4 then describes an experiment which tested the possibility that Blackcaps and Garden Warblers compete for space. The relationship between the two species, as revealed by actual contests between them, is considered in Chapter 5.

3.2. METHODS

3.2.1. The study areas.

Preliminary observations in April and May 1978 soon revealed areas where both species were present in some numbers. Two principal study areas (referred to as the Riverside and Central areas) were selected. Each covered about 15 hectares and contained about 15 warbler pairs. Two areas were used to enable the study of warbler interactions in a greater variety of habitats but both were small enough to permit a thorough survey. Figure 3-1 shows the location of the two major areas within Wytham wood, and those of some other areas which received less intensive study. The Riverside area was situated on a gentle slope (Clay Hill) bordering the River Thames. The general character of much of the area was scrub, with scattered mature trees, chiefly oaks. The Central area, within the Great Wood proper, was predominantly mature deciduous woodland. The distribution of the vegetation within the study areas is shown in Figures 3-7 and 3-11, and in the other principal maps of territory positions.

FIGURE 3-1. WYTHAM WOODS, SHOWING THE LOCATION
OF THE STUDY AREAS



STUDY AREAS

- 1 RIVERSIDE
- 2 CENTRAL (x = Common Piece)
- 3 ROUGH COMMON
- 4 THE MOUNT
- 5 LARCH PLANTATIONS

The Riverside area was unmodified by man during the three-year study period, although the rides and firebreaks were cut each autumn. The Central area experienced a limited amount of forestry activity during the 1978/79 winter, before the warblers arrived in 1979. This involved the removal of the few mature sycamores from the large tract of open woodland in the centre of the study area. The areas felled were very small but the removal of the trunks caused the formation of new "rides" through the undergrowth. By 1980 these new paths were mainly covered in grasses but they lacked any dense vegetation. The clearance of undergrowth, although limited, could have affected warbler numbers locally and this point is discussed in Chapter 4. A few large dead elms were also removed from another part of the Central area (Common Piece) early in 1979 but most of the dead trees there were left and some fell down each winter, making the area progressively more open. No further alterations were made to the habitats in the study areas until after the completion of the study.

3.2.2. The observation and plotting of territory positions

About twelve hours daily were spent in total in the two main study areas during April, May and June each year, generally between 0500 and 1200 hours and between 1600 and 2100 hours (B.S.T.). Not all this time was spent just observing birds. Some of it was taken up by song playback experiments and mist-netting but these activities still permitted the gathering of information on birds' positions. Observations were concentrated into the period up to June each year after field work throughout July and August in 1978 showed that territorial behaviour was scarcely perceptible by then in either species. Most birds appeared to raise only one brood and this had usually fledged by the end of June.

The advantage of concentrating the work on small areas with few birds was that good overall coverage of each territory was possible, even though the tendency of both species to inhabit dense cover and their low vocal output during wet or windy weather (which often occurred in April and May in

1978 and 1979) made certain individuals often difficult to locate.

Territories were not visited in any regular sequence nor for fixed periods of time. This would have standardised the attention which each territory holder received but was found impractical for work with migrant species. Unlike residents, migrants colonise their breeding-areas over a period of weeks and it was important for this study to consider how newly-arrived birds interact with established ones and where they finally settle. A fixed territory-visitation sequence would have had to be altered at frequent intervals throughout April, May and early June to include new birds and it would often have prevented immediate attention being given to the conspicuous interspecific and intraspecific interactions which occurred unpredictably throughout the study areas (Chapter 5).

Territory positions were plotted by repeated observation, using the method recommended by the International Bird Census Committee (Anon. 1969), although on a much more intensive scale than would be needed for census purposes. The method employs different symbols to record singing birds, foraging and other movements, and joint registrations i.e. simultaneous observations of neighbours (registrations are any observations plotted). Observations were recorded on to maps which showed the positions of rides, paths, firebreaks and other major physical features of the study areas. Large orange posts are present in the ground all over the wood marking a hundred-metre grid. The positions of the posts were also shown on the maps and using these and the positions of paths and rides as points of reference it was possible to plot observations quite accurately, probably always to within ten metres of their actual positions.

As many birds as possible were caught and colour-ringed within the study areas. This potentially-lengthy task was simplified by using tape lures, which usually enabled the prompt capture of any males. However, some birds were not captured until they had been used as subjects in song playback experiments. The usefulness of colour-ringing was limited by the

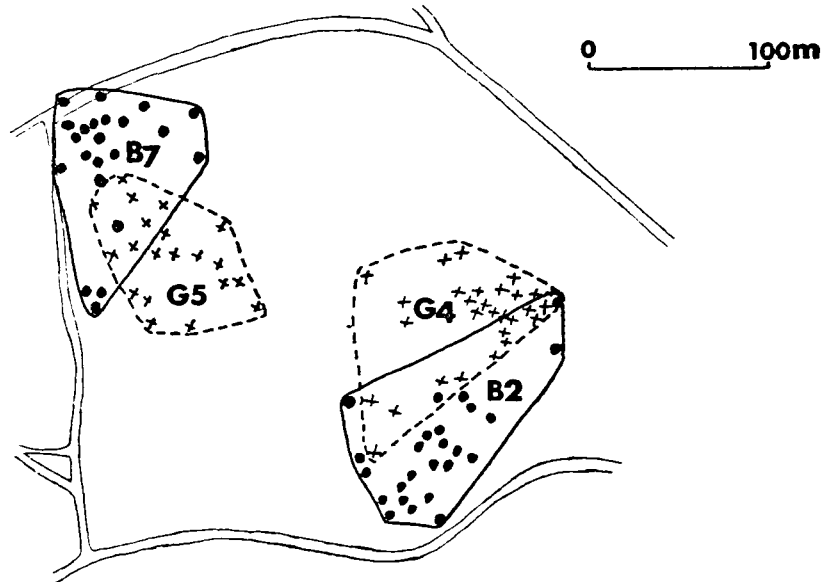
difficulty of observing Sylvia warblers in dense vegetation. In contrast, Phylloscopus warblers, which were also colour-ringed in the Riverside area in 1978 and 1979, proved to be ideal subjects for this technique, their long tarsi and obtrusive behaviour making it easy to see the colour combinations. The marked Blackcaps and Garden Warblers were nevertheless useful in monitoring the territorial behaviour of particular individuals, especially because they enabled confirmation that some changes in territory positions were real and not due to the disappearance of one bird and its replacement by another. A few birds had distinctive voices and were invaluable since their movements could often be traced even when they were themselves concealed in dense thickets.

The drawing of territory boundaries relied upon accurate observations of precisely where birds sang and foraged. Virtually all the observations of foraging birds fell within the area contained by registrations of singing birds so that there was no suggestion that birds foraged outside their territories, as occurs with some species such as Reed and Sedge Warblers (Lack 1946). Hence all sightings were taken as falling within the territories of the respective individuals. The only exceptions to this concerned the initial, often wide-ranging movements of new arrivals; these sometimes took them into the territories of established birds, from where they were usually ejected. Established birds which repeatedly intruded into neighbouring territories were plotted as having overlapping territories with their neighbours. Territory boundaries were drawn initially by the convex polygon method, described in Chapter 2. This method has the advantage of being objective. However it soon became apparent that it can exaggerate the degree of overlap between adjacent territories where repeated observation has shown that the actual overlap is small or non-existent (an example is given in Figure 3-2). It was found that birds often tended to defend well-defined clumps of vegetation, as demarcated by paths, rides, thicket-edges and other discontinuities. As a result, many territories were definitely not convex polygons in shape. For practical purposes it was found convenient to adhere

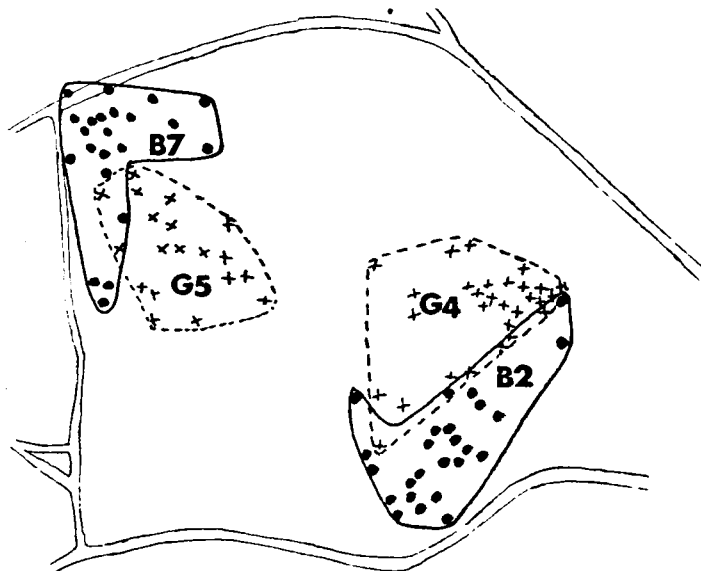
FIGURE 3-2. THE DISADVANTAGE OF THE CONVEX POLYGON METHOD OF DRAWING TERRITORY BOUNDARIES IN EXAGGERATING THE DEGREE OF OVERLAP BETWEEN SOME ADJACENT TERRITORIES

The figure shows registrations of two Blackcaps (●) and two Garden Warblers (×) in the Central Study Area during the period May 6 - Jun 2 1980. All four birds were colour-ringed.

- A. Boundaries drawn by convex polygon method. Substantial overlap occurs between B7 & G5 and between B2 & G4.



- B. Boundaries drawn as suggested by registration positions. Little overlap occurs between territories. (A more eccentric boundary line could be drawn resulting in no overlap at all in either case but observations of the movements of the birds showed that some marginal overlap did occur.



to the convex polygon method in many cases but where fieldwork showed that this was inappropriate the boundaries have been drawn to reflect this fact.

3.3. RESULTS

3.3.1. The arrival of the Blackcap and Garden Warbler populations.

Observations at Wytham began in early March in 1978 and from the beginning of April in 1979 and 1980. The build-up of the warbler populations could only be monitored within the main study areas since only these were visited regularly enough for new arrivals to be detected within one or two days of arrival. It was most unlikely that any birds which established territories in the study areas were overlooked longer than this except in the event that any individuals were present for days on their future territories without singing.

Howard (1907-1914) refers to Blackcaps arriving during the night and proclaiming their presence immediately next morning by song. This probably occurs but it needs to be admitted that any warblers which arrive but do not sing will often go undetected until they do so. This may be more likely to happen very early in the season when few conspecifics have arrived and ownership of particular sites is not in dispute. In 1979 one of the earliest Blackcaps was a male discovered on April 17th feeding in a goat willow bush, where it was regularly taking nectar. The bird was in this area until April 19th and was watched for several hours. It sang no songs during this period although it was defending the bush against Phylloscopus warblers and tits. On April 19th it was mist-netted next to the bush when it responded to playback of Blackcap song. It was colour-ringed and released but not seen again in that area. However on April 30th it was found to have paired and to have established a territory half a kilometre away, and it was now singing frequently. The incident suggests that some early arrivals may lead a clandestine existence before they establish territories. This behaviour is hard to detect except by chance (as above) but it might be expected that later in the season, when available space is rapidly being filled, new arrivals

remain silent only until they locate a suitable, apparently-unoccupied site. They will then sing and try to establish themselves, or otherwise risk being displaced by subsequent arrivals. In short, the monitoring of the build-up of a warbler population detects the established birds on their territories, although some may have actually arrived some days previously.

The arrivals of birds are summarised in Figure 3-3 and the first arrival dates are given in Table 3-1. Cold weather, including settled snow as late as May 2nd, may have delayed the first Garden Warblers in 1979. 1980 was exceptionally warm and sunny in April and May, this perhaps encouraging the early arrival of Blackcaps.

The first male Blackcaps were noted before the first females, a pattern also visible at bird observatories (Davis 1967), but the difference is small and many birds were already paired when the later males arrived in the wood. Male and female Garden Warblers are identical in appearance. However, in 1978 the first male Garden Warbler was in the company of another, silent bird to which it did not react aggressively, and so was apparently already paired. In 1979 and 1980 the earliest male Garden Warblers were apparently paired the day after arrival; in 1980 the second, silent member of such a pair was mist-netted on the day of its arrival and found to have a short wing-length (73 mm.) typical of females. Hence it appears that some Garden Warbler females arrive simultaneously with the earliest males.

The arrival patterns of the two species show some obvious differences. The first Blackcap arrivals always precede those of the first Garden Warblers and by the time the latter appear in early May about 65% of Blackcaps have already established themselves (the figure is an average for the three seasons studied). The build-up of the Blackcap population is slower than that of Garden Warblers. For example, the mean interval (over the three seasons studied) from the first arrivals to the presence of 75% of the breeding population was 24 days (s.d. 6.6) for Blackcaps and 11 days (s.d. 2.9) for Garden Warblers.

FIGURE 3-3. THE ARRIVAL OF MALE BLACKCAPS AND GARDEN WARBLERS IN THE PRINCIPAL STUDY AREAS IN 1978, 1979 AND 1980

The numbers of birds present each day are expressed as a percentage of the total population of each species present on June 15 (June 6 in 1980). Transients of both species, and Blackcaps in the removal zone of 1979 (Chapter 4) are excluded.

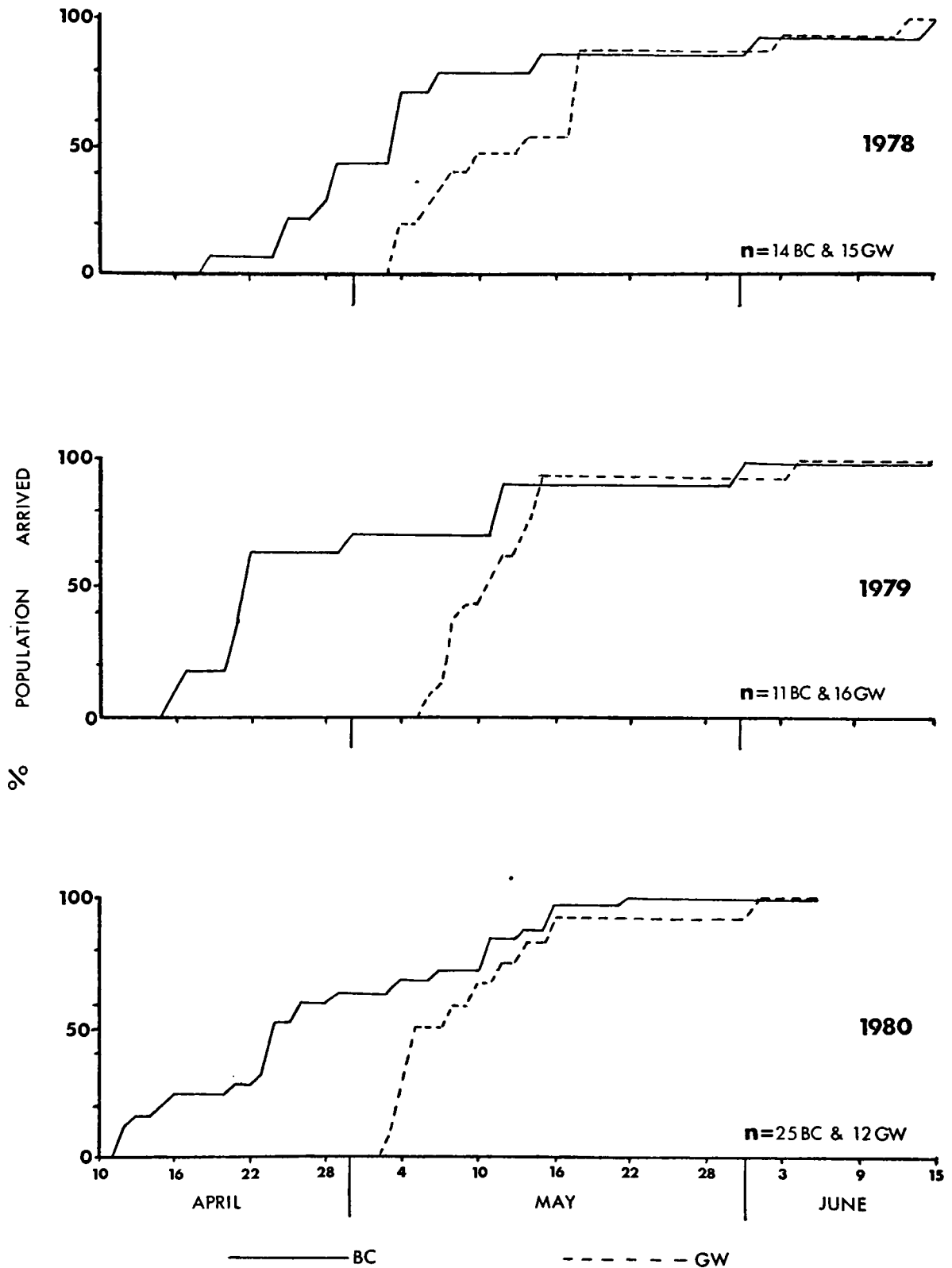


TABLE 3-1. THE DATES OF THE FIRST ARRIVALS OF BLACKCAPS AND GARDEN WARBLERS AT WYTHAM

		1978	1979	1980
BLACKCAPS	First male	APR 19	APR 14	APR 5
	First female	APR 24	APR 15	APR 15
GARDEN WARBLERS	First male	MAY 4	MAY 8	MAY 3
	First female	MAY 4	MAY 9	MAY 4

TABLE 3-2. THE ARRIVAL DATES OF BLACKCAPS AND GARDEN WARBLERS COMPARED BETWEEN WOODLAND HABITATS (the Central study area) AND SCRUB HABITATS (the Riverside study area)

<u>MEAN ARRIVAL DATES ($\pm$ 1 S.D.)</u>			
	YEAR	WOODLAND	SCRUB
BLACKCAP	1980	MAY 1 ($\pm$ 14), n = 14	APR 26 ($\pm$ 9), n = 11
GARDEN WARBLER	1979	MAY 10 ($\pm$ 3), n = 9	MAY 12 ($\pm$ 10), n = 7
GARDEN WARBLER	1980	MAY 5 ($\pm$ 3), n = 5	MAY 13 ($\pm$ 11), n = 7

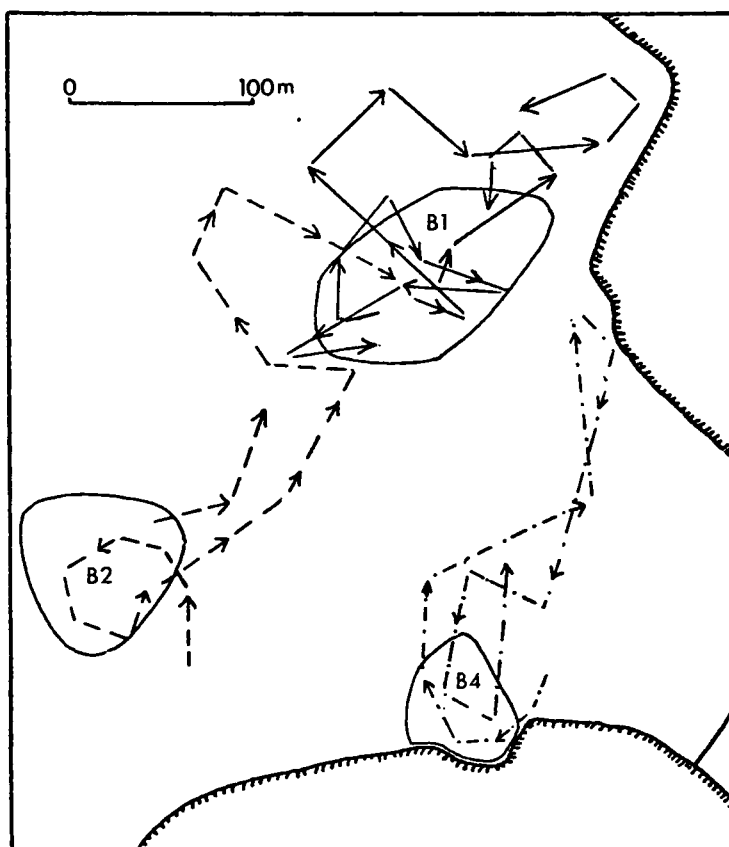
The arrival dates do not differ significantly between woodland and scrub for either species in either year (Mann-Whitney U-test, 2-tailed, $p > 0.05$).

Mean arrival dates in the Central area (mainly woodland) and the Riverside area (mainly scrub) are compared in Table 3.2. The comparison was only possible for the two species in 1980, and for Garden Warblers also in 1979, because in 1979 Blackcap populations in the Central area were artificially manipulated (Chapter 4) and in 1978 the Central area was only studied from mid-May, when most birds were already established. The mean arrival dates do not differ significantly between the two areas for either species. However, the spread of dates is smaller for woodland Garden Warblers than for scrub Garden Warblers, and the matter merits further investigation involving larger samples.

3.3.2. Territory establishment by Blackcaps

Bairlein (1978), observing colour-ringed Blackcaps breeding in southwest Germany, distinguished three forms of territory establishment. The first involved extensive roving with subsequent occupation of the breeding territory, the second entailed occupation of a large area which later shrank to give the eventual breeding territory and thirdly some, chiefly older birds, directly settled in their breeding territories. Observations during the present study do not suggest that territory establishment patterns fall into discrete categories. Conspicuous wandering by Blackcaps was only noted early in the season, chiefly in April, when much of the available habitat was still unoccupied. Figure 3-4 shows some of these movements by three males in the Central area in April 1980. Such birds interrupted their movements with frequent bursts of song and long bouts of foraging, principally for aphids on sycamore buds. At the time few Blackcaps were present in the wood and intraspecific encounters were infrequent. When they occurred birds sometimes chased each other but on several occasions males were visible feeding close together without any obvious antagonism, suggesting that territorial behaviour had not yet begun in earnest. As the season advances subsequent arrivals find more of the wood already occupied by Blackcaps and these later birds do not appear to wander extensively but rather remain within their eventual breeding

FIGURE 3-4. AN EXAMPLE OF THE WIDE-RANGING MOVEMENTS SHOWN BY
EARLY BLACKCAP ARRIVALS



The movements of 3 male Blackcaps in the Central study area during April 12 - 21 1980 are shown in relation to their eventual breeding-season territories. No other Blackcaps had arrived at the time. B1 and B2 were colour-ringed, and B4 unringed, when the observations were made.

~~~~~ wood edge

territory boundaries. It seems highly likely however that late-arriving male Blackcaps do rove widely until they find a suitable, apparently-unoccupied area, but that they do so in silence in order to avoid frequent fights with established birds. Such birds would be very hard to detect.

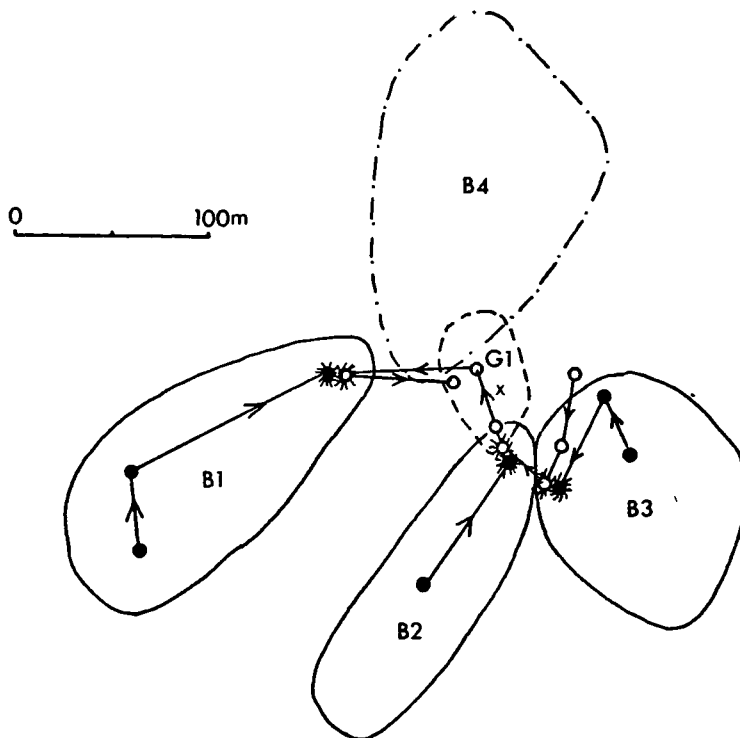
### 3.3.3. Territory establishment by Garden Warblers

As noted above, some 65% of male Blackcaps were already established in the wood when the first Garden Warblers arrived. The Garden Warblers eventually settled in areas largely unoccupied by Blackcaps, as described in detail below. Observation alone can not reveal whether this behaviour resulted from differences in habitat selection between the two species or whether the earlier-established Blackcaps prevented Garden Warblers from settling in areas which they would otherwise have used. This key problem was investigated experimentally (Chapter 4). It was quite obvious in the field however, that Blackcaps resisted any intrusions into their territories by the newly-arrived Garden Warblers and that, with rare exceptions, such Garden Warblers eventually settled in areas wholly or chiefly outside the Blackcap territory boundaries.

Figure 3-5 describes an example of the types of interactions which occurred in May when the Garden Warblers arrived in the wood. The movements of a Garden Warbler (G1) on the day of its arrival (May 14th) in the vicinity of three Blackcap territories (B1 - 3) are shown, as are those of the three Blackcaps. G1 intruded into all the Blackcap territories and was chased each time by the territory-holders until it withdrew. It eventually established itself outside the Blackcap territory boundaries. The habitat was mature, closed-canopy sycamore woodland with a dense understorey of brambles, nettles and sycamore and ash saplings. G1 was visited almost daily for the rest of May and June and periods of several hours were spent in following it about. It was never seen to leave the small area (0.25 h.) shown in Figure 3-5. A successful nest was found near the centre of this territory on June 18th, when the young were leaving it, and a second nest with three

FIGURE 3-5. INTERACTIONS BETWEEN A NEWLY-ARRIVED GARDEN WARBLER (G1)  
AND THREE PREVIOUSLY-ESTABLISHED BLACKCAPS (B1 - 3) IN  
AN AREA OF MATURE, CLOSED-CANOPY SYCAMORE WOODLAND

Observations made on 14 May 1978 near the Riverside study area.



KEY. ○ → movements of G1 ● → movements of B1 - 3  
 \* position of chases of G1 by Blackcaps  
 x eventual nest-site of G1  
 ○ Blackcap territory boundaries  
 - - - - - eventual territory boundary of G1

G1 entered the territories of B1, B2 and B3 several times between 0700 and 1300 hours, singing loudly. It was chased every time by the territory holders and withdrew immediately. G1 spent most time foraging and singing within the area where it eventually established its territory.

NOTE. A fourth Blackcap (B4) was present where shown during late April but then disappeared. The area was not seen to be used subsequently by any warblers. The habitat in the territory of B4 differed from that of all the other *Sylvia* territories in that the undergrowth was sparse, chiefly dogs mercury, so that the area was perhaps less suitable than that settled by B1 - 3 and G1.

eggs was found fifteen metres away on July 5th, but these were taken by a predator. The territory of G1 was appreciably smaller than those of its Blackcap neighbours.

The arrival and establishment of G1 has been described in some detail as an example of a Garden Warbler apparently attempting to settle in an area occupied by Blackcaps but, being compelled to withdraw, eventually settling in a vacant area nearby. Further examples of such interactions are given in section 3.3.4 and in Chapter 5.

The extensive roving behaviour of the first Blackcap arrivals was only occasionally exhibited by Garden Warblers. Instead most Garden Warblers were first observed when they sang on or near their eventual territories. Garden Warblers thus resembled the later-arriving Blackcaps in that they appeared to occupy vacant areas directly. A likely interpretation of this difference between the early arrivals of both species is that the presence of established Blackcaps apparently deters Garden Warblers from overt wandering over wide areas (although they may still do so clandestinely) in the same way that late Blackcap arrivals are also apparently constrained to remain within particular areas.

#### 3.3.4. The relative positions of the territories of Blackcaps and Garden Warblers

In some areas habitat characteristics appear to be of major importance in determining where Blackcaps and Garden Warblers establish territories. In others, intraspecific and interspecific interactions appear to modify the spacing pattern of the two species initially determined by habitat selection. Examples of these different situations are described in turn.

##### A. Territory positions determined principally by differences in habitat selection between the two species.

Observations made at Rough Common in 1978 suggest that in this locality habitat played a major part in determining the positions of Blackcap and Garden Warbler territories. The different habitats there occur

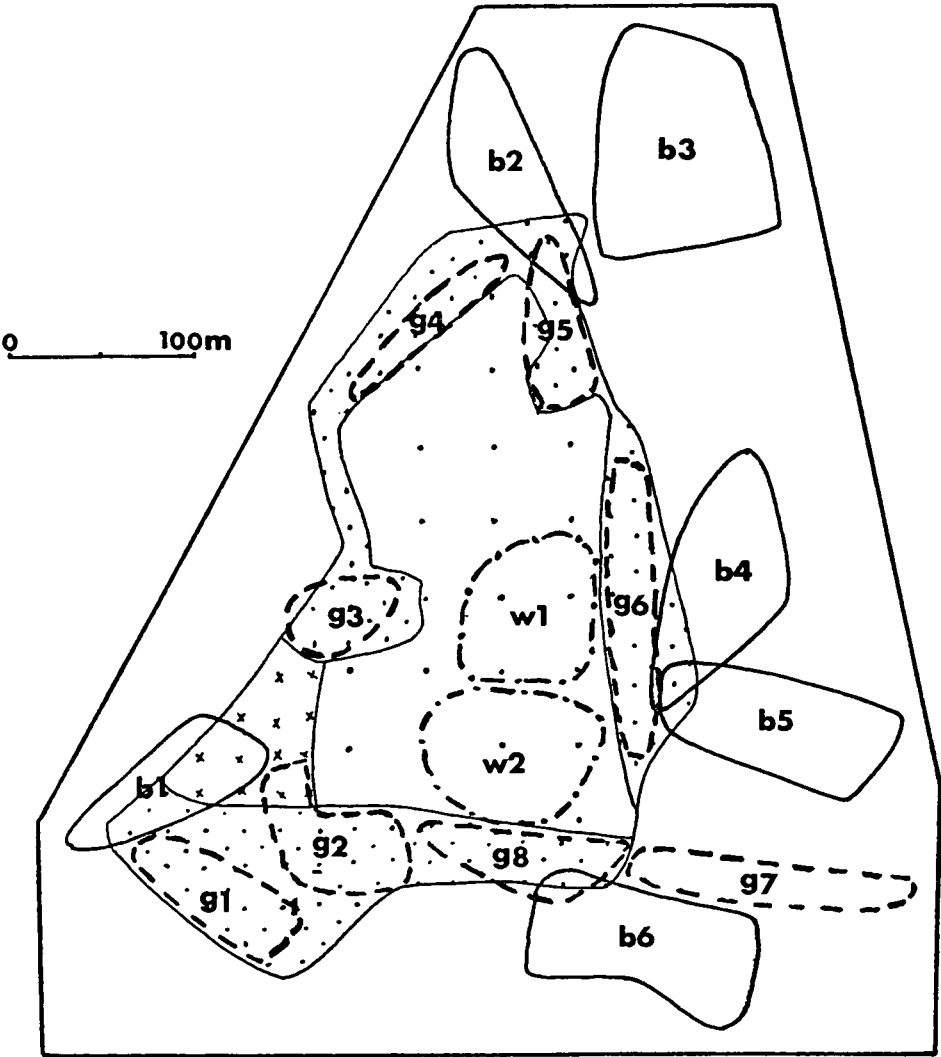
as discrete and extensive tracts (Figure 3-6). The central part of the Common consists of grassland and large patches of low ( $< 2$  metres) bramble and elder scrub. This central area of low vegetation is bordered by tall elder and thorn scrub, some four metres tall. Closed canopy deciduous woodland surrounds the belt of tall scrub but some of it comprises extensive plantations of young beech and chestnut, with no undergrowth, and is probably unsuitable for warblers. Frequent observations in May and June 1978 revealed the presence of six Blackcap, eight Garden Warbler and two Whitethroat territories. The Blackcaps were all in the deciduous woodland, avoiding the monoculture plantations but also leaving some other areas vacant. Seven of the Garden Warblers settled in the tall scrub bordering the open Common and they appeared to confine their activities almost exclusively to this habitat, intruding only marginally into the surrounding woodland. The eighth Garden Warbler (G7) occurred in a mixture of hornbeam woodland and thorn scrub bordering a ride leading into the Common. The two Whitethroats occurred in the low scrub in the centre of the Common.

When the first Garden Warbler arrived (on May 4th) only two Blackcaps (B1 and B2) were known to be present, both of them in deciduous woodland. The scrub into which the Garden Warblers eventually settled was definitely vacant of Sylvia warblers until they arrived, as were tracts of the woodland in which they did not settle and which were later partly occupied by Blackcaps. Intraspecific interactions were frequently seen between the Garden Warblers but only one interspecific interaction was observed. This happened on May 18th when a Blackcap was seen in the territories of G1 and G2. Both Garden Warblers and the Blackcap were singing and tac-tac calls were heard from the Garden Warblers only. The Blackcap was seen to chase the Garden Warblers several times during the course of an hour. It was then caught, colour-ringed and released, but was not seen again in the area, even though it was apparently dominant over the Garden Warblers.

The situation at Rough Common strongly suggests that the three

FIGURE 3-6. SYLVIA TERRITORIES AROUND ROUGH COMMON : MAY - JUNE 1978

Blackcaps B1 - 6, Garden Warblers G1 - 8, Whitethroats W1 - 2.  
Territories are numbered in clockwise order.



HABITAT KEY

- |                                                                  |                                                            |
|------------------------------------------------------------------|------------------------------------------------------------|
| <input type="checkbox"/> deciduous woodland                      | <input type="checkbox"/> low scrub                         |
| <input checked="" type="checkbox"/> dead elms, elder understorey | <input checked="" type="checkbox"/> tall thorn/elder scrub |

Sylvia species present were primarily segregated according to habitat.

Shorter visits to the area in 1979 and 1980 revealed essentially the same pattern of territories in those years. In all three seasons the central part of the Common held only Whitethroat territories, Garden Warblers were present in the tall scrub fringe and Blackcaps in the surrounding woodland, although in 1980 one Blackcap territory included both woodland and a portion of the adjacent scrub. Other warbler species at Rough Common also showed strong segregation by habitat. Grasshopper Warblers occurred in the central low scrub, Willow Warblers in the tall scrub belt and Chiffchaffs in the deciduous woodland, with one Wood Warbler territory there each year in an area of mature beeches with little undergrowth. In each of the three years Garden Warblers used all of the tall scrub fringing the Common and Blackcaps used much of the surrounding woodland. Thus the possibility arises that subsequent Garden Warbler and Blackcap arrivals were excluded from the scrub and at least part of the woodland by established birds of both species. If this occurred it could be tested by removing Blackcaps from the woodland to see if they were excluding any Garden Warblers, and by removing Garden Warblers from the scrub to see if they were keeping-out any late-arriving Blackcaps.

B. Territory positions determined partly by habitat preferences and intraspecific interactions but also influenced by interspecific interactions

1. Observations in the Riverside area.

Of those areas of Wytham wood studied the Riverside area contained the greatest mixture of habitats. In particular, blocks of hawthorn, blackthorn and willow scrub bordering the Thames were separated from similar vegetation further away by a fifty metre-wide belt of deciduous woodland, chiefly maple with a hazel understorey. The positions of Blackcap and Garden Warbler territories were carefully mapped in all three years of the study. They are superimposed on habitat maps of the area in Figure 3-7.

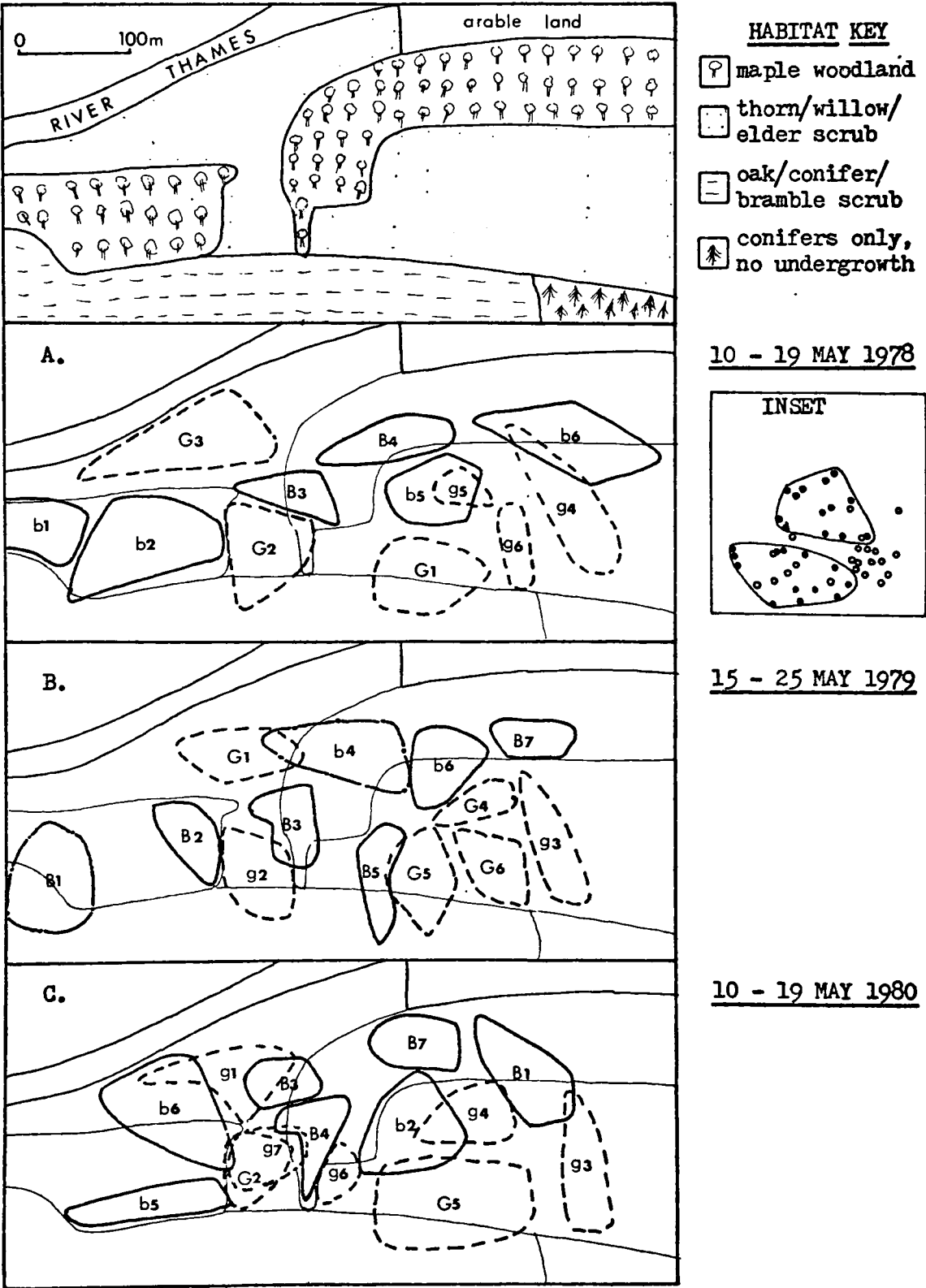
The territories of both species change in position and extent as the breeding season elapses, as described below. The effect of these shifts is to obscure the pattern which exists in the siting of territories

**FIGURE 3-7. THE POSITIONS OF BLACKCAP AND GARDEN WARBLER TERRITORIES  
IN THE RIVERSIDE STUDY AREA IN 1978, 1979 AND 1980**

- 
 Blackcap territories
 
 Garden Warbler territories
- 
 Positions of the territories of two Blackcaps which were known to be present but which were not actually observed during the period mapped

The inset to Figure A. gives the registrations of G5 (•) shown in relation to those of B4 and B5 (•), during the period 26 May - 15 June. The territory boundaries of the two Blackcaps are also shown.

Capitals denote colour-marked birds. Except for 1978 Blackcaps, territories are numbered in the order of arrival of the holders.





relative to each other. Figure 3-7 is an attempt to minimise the consequences of temporal changes in territory positions by summarising registrations obtained during a short portion of the breeding season. Periods of about ten days were chosen, these still being long enough to enable enough observations to be accumulated to delimit the positions of most territories.

The periods mapped each fall at a time when most birds of both species were already established in the area but were still very vocal, making it relatively easy to plot their territories. The Figure reveals that most Blackcap territories were located in maple woodland although some of these extended into the adjacent scrub. These extensions were mainly small. Even the largest (B6 in 1980) was plotted on the basis of a minority of registrations, B6 spending most time in the maple woodland. However, one Blackcap territory each year was wholly situated in the thorn scrub although in about the same place each season, in an area which included a large oak and several isolated maples. This scrub territory (B5 in 1978 and 1979, and B2 in 1980) was probably occupied by a different individual each year. All Garden Warbler territories were situated in the scrub, with only marginal extensions into the maple woodland. Much of the lowest scrub near the river, and all of a dense conifer plantation with no undergrowth, was not used by either species in any of the three years. Some of the small gaps visible between territories in Figure 3-7 disappear when observations from a longer period of mapping are plotted (Figure 3-10) and others suggest a tendency for males to sing mainly along boundaries with neighbours (e.g. B4 & B6 in 1978 and B6 & B7 in 1979). It is probably true to say that all of the suitable habitat available was used by one species or the other every year.

The relative positions of Blackcap and Garden Warbler territories is suggestive of a high degree of intra- and interspecific territoriality. None of the Blackcap territories overlapped with those of other Blackcaps, although such overlaps were sometimes noted briefly early in the season when territories were being established. Similarly, Garden

Warbler territories did not overlap with those of other Garden Warblers, with the conspicuous apparent exception of G2 and G7 in 1980, whose territories appear almost completely superimposed. The circumstances of this overlap are described in detail below. Blackcap and Garden Warbler territories were mainly well separated in the three seasons, overlaps usually being peripheral and small (Table 3-3). An exception is that of B5 and G5 in 1980, where G5 is plotted as almost wholly within the territory of B5. This case is also considered further in more detail.

The relative distribution of Blackcap and Garden Warbler territories in the Riverside area may be compared with that of Chiffchaffs and Willow Warblers in the same locality. The two Phylloscopus species were colour-ringed and their territories mapped during April and early May 1979 (Figure 3-8). Both occurred at higher densities in the area than did the Sylvia warblers but there was no evidence whatsoever of interspecific territoriality between them (or any other warbler species). Chiffchaff territories were established first, some in early April (mid-March in 1978), and the Willow Warblers later established territories which showed large, sometimes total overlaps with some of the Chiffchaff territories. The two species largely ignored each other and could often be seen singing and feeding in close proximity. Chiffchaffs occurred in the maple woodland and taller scrub with Willow Warblers chiefly in the scrub, including the lowest formations near the river. In general most Willow Warblers used low scrub and Chiffchaffs the tall vegetation but the two species overlapped extensively in intermediate vegetation. Hence, although some segregation on habitat grounds could be identified, the overall overlap between the two species was high (Table 3-4).

#### Interactions between Blackcaps and Garden Warblers in the Riverside area

Short-term observations (Figure 3-7 and Table 3-3) show that most Blackcap and Garden Warbler territories do not overlap with those of either species. The Figure does show some instances of overlap requiring

TABLE 3-3. AREA USAGE BY BLACKCAPS AND GARDEN WARBLERS IN THE RIVERSIDE STUDY AREA

Based on Figure 3-7. Areas in hectares.

A. The overall overlap between the two species.

| YEAR | TOTAL AREA USED<br>BY BLACKCAPS | TOTAL AREA USED<br>BY GARDEN WARBLERS | TOTAL OVERLAP<br>BETWEEN THE<br>TWO SPECIES | OVERLAP AS %<br>OF TOTAL AREA<br>USED |
|------|---------------------------------|---------------------------------------|---------------------------------------------|---------------------------------------|
| 1978 | 2.97                            | 2.70                                  | 0.18                                        | 3.3 %                                 |
| 1979 | 2.71                            | 2.02                                  | 0.10                                        | 2.2 %                                 |
| 1980 | 3.05                            | 2.73                                  | 0.42                                        | 7.3 %                                 |

The comparable overlap figure for Willow Warblers and Chiffchaffs in 1979 is 24.6 %; Table 3-4.

B. The overlap between individuals whose territories overlapped with those of the other species.<sup>1</sup>

|                                                                                                 |                         |                        |                         |
|-------------------------------------------------------------------------------------------------|-------------------------|------------------------|-------------------------|
| Overlap of Blackcaps (n) with Garden Warblers expressed as a % of the BLACKCAP territory areas. | 1978<br>16.4 %<br>n = 2 | 1979<br>8.9 %<br>n = 3 | 1980<br>19.1 %<br>n = 5 |
|-------------------------------------------------------------------------------------------------|-------------------------|------------------------|-------------------------|

|                                                                                                       |                                       |                        |                         |
|-------------------------------------------------------------------------------------------------------|---------------------------------------|------------------------|-------------------------|
| Overlap of Garden Warblers (n) with Blackcaps expressed as a % of the GARDEN WARBLER territory areas. | 1978 <sup>ii</sup><br>26.1 %<br>n = 2 | 1979<br>8.5 %<br>n = 3 | 1980<br>14.9 %<br>n = 6 |
|-------------------------------------------------------------------------------------------------------|---------------------------------------|------------------------|-------------------------|

- NOTES i. This comparison is necessary where two species appear to be partly segregated by habitat. In this circumstance the size of the overall overlap figure for a given area will reflect the relative abundance in that area of habitat preferred by one species or the other alone and of habitat occupiable by both species, since overlap will only occur in the latter.
- ii. This relatively large figure is mainly due to the overlap between B5 and G5 described in the text. It is still nearly half the size of the comparable overlap figure for Chiffchaffs and Willow Warblers (Table 3-4 B).

TABLE 3-4. AREA USAGE BY CHIFFCHAFFS AND WILLOW WARBLERS IN THE RIVERSIDE STUDY AREA IN 1979

Based on Figure 3-8. Areas in hectares.

A. The overall overlap between the two species.

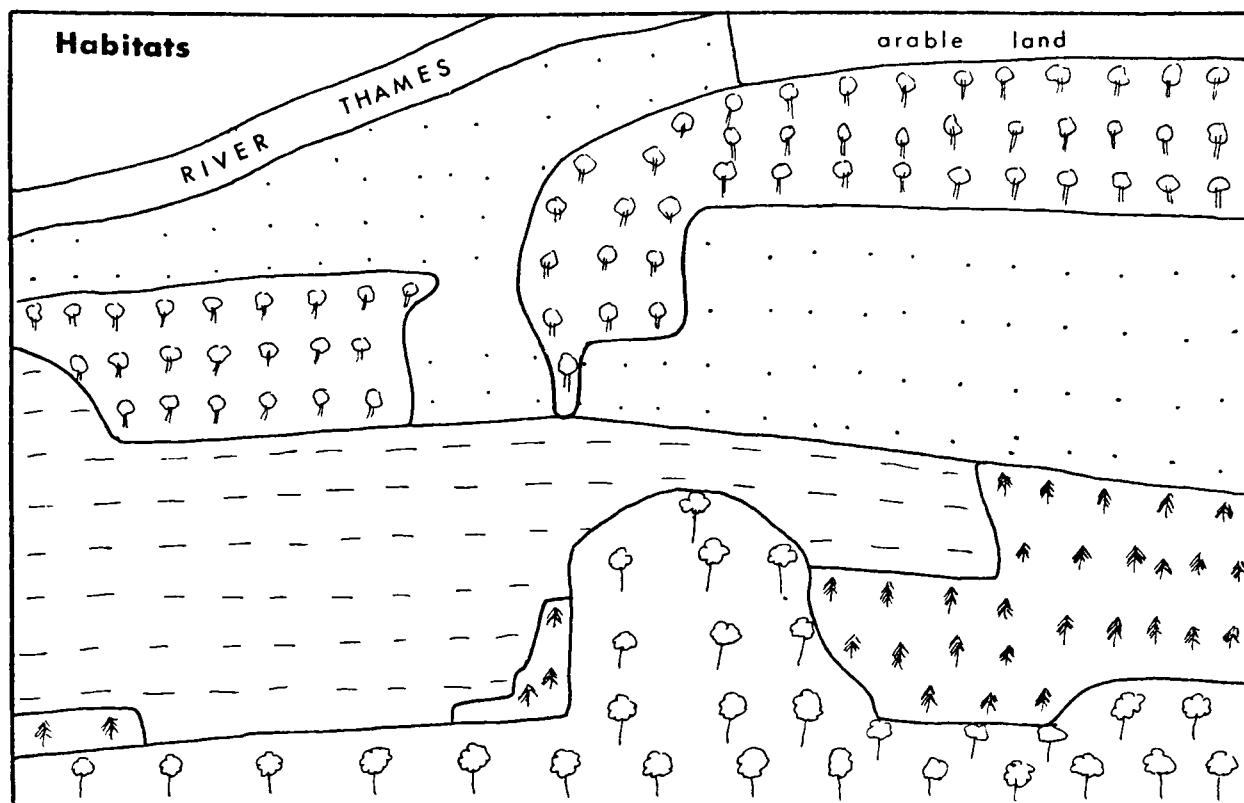
| TOTAL AREA USED<br>BY CHIFFCHAFFS | TOTAL AREA USED<br>BY WILLOW WARBLERS | TOTAL OVERLAP BETWEEN<br>THE TWO SPECIES | OVERLAP AS %<br>OF TOTAL AREA<br>USED |
|-----------------------------------|---------------------------------------|------------------------------------------|---------------------------------------|
| 7.03                              | 6.93                                  | 2.76                                     | 24.6 %                                |

B. The overlap between individuals whose territories overlapped with those of the other species.

|                                                                                                                 |               |
|-----------------------------------------------------------------------------------------------------------------|---------------|
| Overlap of Willow Warblers (n) with Chiffchaffs expressed as a percentage of the WILLOW WARBLER territory areas | 49.9%, n = 11 |
|-----------------------------------------------------------------------------------------------------------------|---------------|

|                                                                                                             |               |
|-------------------------------------------------------------------------------------------------------------|---------------|
| Overlap of Chiffchaffs (n) with Willow Warblers expressed as a percentage of the CHIFFCHAFF territory areas | 43.2%, n = 13 |
|-------------------------------------------------------------------------------------------------------------|---------------|

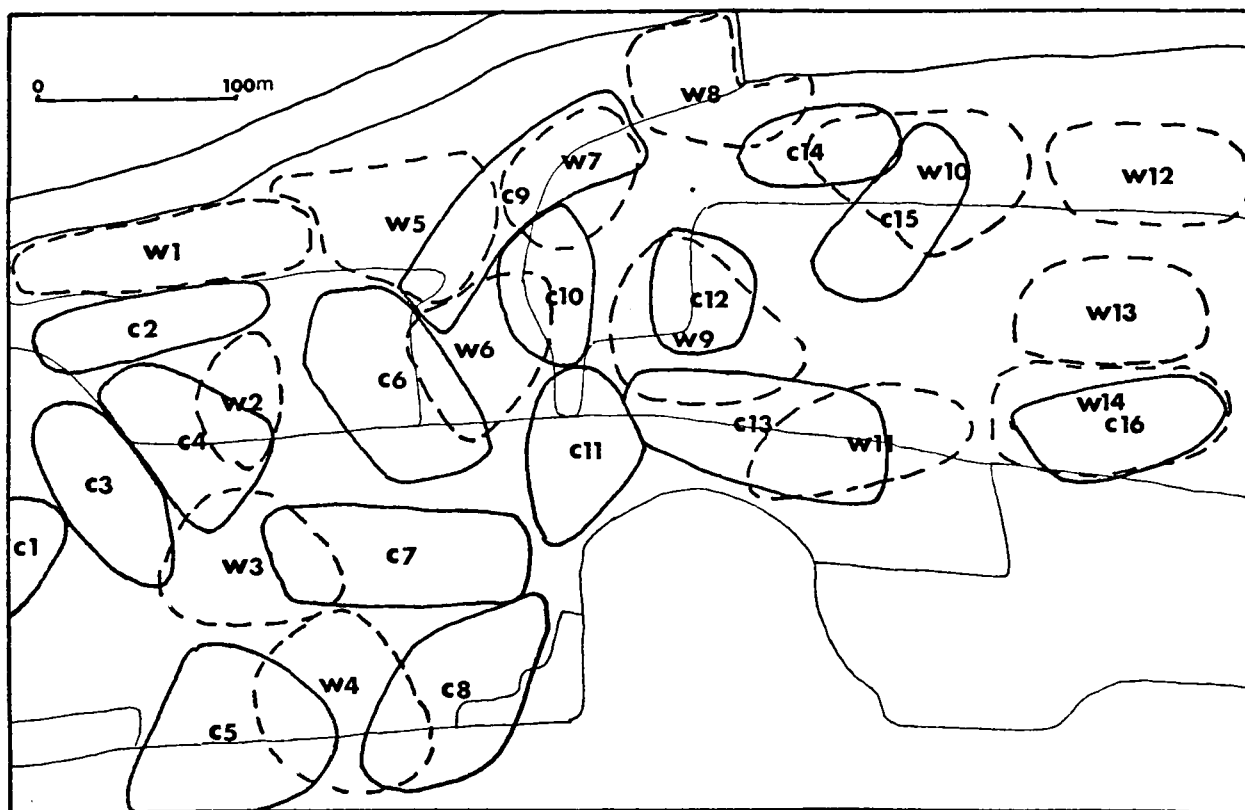
**FIGURE 3-8. THE POSITIONS OF WILLOW WARBLER AND CHIFFCHAFF TERRITORIES**  
**IN THE RIVERSIDE STUDY AREA DURING THE PERIOD 16 - 26 APRIL**  
**1979**



**KEY**

-  maple woodland
-  thorn/willow/elder scrub
-  oak/conifer/bramble scrub
-  conifers only. no undergrowth.
-  tall sycamore woodland. little undergrowth.

**TERRITORIES** Willow Warblers W1 - 14. Chiffchaffs C1 - 16.



explanation however and these are now considered, together with the wider question of whether Garden Warblers avoid Blackcap-occupied habitat when setting-up territories.

In 1978 the only really large overlap observed was between G5 and B5. Both were unringed males whose territories fell between those of G1 and B4, which were colour-ringed. B5 was present since at least May 4th, frequenting dense thorn thickets with a few scattered maples. G5 arrived on about May 9th and settled in the densest thickets at one end of the territory of B5. It was present there throughout May but was rather inconspicuous, not being heard at all on many days. In early June, G5 (or perhaps another male which had replaced it) became much more vocal and obvious, ranging over a wider area within the territory of B5 (which had itself shifted to include a portion of maple woodland) but with registrations concentrated in dense thorn thickets outside the Blackcap's territory (Figure 3-7; inset). No aggressive interactions were noted between G5 and B5 except that on May 15th B5 and its mate were sitting silently at the top of a maple when G5 approached them singing vigorously. G5 ascended the tree to within two metres of the Blackcaps which then flew off leaving the Garden Warbler singing alone. The observations of G5 and B5 are open to a number of possible interpretations. Possibly some individual warblers are not interspecifically-territorial, or are only weakly so. Perhaps too the fact that G5 and B5 inhabited the densest thorn thickets meant that they found it difficult to locate each other precisely and so to defend boundaries which were clearly mutually-exclusive.

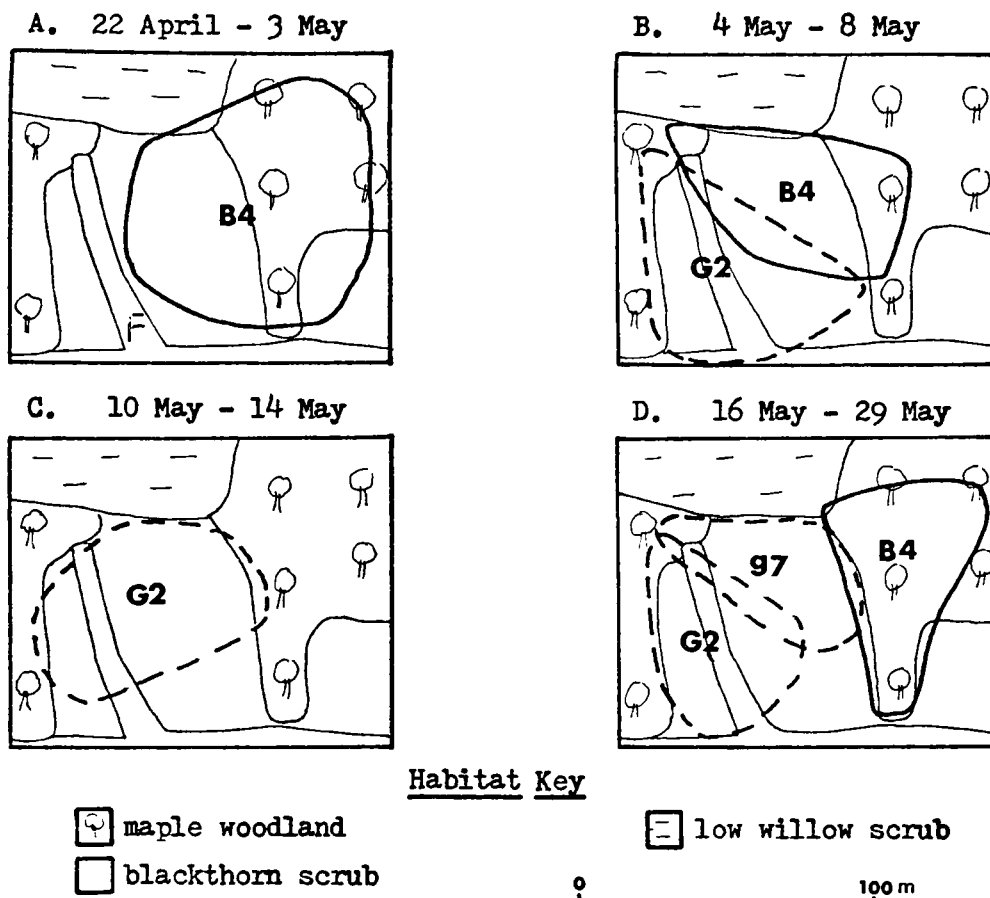
In 1979 no large overlaps occurred between Blackcaps and Garden Warblers although the corner of G5 nearest to B5 was in dispute (see also Figure 3-10), and some aggressive interactions occurred here. However the registrations of B5 largely fell outside the boundaries of G5.

In 1980 there was once again an overlap between a Blackcap and a Garden Warbler in the dense thorn scrub used by G5 and B5 in 1978, although

it was less pronounced on this occasion. Also in 1980 G1 overlapped with the territory of B3 but both seemed to show some temporal segregation at least since they were never seen together in their area of overlap. G1 and B6 did not normally overlap. The extension of the territory of G1 into that of B6 shown in Figure 3-7 (c) is due to observations made on May 19th. G1 was singing in riverside scrub when B6 emerged from the maple belt and flew towards G1. Several chases occurred following which G1 returned to the centre of its territory and B6 remained in the riverside vegetation. The large overlap between G2 and G7 was more apparent than real. The events which occurred are summarised in Figure 3-9.

It remains to be considered whether newly-arrived Garden Warblers in the Riverside area settled in areas which were vacant of Blackcaps at the time of the formers' arrivals. The area was visited frequently during the whole of April and May 1979 and 1980 so that it is possible to show the positions of Blackcap territories before any Garden Warblers arrived (i.e. during April and early May) and also after the Garden Warblers had settled (Figure 3-10). However, it is difficult to depict the relative positions of Garden Warbler territories and previously-established Blackcap territories concisely because the main Garden Warbler arrivals were spread over a period of two or three weeks during which shifts in territory positions of both Blackcaps and the earlier-arrived Garden Warblers occurred. In 1979 too, one Blackcap (B7) arrived after the first Garden Warblers settled in the area. In order to accommodate these events it is necessary for Figure 3-10 to span longer periods of time than Figure 3-7 and hence some of the overlaps between territories are due partly or wholly to temporal shifts in positions. Mapping problems of this nature are a consequence of trying to summarise what is essentially a highly-dynamic situation in a static manner; even the short-term maps can not take full account of the day to day shifts in boundaries and the effect of arrivals of new birds or the disappearance of established ones.

**FIGURE 3-9. INTERACTIONS BETWEEN A BLACKCAP (B4) AND TWO GARDEN WARBLERS (G2 & G7) IN THE RIVERSIDE STUDY AREA IN 1980**



- A.** Before any Garden Warblers arrived B4 was holding a territory in maple woodland and adjacent blackthorn scrub bordering a short firebreak (F), in an area used largely by Garden Warblers in both 1978 and 1979 (see Figure 3-7).
- B.** G2 arrived on May 4th. The territory of B4 showed some contraction over the next five days, with G2 and B4 mainly inhabiting opposite sides of the firebreak. When G2 sang B4 responded at first by approaching to the edge of its side of the firebreak singing loudly, at which G2 stopped singing temporarily. However, by May 6th long mutual vocal contests across the firebreak were taking place and G2 was seen to make occasional incursions into the territory of B4, but only when the latter was neither visible nor audible.
- C.** B4 apparently disappeared. It was searched-for daily but was neither seen nor heard. G2 extended its territory to include the scrub portions of B4's territory and the adjacent woodland fringe.
- D.** G7 arrived on May 16. Frequent chases occurred between G7 and G2 in which G7 emerged as the dominant of the two. Thereafter G2's territory shrank and G7 settled between G2 and B4. The latter was confirmed now to be still present, but confining itself to the maple woodland only.

- NOTES** 1. B4 was colour-ringed on May 1st. It was a first-year bird and was distinguishable from other Blackcap males because it had an unusual ending to many of its songs. Furthermore its crown looked dark brown and not black as a result of the late retention of scattered juvenile feathers among the black crown plumage.
2. G2 was colour-ringed on May 6th. G7 was unmarked.

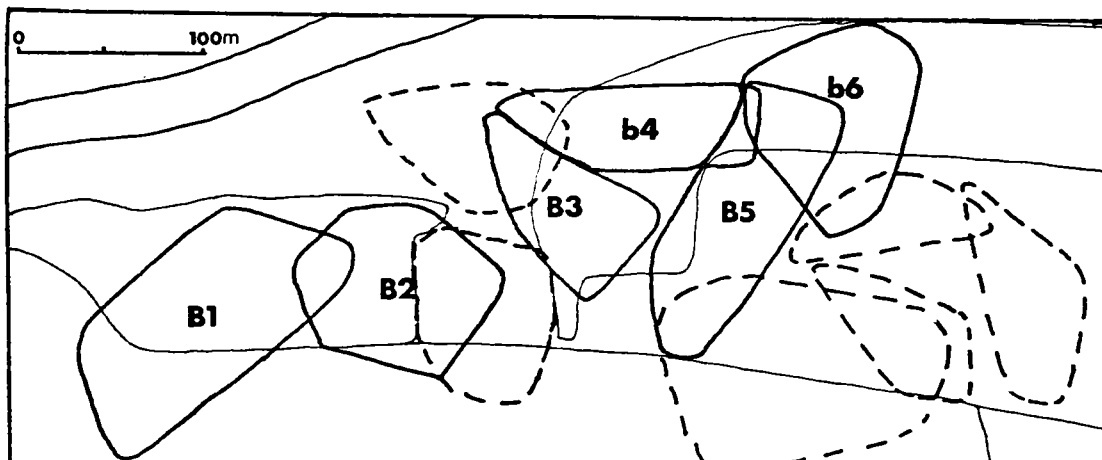
**FIGURE 3-10. THE POSITIONS OF BLACKCAP TERRITORIES IN THE RIVERSIDE STUDY AREA IN ADVANCE OF THE GARDEN WARBLER ARRIVALS IN 1979 AND 1980, COMPARED WITH THE RELATIVE POSITIONS OF THE TERRITORIES OF BOTH SPECIES EACH YEAR AFTER THE GARDEN WARBLERS HAD ESTABLISHED THEMSELVES**

The figure indicates the overlap which would have occurred each year had the Blackcap territories remained in their "April" positions after the Garden Warblers arrived. The actual relative positions of the territories of the two species during May are also shown.

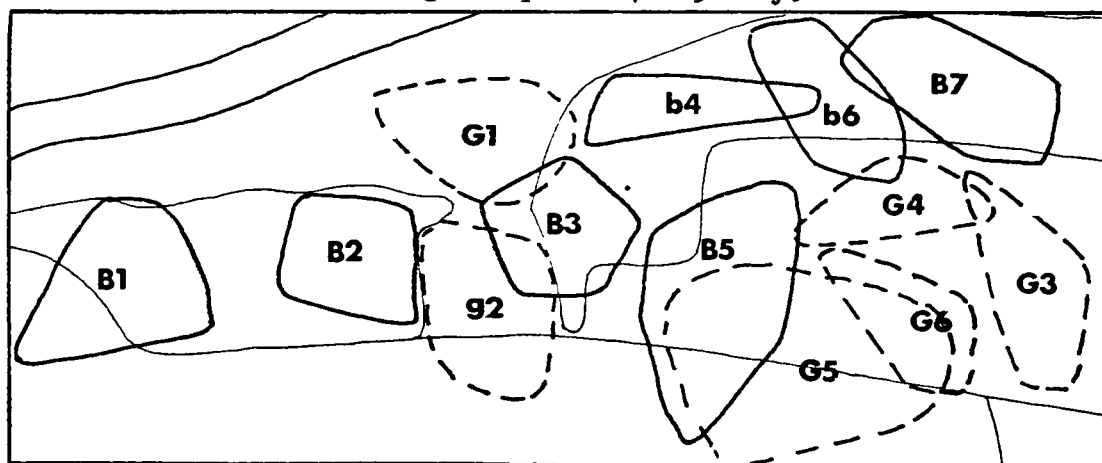
Blackcap territories (—) Garden Warbler territories (---) Territories are numbered in the order of arrival of the holders. Capitals denote colour-marked birds. The boundaries of the major blocks of different habitats (as shown in Figure 3-7) are indicated.

**A. 1979**

- i. The territory positions of Blackcaps before the Garden Warblers arrived, with the eventual Garden Warbler territory positions superimposed. The periods mapped are; Blackcaps 21 April - 6 May, Garden Warblers 7 - 30 May.



- ii. The relative positions of the territories of both Blackcaps and Garden Warblers during the period 7 - 30 May.



**NOTE** In Figure ii most of the registrations of B5 were peripheral to the territory of G5 (see inset) but frequent fights occurred between them in the area of overlap. Indeed it seems likely that the large number of registrations of G5 in that area resulted from the amount of time that it spent there defending its boundary against B5. G5 & G6 did not overlap at all. G5 had confined itself to a smaller area by the time G6 arrived and the final territories were quite separate.

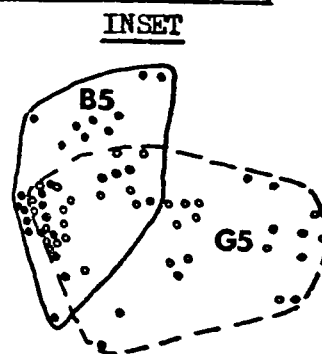
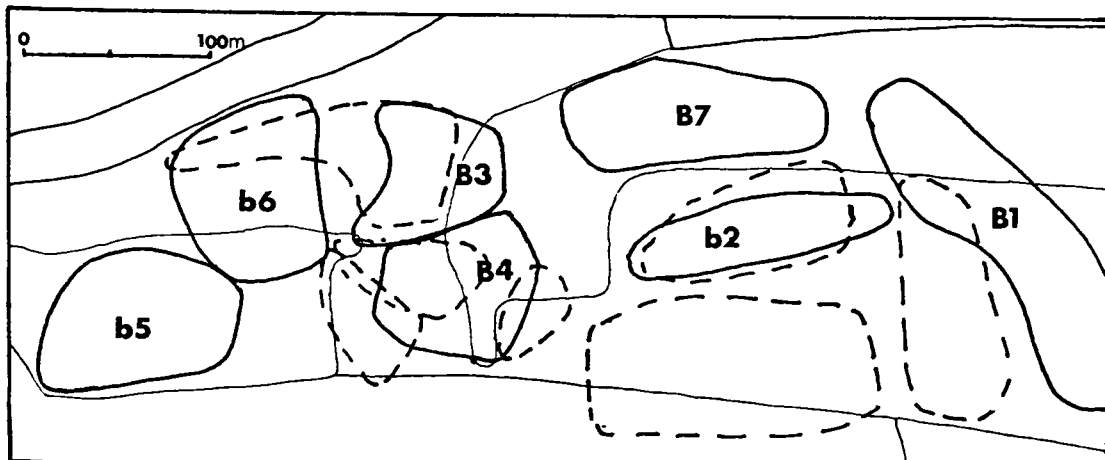




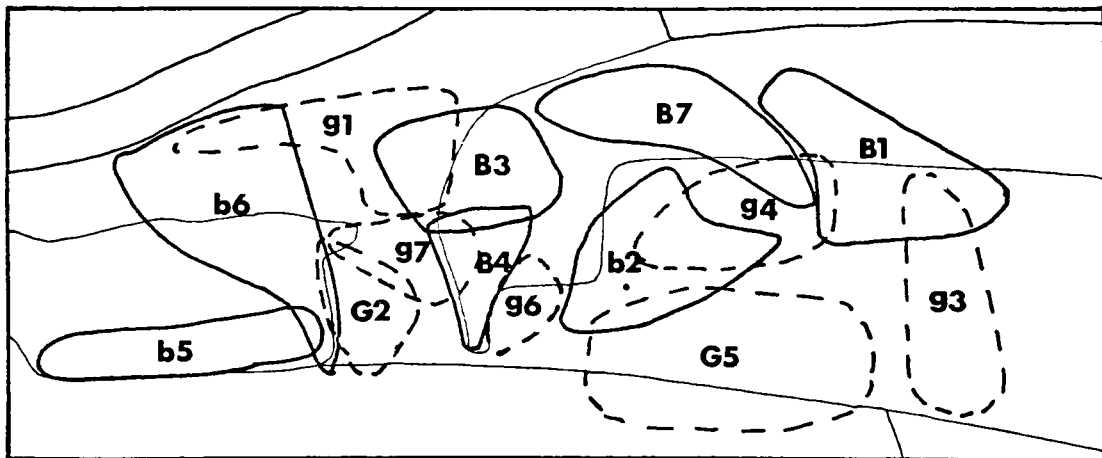
FIGURE 3-10. (continued)

B. 1980

- i. The territory positions of Blackcaps before the Garden Warblers arrived, with the eventual Garden Warbler territory positions superimposed. The periods mapped are; Blackcaps 15 April - 3 May, Garden Warblers 6 - 26 May.



- ii. The relative positions of the territories of both Blackcaps and Garden Warblers during the period 6 - 26 May.



In both years Garden Warblers settled only in scrub; they avoided the maple woodland or were excluded from it by the Blackcaps, whose territories were mainly located there. Because of this, the overlap that would have occurred between the two species had the Blackcap territories remained in the positions they held before any Garden Warblers arrived is low; 70 - 80 % of the area settled by Garden Warblers was vacant, i.e. unclaimed by Blackcaps, when the former arrived (Table 3-5A). The actual overlap which was observed once all individuals of the two species had settled was a little lower (Table 3-5B) because of some shrinkage in Blackcap territory areas. In the case of B4 in 1980 (Figure 3-9) it appeared that the reduction in size of the Blackcap territory was caused by the arrival of the Garden Warblers. This was not thought to occur generally. An alternative explanation for such apparent displacements could always be that Blackcap territories contract and peripheral areas are abandoned, as the core of the territory becomes more productive. The fact that some Blackcaps which lacked Garden Warbler neighbours (e.g. B1 in 1979 and B5 in 1980; Figure 3-10) also reduced their territory areas, and that in some other cases (e.g. B2, B3 & B4 in 1979) the contraction affected all the territory boundaries and not just those shared with Garden Warbler neighbours, supports the impression that displacement of Blackcaps by Garden Warblers is not the main cause of the observed reductions in Blackcap territory sizes. More observations, of isolated Blackcaps, are required to confirm this.

To summarise, the situation in the Riverside area suggests that a difference in habitat selection partly explains the siting of the territories of the two species, most Blackcaps selecting maple woodland when they arrive in April and Garden Warblers settling in scrub when they arrive in May. Unlike at Rough Common, the habitats in the Riverside area were intermixed and this probably explains why interspecific interactions were relatively frequent there. The observed situation is not unambiguous since it is possible that Garden Warblers would settle in the woodland if Blackcaps were not already occupying it. Some Garden Warblers did indeed

**TABLE 3-5. THE SITTING OF GARDEN WARBLER (GW) TERRITORIES IN THE RIVERSIDE AREA IN RELATION TO THE POSITIONS OF BLACKCAP (BC) TERRITORIES**

Based on Figure 3-10. Areas in hectares.

| A.<br>YEAR | TOTAL AREA USED<br>BY BC BEFORE ANY<br>GW ARRIVED (= A) | TOTAL AREA USED<br>BY GW<br>(= B) | TOTAL OVERLAP<br>BETWEEN<br>A AND B | OVERLAP AS % OF           |                           | TOTAL AREA<br>USED BY THE<br>TWO SPECIES |
|------------|---------------------------------------------------------|-----------------------------------|-------------------------------------|---------------------------|---------------------------|------------------------------------------|
|            |                                                         |                                   |                                     | BC TERRITORY AREAS<br>(A) | GW TERRITORY AREAS<br>(B) |                                          |
| 1979       | 4.08                                                    | 3.34                              | 0.66                                | 16.2 %                    | 19.8 %                    | 9.8 %                                    |
| 1980       | 3.95                                                    | 3.12                              | 0.98                                | 24.8 %                    | 31.4 %                    | 16.1 %                                   |

| B.<br>YEAR | TOTAL AREA USED<br>BY BC AFTER GW<br>ARRIVED (= C) | TOTAL AREA USED<br>BY GW<br>(= B) | TOTAL OVERLAP<br>BETWEEN<br>C AND B | OVERLAP AS % OF           |                           | TOTAL AREA<br>USED BY THE<br>TWO SPECIES |
|------------|----------------------------------------------------|-----------------------------------|-------------------------------------|---------------------------|---------------------------|------------------------------------------|
|            |                                                    |                                   |                                     | BC TERRITORY AREAS<br>(C) | GW TERRITORY AREAS<br>(B) |                                          |
| 1979       | 3.37                                               | 3.34                              | 0.52                                | 15.4 %                    | 15.6 %                    | 8.4 %                                    |
| 1980       | 3.61                                               | 3.12                              | 0.82                                | 22.7 %                    | 26.3 %                    | 13.9 %                                   |

sing in the maple belt each year but none remained there for more than a couple of days, suggesting that they were either transients or were displaced by Blackcaps. The occurrence of frequent fights between Blackcaps and Garden Warblers whenever they did encounter each other further reinforces the idea that the ground-pattern of territory positions is also partly due to interspecific interactions (Chapter 5). Perhaps also the Blackcaps established in the woodland, and late-arriving Blackcaps, would make use of the scrub in May if it were not already being defended by Garden Warblers. Removal of the Garden Warblers from the scrub would show whether they were effectively keeping-out any Blackcaps. It would also be of interest to determine the relative productivity of woodland and scrub at different stages of the breeding season to diagnose which habitats are best able to provide the food needs of Blackcaps and Garden Warblers (if there is a difference), and hence are desirable on grounds of food-availability.

## 2. Observations in the Central area.

The Central area was the most uniform in vegetational characteristics of the parts of the wood studied. However the density of the canopy and undergrowth showed clear differences between certain parts of the area and this appeared to influence the settling pattern of Blackcaps and Garden Warblers. Closed-canopy sycamore woodland formed a ring around the area, broken only by a young elm plantation (Common Piece), in which most trees were dead, and a tract of mature larch/spruce plantation. The central part of the area was open oak woodland. In some parts under the sycamore canopy there was only a sparse cover of grass and dogs mercury, with thin patches of bramble, although in other tracts a denser undergrowth of bramble and elder was present. The open woodland in the centre of the area was covered in dense bramble thickets, in places over a metre deep, with extensive tracts of young ash and sycamore saplings. The Common Piece was also fairly open, with dense bramble clumps and elder thickets.

The area was studied from late May in 1978, when its potential was discovered. In 1979 it was used as the study plot for a removal experiment. In 1980 the area was intensively worked throughout April, May and up to June 6th. The 1978 and 1980 observations are considered here and those relating to the removal experiment are presented in Chapter 4.

The territory positions of the two species in 1978 are given in Figure 3-11A. The area was "discovered" relatively late in the season and so the Figure covers observations from late May until mid June, by when both species had fledged their young. The need to give a map for such a long period arises from a relative shortage of observations, vocal activity of the two species declining greatly after the end of May so that registrations were harder to obtain. Nevertheless, even if temporal shifts caused changes in territory boundaries over the period mapped, the territory positions still suggest a high degree of interspecific territoriality, with little overlap between Blackcaps and Garden Warblers (Table 3-6).

The territory positions in 1980 are shown for a short period at the height of the breeding season, hence minimising changes in relative positions caused by temporal shifts (Figure 3-11B). The justification for the boundaries plotted for B7 and B2 is given in Figure 3-2. Again, only small overlaps were observed between the territories of Blackcaps and Garden Warblers (Table 3-6).

Figures 3-11A and 3-11B are not entirely comparable because they cover different parts of the breeding season. Also, the first Blackcaps arrived much earlier relative to Garden Warblers in 1980 than was the case in 1978. Nevertheless a similarity in the siting of territory positions emerges between the two seasons, most Blackcaps occurring in closed-canopy woodland and Garden Warblers in the more open areas, suggesting an influence of habitat on the siting of territories in the two species. The areas marked A, B and C in the Figure

**FIGURE 3-11. THE POSITIONS OF BLACKCAP AND GARDEN WARBLER TERRITORIES  
IN THE CENTRAL STUDY AREA IN 1978 AND 1980**

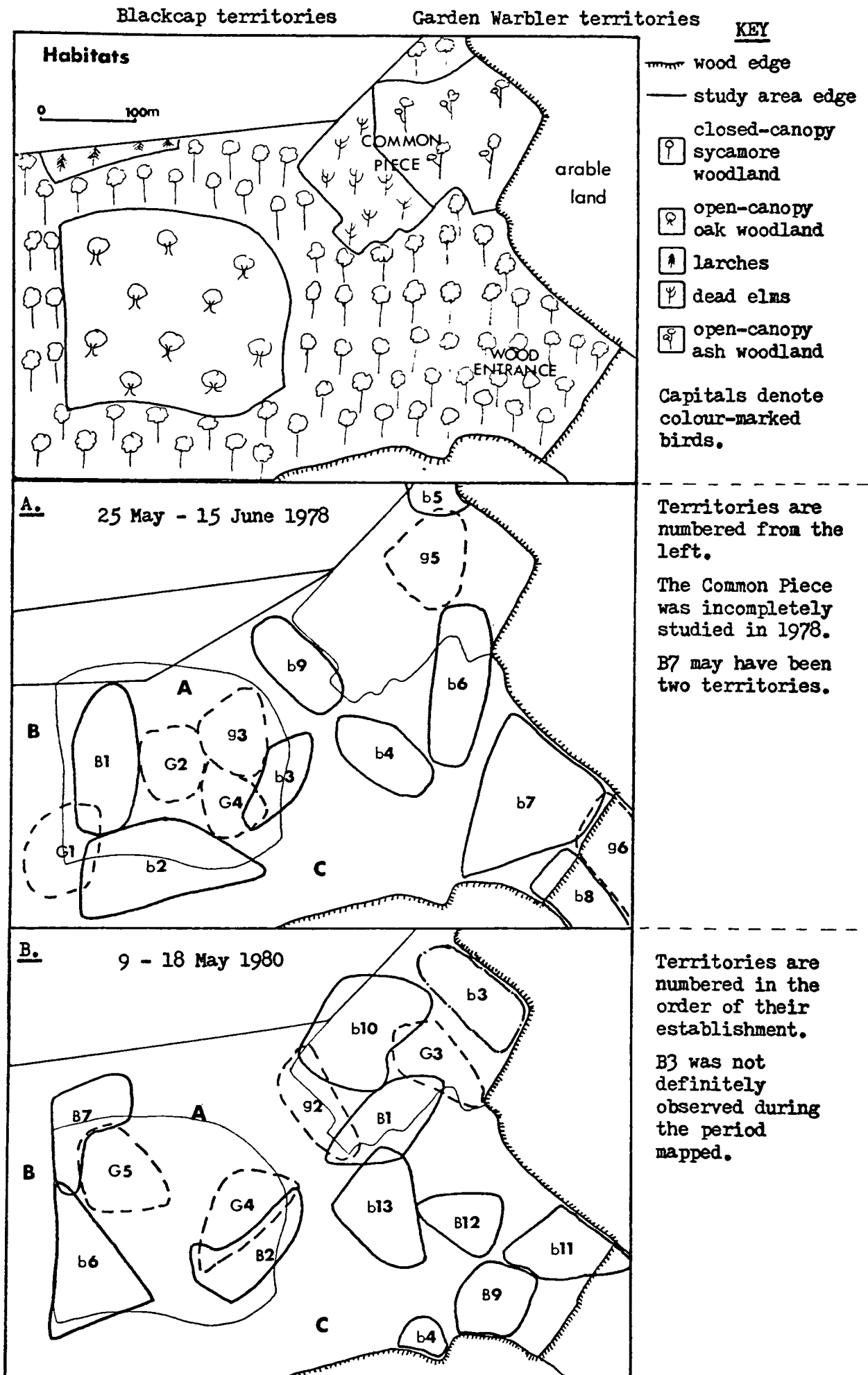


TABLE 3-6. AREA USAGE BY BLACKCAPS AND GARDEN WARBLERS IN THE CENTRAL STUDY AREA

Based on Figure 3-11. Areas in hectares.

A. The overall overlap between the two species.

| YEAR | TOTAL AREA USED<br>BY BLACKCAPS | TOTAL AREA USED<br>BY GARDEN WARBLERS | TOTAL OVERLAP<br>BETWEEN THE<br>TWO SPECIES | OVERLAP AS %<br>OF TOTAL AREA<br>USED |
|------|---------------------------------|---------------------------------------|---------------------------------------------|---------------------------------------|
| 1978 | 5.91                            | 2.67                                  | 0.26                                        | 3.1 %                                 |
| 1980 | 6.91                            | 2.32                                  | 0.35                                        | 4.0 %                                 |

B. The overlap between individuals whose territories overlapped with those of the other species.

|                                                                                                 |                        |                         |
|-------------------------------------------------------------------------------------------------|------------------------|-------------------------|
| Overlap of Blackcaps (n) with Garden Warblers expressed as a % of the BLACKCAP territory areas. | 1978<br>6.5 %<br>n = 3 | 1980<br>11.7 %<br>n = 4 |
|-------------------------------------------------------------------------------------------------|------------------------|-------------------------|

|                                                                                                       |                         |                         |
|-------------------------------------------------------------------------------------------------------|-------------------------|-------------------------|
| Overlap of Garden Warblers (n) with Blackcaps expressed as a % of the GARDEN WARBLER territory areas. | 1978<br>16.5 %<br>n = 2 | 1980<br>15.1 %<br>n = 4 |
|-------------------------------------------------------------------------------------------------------|-------------------------|-------------------------|

were the only parts of the study area where there was little or no undergrowth. They were avoided by both species in all three years of the study. Otherwise, most of the apparently-suitable habitat was used by either species every year.

It is apparent from Figure 3-11 that much of the area used by G1 and G4 in 1978 was settled by B6 and B2 respectively in 1980 and that the area used by B1 and B9 in 1978 was largely used by G5 and G2 respectively in 1980. (Figure 3-9 is another instance of a Blackcap settling in an area previously occupied by Garden Warblers.) Cody(1978: 372) also gives an example of a particular habitat patch changing ownership between a Garden Warbler and a Blackcap in successive years. These observations are clear evidence that certain areas of habitat are acceptable to the two species, although not necessarily equally suited to them both.

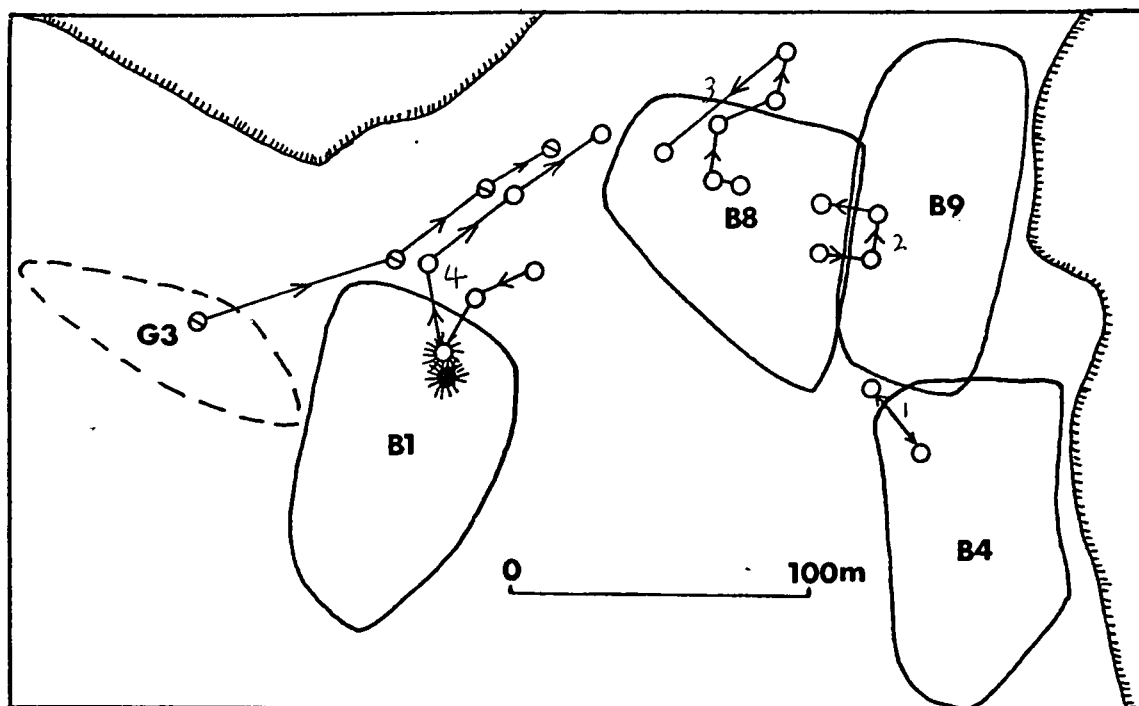
#### Interactions between Blackcaps and Garden Warblers in the Central area.

Frequent contests occurred between Blackcaps and Garden Warblers where their territories were adjacent, as well as during the period when Garden Warblers were settling in the area. In 1980, a good example was seen of a Garden Warbler making persistent attempts to settle in an area of closed-canopy deciduous woodland occupied by Blackcaps, and eventually being prevented from doing so (Figure 3-12). The incident provides circumstantial evidence of a Garden Warbler being totally-displaced from an area by previously-established Blackcaps.

The observations in 1980 enable examination of the question whether the Garden Warblers selected areas vacant of Blackcaps when establishing their territories (Figure 3-13). 73 % of the area in which Garden Warblers settled had not been claimed already by Blackcaps (Table 3-7), and the separation of the territories of the two species became even more pronounced as the season progressed (Figure 3-13B, C).



**FIGURE 3-12. THE ATTEMPTED SETTLEMENT OF A GARDEN WARBLER (G1) IN THE CENTRAL STUDY AREA IN 1980, AND ITS APPARENT DISPLACEMENT BY PREVIOUSLY-ESTABLISHED BLACKCAPS AND A GARDEN WARBLER**



**KEY** ○ —→ Registrations and movements of G1  
 ○ —→ Registrations and movements of G3      〰 wood edge  
 ☆ Interaction between G1 and B1

The locations of the events described below are numbered. B1, B8, B9 and G3 were colour-ringed at the time of the observations.

1. May 3 (0630 - 0730 hours). G1 was first noted, singing a subdued song high in the sycamore canopy. It was approached in turn by singing Blackcaps (B4, B8 & B9). On each approach G1 stopped singing and backed off, only to resume singing a little further away shortly afterwards.

2. May 4 (1000 - 1100). G1 was singing in conjunction with B4 and B9, both of which approached it. G1 stopped singing each time a Blackcap approached. B8 was not seen.

3. May 7 (0545 - 0730). G1 was singing and moving about within the territory of B8 but the latter was not seen at the time, although it was present later in the day.

4. May 7 (1030 - 1130). G1 entered the territory of B1 and was at once approached and chased-out by that bird. G3, presumably attracted by the song of G1, left its previously-known territory boundaries and chased G1 for a distance of about 100 metres.

May 8 (0600 - 0630; not mapped). G1 again approached G3 and was chased by it. G1 sang loudly after this contest and this attracted B1 which attacked G3 and chased it back to its territory, which it had left when pursuing G1.

G1 was not seen again. It presumably went to settle elsewhere. The possibility exists of course that more than one individual was involved in the sightings of G1. Whether or not this was so, the observations suggest that previously-established Blackcaps and a Garden Warbler were able to prevent any new Garden Warblers from settling in the area.

FIGURE 3-13. THE POSITIONS OF BLACKCAP TERRITORIES IN THE CENTRAL STUDY AREA IN 1980 IN ADVANCE OF THE GARDEN WARBLER ARRIVALS, COMPARED WITH THE RELATIVE POSITIONS OF THE TERRITORIES OF BOTH SPECIES AFTER THE GARDEN WARBLERS HAD ESTABLISHED THEMSELVES

Blackcap territories ( ) Garden Warbler territories  
Territories are numbered in the order of arrival of the holders. Capitals denote colour-marked birds. The boundaries of the major blocks of different habitats (as shown in Figure 3-11) are indicated.

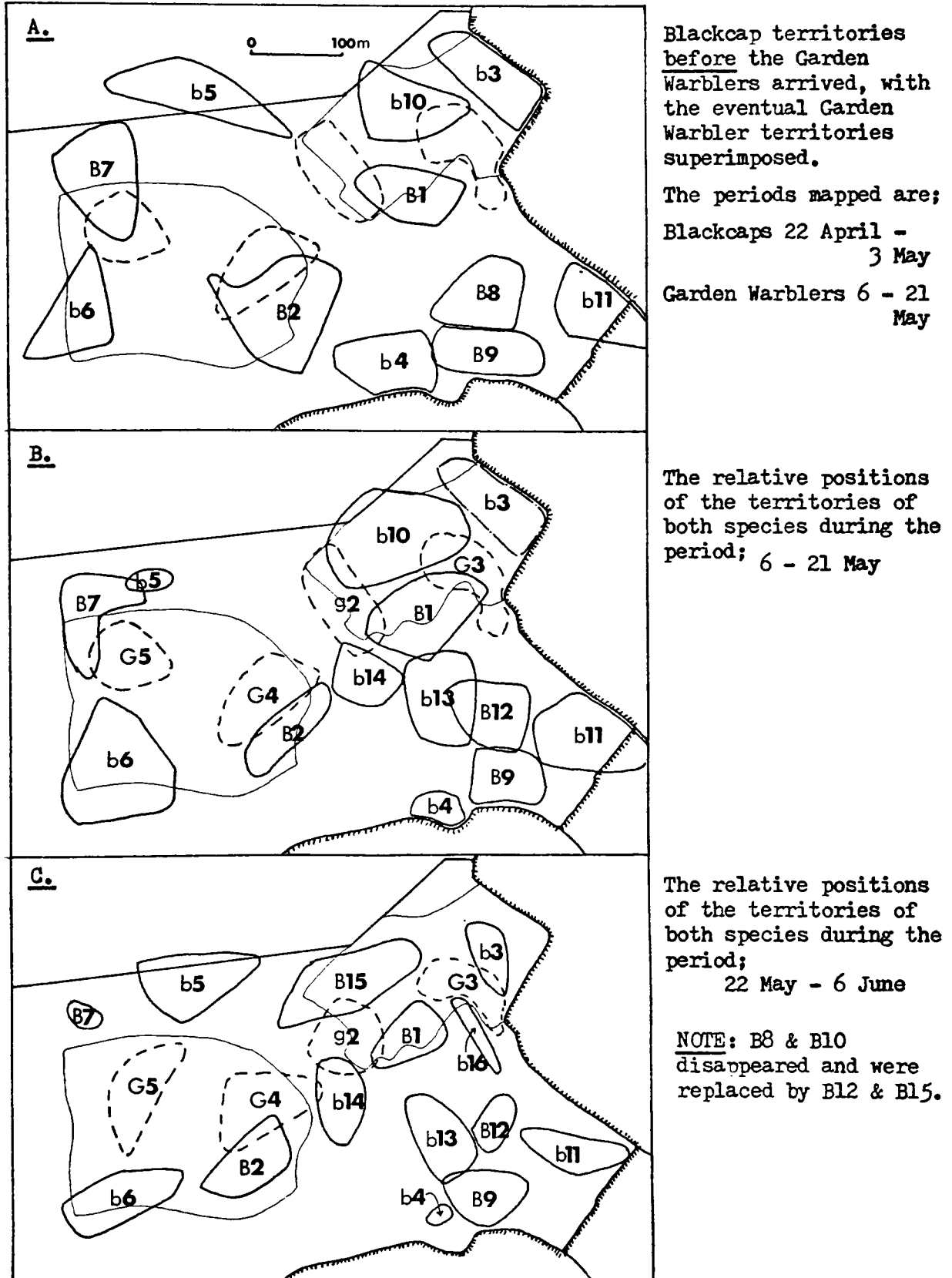


TABLE 3-7. THE SITING OF GARDEN WARBLER (GW) TERRITORIES IN THE CENTRAL STUDY AREA IN 1980 IN RELATION TO THE POSITIONS OF BLACKCAP (BC) TERRITORIES

Based on Figure 3-13a,b. Areas in hectares.

| <u>A.</u>                                         |                             |                               |                        |                                        |                                    |
|---------------------------------------------------|-----------------------------|-------------------------------|------------------------|----------------------------------------|------------------------------------|
| TOTAL AREA USED BY BC BEFORE ANY GW ARRIVED (= A) | TOTAL AREA USED BY GW (= B) | TOTAL OVERLAP BETWEEN A AND B | BC TERRITORY AREAS (A) | OVERLAP AS % OF GW TERRITORY AREAS (B) | TOTAL AREA USED BY THE TWO SPECIES |
| 6.88                                              | 2.31                        | 0.62                          | 9.0 %                  | 26.8 %                                 | 7.2 %                              |
| <u>B.</u>                                         |                             |                               |                        |                                        |                                    |
| TOTAL AREA USED BY BC AFTER GW ARRIVED (= C)      | TOTAL AREA USED BY GW (= B) | TOTAL OVERLAP BETWEEN C AND B | BC TERRITORY AREAS (C) | OVERLAP AS % OF GW TERRITORY AREAS (B) | TOTAL AREA USED BY THE TWO SPECIES |
| 7.01                                              | 2.31                        | 0.52                          | 7.4 %                  | 22.5 %                                 | 5.6 %                              |

### 3.3.5. The territory sizes of Blackcaps and Garden Warblers

Blackcap territories were significantly larger than Garden Warbler territories in the Central area (in deciduous woodland) and around Rough Common (where Garden Warblers were in scrub and Blackcaps in deciduous woodland) but territory sizes in the Riverside area were not significantly different between the two species (Table 3-8). The significance of these observations can only be speculated-at in the absence of some comparative measure of territory qualities. Any relationship between territory size and the quantity of any resource provided by the territory is likely to be only approximate, if at all evident, except in uniform habitats such as reed-beds. Nevertheless, Cody (1978) found an inverse relationship between territory sizes of Garden Warblers and Willow Warblers in Sweden and insect densities, the latter measured by using Tanglefoot plaques. In general he found small territories where insect densities were high, and vice-versa, but the pattern was also influenced by the number of co-occupant warbler species.

In Wytham some very large territories (e.g. G5 and B7 in Figure 3-10A) included open grass- and bracken-covered stretches which were not used by the warblers. Conversely, some very small territories such as the Garden Warbler ones around Rough Common, consisted entirely of dense thorn thickets, so that all parts of the territories provided foraging and nesting opportunities. Ideally, an assessment of territory quality in Blackcaps and Garden Warblers, and other species inhabiting complex habitats, should consider the volume of usable vegetation present in each territory, among other variables.

#### Seasonal changes in territory sizes.

The wide-ranging behaviour shown by early Blackcap arrivals has already been described. The territories eventually established in



advance of the Garden Warbler arrivals were often larger than those defended once the Garden Warblers had settled. However, in a few cases, extended observations suggested that some Blackcap territories were larger in May than they had been in April. Since territories were not visited for fixed periods of time it is impossible to ascertain whether some of the territory size changes detected were real or whether they resulted from different amounts of attention being given to different territory holders. Not all birds were colour-ringed and so some changes in territory size could also have been associated with changes in occupancy.

In the Riverside area the overall trend was for no significant change in the size of Blackcap territories, compared between the periods before and after the arrival of Garden Warblers, although in most cases shrinkages in territory areas were recorded (Table 3-9A). By early June many Blackcaps had fledged young and abandoned their territories, some of which were then taken over by other Blackcaps. An unknown but probably small proportion of Blackcaps had second broods, but little data was gathered on this point. Most Garden Warblers remained on their territories until mid-June and a significant reduction in their territory-sizes was evident as the season progressed (Table 3-9B).

Territory sizes at different stages of the breeding season were studied in more detail in the Central area in 1980. Most birds were marked and the occupancy of particular sites was thus monitored without ambiguity (Table 3-10). The four Garden Warblers present showed no significant changes in territory size over the period studied. After some early extensive wanderings, Blackcaps established territories which remained fairly stable in size between April and mid-May. However, those Blackcaps which were still present on their territories during late May and early June were then defending significantly smaller areas (Figure 3-13C).

TABLE 3-9. THE TERRITORY SIZES OF BLACKCAPS AND GARDEN WARBLERS IN THE RIVERSIDE STUDY AREA AT DIFFERENT STAGES OF THE BREEDING SEASON

A. Territory sizes of 13 Blackcaps before and after the arrival of Garden Warblers (GW).

| BIRD                | TERRITORY SIZE (hectares) |                  | % change in area from before to after GW arrivals |
|---------------------|---------------------------|------------------|---------------------------------------------------|
|                     | Before GW arrival         | After GW arrival |                                                   |
| 1979 (B1)           | 1.02                      | 0.56             | - 45.1 %                                          |
| B2                  | 0.60                      | 0.41             | - 31.7 %                                          |
| B3                  | 0.44                      | 0.43             | - 2.3 %                                           |
| B4                  | 0.54                      | 0.29             | - 46.3 %                                          |
| B5                  | 0.79                      | 0.77             | - 2.5 %                                           |
| B6                  | 0.69                      | 0.41             | - 40.6 %                                          |
| 1980 B1             | 0.95                      | 0.63             | - 33.7 %                                          |
| B2                  | 0.39                      | 0.55             | + 41.0 %                                          |
| B3                  | 0.42                      | 0.48             | + 14.3 %                                          |
| B4                  | 0.47                      | 0.32             | - 31.9 %                                          |
| (B5)                | 0.59                      | 0.32             | - 45.8 %                                          |
| B6                  | 0.61                      | 0.83             | + 36.1 %                                          |
| B7                  | 0.52                      | 0.48             | - 7.7 %                                           |
| Mean Territory Size | 0.62                      | 0.50             |                                                   |
| Standard Deviation  | 0.20                      | 0.17             |                                                   |

Territory sizes do not differ significantly between the two periods (Wilcoxon Test, 2-tailed,  $p > 0.05$ ).

NOTES 1. The data is based on Figure 3-10.

2. 1978 is omitted since Blackcap territory areas before the Garden Warbler arrivals were inadequately known in that year.

3. The birds in parentheses had no Garden Warbler neighbours but their territories nevertheless show a reduction in size between the two periods.

TABLE 3-9. (Continued)

B. Territory sizes of Garden Warblers compared between different stages of the breeding season.

| BIRD                      | TERRITORY SIZE (hectares) |      | % change in area from<br>May to June |
|---------------------------|---------------------------|------|--------------------------------------|
|                           | MAY                       | JUNE |                                      |
| 1978 G1                   | 0.58                      | 0.42 | - 27.6 %                             |
| G2                        | 0.77                      | 0.48 | - 37.7 %                             |
| G3                        | 1.40                      | 0.49 | - 65.0 %                             |
| G4                        | 0.70                      | 0.50 | - 28.6 %                             |
| G6                        | 0.42                      | 0.31 | - 26.2 %                             |
| 1979 G1                   | 0.51                      | 0.40 | - 21.6 %                             |
| G2                        | 0.54                      | 0.37 | - 31.5 %                             |
| G5                        | 1.23                      | 0.21 | - 82.9 %                             |
| G6                        | 0.33                      | 0.32 | - 3.0 %                              |
| Mean<br>Territory<br>Size | 0.72                      | 0.39 |                                      |
| Standard<br>Deviation     | 0.36                      | 0.10 |                                      |

The trend for a reduction in territory size between May and June is significant (Wilcoxon Test, 2-tailed,  $p < 0.01$ ).

- NOTES
1. The periods actually compared are May 5 - 25 with May 26 - June 15 in 1978 and May 7 - 30 with May 31 - June 15 in 1979. This was done to make allowance for differences between the periods in the number of days in which the area was surveyed.
  2. Not all territories were traceable in June and so some birds are omitted. G5 in 1978 is omitted because there was reason to doubt that its site was occupied by the same individual in both months.



TABLE 3-10. THE TERRITORY SIZES OF BLACKCAPS AND GARDEN WARBLERS IN THE CENTRAL STUDY AREA COMPARED BETWEEN DIFFERENT STAGES OF THE BREEDING SEASON IN 1980

A. BLACKCAP TERRITORY SIZES (hectares)

| <u>BIRD</u>               | 1.<br>APR - MAY 5 | 2.<br>MAY 6 - MAY 21 | 3.<br>MAY 22 - JUN 6 | % change in area from<br>period 2 to period 3. |
|---------------------------|-------------------|----------------------|----------------------|------------------------------------------------|
| B1                        | 0.61              | 0.80                 | 0.36                 | - 55.0 %                                       |
| B2                        | 1.15              | 0.41                 | 0.43                 | + 4.9 %                                        |
| B3                        | 0.56              | -                    | 0.25                 |                                                |
| (B4)                      | 0.59              | 0.15                 | 0.03                 | - 80.0 %                                       |
| B6                        | 0.65              | 1.15                 | 0.57                 | - 50.4 %                                       |
| B7                        | 0.86              | 0.56                 | 0.07                 | - 87.5 %                                       |
| (B9)                      | 0.55              | 0.46                 | 0.37                 | - 19.6 %                                       |
| B10                       | 0.74              | 1.26                 | -                    |                                                |
| (B11)                     | 0.50              | 0.72                 | 0.34                 | - 52.8 %                                       |
| (B12)                     | -                 | 0.53                 | 0.17                 | - 67.9 %                                       |
| (B13)                     | -                 | 0.70                 | 0.43                 | - 38.6 %                                       |
| B14                       | -                 | 0.33                 | 0.35                 | + 6.1 %                                        |
| Mean<br>Territory<br>Size | 0.69              | 0.64                 | 0.31                 |                                                |
| Standard<br>Deviation     | 0.20              | 0.34                 | 0.16                 |                                                |

Territory sizes do not differ significantly between periods 1 and 2 (Wilcoxon Test, 2-tailed,  $p > 0.05$ ,  $n = 8$ ). Territory areas are significantly smaller in period 3 than in either period 1 or period 2 (Wilcoxon Test, 2-tailed,  $p < 0.01$ ,  $p = 0.01$ ;  $n = 7$ ,  $n = 10$  respectively).

NOTES 1. Period 1 is the time preceding the Garden Warbler arrivals.

2. - = absent during the period. The absence of B3 during most of May may have involved a change in territory occupant. B8 disappeared during period 1 and B5 was inadequately studied. Both are omitted.

3. Birds in parentheses had no Garden Warblers as neighbours.

4. The data is based on Figure 3-13.

B. GARDEN WARBLER TERRITORY SIZES (hectares)

| <u>BIRD</u>         | MAY 6 - MAY 21 | MAY 22 - JUN 6 |
|---------------------|----------------|----------------|
| G2                  | 0.61           | 0.51           |
| G3                  | 0.60           | 0.41           |
| G4                  | 0.63           | 0.66           |
| G5                  | 0.47           | 0.53           |
| Mean Territory Size | 0.58           | 0.53           |
| Standard Deviation  | 0.07           | 0.10           |

### 3.3.6. Philopatry in Blackcaps and Garden Warblers at Wytham

Significantly more Garden Warblers than Blackcaps, ringed as adults during the breeding season, were present in the wood the year after (Table 3-11). The recovery rate for Garden Warblers (30%) is similar to that recorded for males in southern Finland (25%, Solonen 1979), and most of the birds ringed at Wytham were males. The recovery rate for Blackcaps (4.8%) is much lower than that recorded in southwest Germany (40%, Bairlein 1978). More years' data is needed to establish whether the two species differ in breeding site fidelity in Britain generally, to the extent found in the present study. For both species, fledged juveniles and adults caught after the breeding season gave negligible return data. For Garden Warblers at least, there are indications that returning birds remained faithful to the habitat which they occupied when they were ringed (Table 3-12), but for both species the data available on this point is sparse.

76% of 71 recoveries within Britain of Blackcaps ringed there in the breeding season were within 25 kilometres of the ringing site. This suggests that they at least return to the same general area to breed in successive years, particularly since fidelity to specific sites is underestimated by ringing recoveries because many ringers do not report recaptures of "their own" birds (Langslow 1979).

### 3.4. DISCUSSION

The observations at Wytham suggest that Blackcaps and Garden Warblers are interspecifically territorial in areas where both species are in similar habitats. In areas where scrub adjoins woodland, most Blackcap territories are situated in the woodland but many Garden Warblers settle in the scrub. The many Blackcaps which arrive before the earliest Garden Warblers settle chiefly in woodland. This may be because Blackcaps prefer woodland but it is also possible that the alternative habitat, scrub, is less able to support warblers until later in the season, when the Garden Warblers which mainly use it are arriving. A comparative study of food-availability

TABLE 3-11. SIGHTINGS AND RECAPTURES IN SUCCESSIVE YEARS OF BLACKCAPS AND GARDEN WARBLERS RINGED AT WYTHAM DURING 1978 AND 1979

The table presents the pooled observations of 1979 and 1980. Observed birds include retraps as well as sightings of colour-ringed individuals. The numbers observed are given as a fraction of the numbers ringed.

| RINGED<br>AS                      | OBSERVED AFTER 1 YEAR |                    | OBSERVED AFTER 2 YEARS |                    |
|-----------------------------------|-----------------------|--------------------|------------------------|--------------------|
|                                   | BLACKCAPS             | GARDEN<br>WARBLERS | BLACKCAPS              | GARDEN<br>WARBLERS |
| Adults during the breeding season | 3/63(4.8%)            | 12/40(30.0%)       | 1/14(7.1%)             | 3/19(15.8%)        |
| Adults after the breeding season  | 0/29                  | 0/6                | 0/15                   | 1/3 (33.3%)        |
| Fledged juveniles                 | 1/62(1.6%)            | 0/22               | 0/40                   | 0/15               |
| Pulli                             | 0/22                  | 0/18               | 0/15                   | 0/12               |

Significantly more adult Garden Warblers than adult Blackcaps were observed one year after ringing ( $\chi^2 = 10.58$ , d.f. = 1,  $p < 0.01$ ) but the difference after two years is not significant (Fisher Exact Test,  $p = 0.45$ ).

#### NOTES

1. The only Blackcap present two years after ringing was not observed in the intervening year. Two of the four Garden Warblers ringed in 1978 and recovered in 1980 were similarly not observed in 1979.
2. Blackcaps removed from the wood in 1979 and released elsewhere (Chapter Four) are not included. None was known to have returned in 1980.
3. In addition to the above, a juvenile Blackcap and a yearling male Blackcap ringed at Wytham on August 28 1978 and 19 May 1979 respectively were recovered after one year in Lincolnshire (162 km NE) and Wiltshire (62 km SW) respectively, both in May. This could be taken as evidence of weak philopatry by Wytham Blackcaps but the first bird could have been born in Lincolnshire and caught on passage through Wytham and the second might have been on its way back to the wood .
4. In 1979 a Garden Warbler pullus was recovered dead just outside the wood 50 days after ringing. Rings of two Garden Warbler pulli ringed in 1978 were recovered shortly after in a nearby Sparrowhawk nest (T.Geer, pers. comm.).

TABLE 3-12. HABITAT FIDELITY IN BLACKCAPS AND GARDEN WARBLERS RETURNING  
TO WYTHAM WOOD IN SUCCESSIVE YEARS

A. GARDEN WARBLERS

|                             |          | Habitat where recovered. |       |
|-----------------------------|----------|--------------------------|-------|
|                             |          | Woodland                 | Scrub |
| Habitat<br>where<br>ringed. | Woodland | 5                        | 1     |
|                             | Scrub    | 1                        | 6     |

- NOTES
1. Birds recovered in the same habitat were all found on territories very close to, or coincident with, the territories where they were ringed.
  2. Of the two birds which switched habitat, the bird ringed in scrub was recovered in the woodland immediately adjacent to it and it is uncertain which habitat it was using in either year. The second bird was probably a genuine case of a change of nesting habitat. It was a female paired to a male in the Central study area in 1978 and recovered in 1979 in scrub at Rough Common, 1000 metres away, apparently paired to a male there.
  3. Two birds which were present in all three years of the study remained faithful to their original territory positions, one in wood and one in scrub, every year.

B. BLACKCAPS

|                             |          | Habitat where recovered. |       |
|-----------------------------|----------|--------------------------|-------|
|                             |          | Woodland                 | Scrub |
| Habitat<br>where<br>ringed. | Woodland | 3                        | 1     |
|                             | Scrub    | 0                        | 0     |

- NOTES
1. One male was caught in the same area where it was ringed. The two other birds, one male and one female, recovered in woodland were 1000 metres and 1500 metres away respectively from the place of ringing, and they both remained in the new sites for the breeding season.
  2. The bird (male) recovered in scrub was 700 metres away from its woodland territory of the previous year but it was uncertain whether it was breeding in the scrub where it was recovered.

in scrub and deciduous woodland, combined with an investigation of territory sizes in these two major habitats, is needed to reveal whether there are any seasonal or general differences between the habitats regarding their capacity to support warblers.

This study has shown that both Blackcaps and Garden Warblers obtain all or most of their food within their territory boundaries, in addition to nesting there. Courtship and mating also occurs inside the territories (Howard 1910-1914). Possibly, therefore, interspecific territoriality between Blackcaps and Garden Warblers is associated with competition for food between the two species.

With rare exceptions, Garden Warblers establish their territories outside Blackcap-occupied habitat. This could mean that Blackcap habitat is unsuitable for Garden Warblers and is avoided by them. However, cases were observed of Garden Warblers apparently trying to settle within Blackcap territories and being attacked and displaced by the resident Blackcaps, suggesting that some Blackcaps exclude Garden Warblers from areas where the habitat is suitable for the two species. Certain habitat patches were used by Blackcaps in one year and by Garden Warblers in another. Similarly, Solonen (1979) found that naturally-vacated territories of either species were usually soon occupied by other pairs, usually Garden Warblers. Such observations demonstrate that at least some habitat is occupiable by both species and that the presence of only one of them is often due to interspecific territoriality.

Blackcaps are clearly dominant over Garden Warblers in interspecific interactions (see also Chapter 5), contrary to the conclusion of Cody (1978). The relationship between the two species is also different from that found between Sedge and Reed Warblers, a well-studied species-pair in which one species arrives before the other on the breeding grounds and which are interspecifically territorial. Here the later-arriving Reed Warblers are often dominant over the previously-established Sedge Warblers (Catchpole

1972, Brown & Davies 1949) and their arrival results in territory shifts by the Sedge Warblers, or even the total displacement of the latter from some types of habitat (Svensson 1978). However, unlike Blackcaps and Garden Warblers, Reed and Sedge Warblers often feed outside their territory boundaries (Lack 1946), so that the two territory-systems are not entirely comparable. Once established, Garden Warblers are not displaced by later-arriving Blackcaps, suggesting that interspecific territoriality between the two species is mutual or, again, that the habitats in which Garden Warblers settle are mainly avoided by Blackcaps.

Territory-mapping usually revealed little overlap between adjacent Blackcap and Garden Warbler territories but such overlaps were nevertheless more conspicuous than those found between conspecific neighbours. Perhaps territory boundaries are defended more vigorously against conspecific intruders than against those of another species; this is quite likely since conspecific intruders represent competition for mates, which those of other species do not. However, overlaps between territories of different species are easier to detect than overlaps between conspecifics since in the latter case boundary registrations may sometimes be assigned to the wrong territory, whereas in the former case the identity of individuals is never in doubt. It is possible therefore that overlaps between conspecifics were underestimated relative to those between the two species.

CHAPTER FOUR

AN EXPERIMENTAL TEST  
OF THE HYPOTHESIS THAT  
BLACKCAPS AND GARDEN WARBLERS  
COMPETE FOR SPACE

## CHAPTER FOUR

### AN EXPERIMENTAL TEST OF THE HYPOTHESIS THAT BLACKCAPS AND GARDEN WARBLERS COMPETE FOR SPACE

#### 4.1. INTRODUCTION

Two alternative hypotheses could explain why Blackcap and Garden Warbler territories do not generally overlap. Firstly, the two species may select different habitats which are patchily-distributed and which do not themselves overlap. Secondly, the two species may compete for the same habitat and defend mutually-exclusive territories. The latter hypothesis is supported by observations of interspecific interactions but the critical test of it is to perform a removal experiment to see if one species will replace the other in the same locality. Blackcaps generally establish their territories before Garden Warblers do so; about 65% of Blackcaps have territories even before the first Garden Warblers arrive in spring. A removal experiment was carried out to see whether Garden Warblers were being excluded from some areas by the presence there of the earlier-established Blackcaps. Removal experiments involving birds are rare (Connell 1975) and, so far as I am aware, this is the first study to have used the technique in investigating interspecific territoriality in the breeding season.

#### 4.2. METHODS

The experiment was carried out in a large part of the Central study area in 1979. The positions of Blackcap and Garden Warbler territories were mapped in this area both in 1978 and 1980, which provided information on the natural (i.e. unmanipulated) distribution and abundance of the two species within the removal zone. Observations in the Riverside study area provided some information on the relative abundance of the two species in the wood each year, for control purposes.

In 1979 the removal zone was visited from the beginning of April and the positions of Blackcap territories observed as they became established. Territory mapping continued until May 8th, when the first



Garden Warbler arrived in the area. The Blackcaps in the removal zone were not used as subjects in song playback experiments, nor were they colour-ringed, since such disturbance might have made them harder to catch later. The mapping of Blackcap territories before removals began provided a useful indication of some of the areas which would have been occupied by Blackcaps in the removal zone in 1979.

The removal of Blackcaps began with the arrival of the first Garden Warblers. All the established Blackcaps were removed and any others which tried to settle in the removal zone were also captured as soon as possible after they had been detected. Playback of Blackcap song was used to attract birds into mist-nets. The method was highly effective, usually permitting the immediate capture of territory holders, even replacement ones which had only been present for a few hours. Replacement birds were nearly always caught on the day they arrived. However, a time-lag of several hours occurred sometimes before the birds were detected, their prospective territory positions pinpointed and the netting procedure carried out (the mean time of capture for the replacement Blackcaps was 12.15 hours; s.d. 3.5,  $n = 18$ ). This meant that the removal zone was not totally Blackcap-free, although (with two exceptions) it did lack well-established birds, and hence that competition for space could still have occurred briefly between newly-arrived Blackcaps and Garden Warblers. This possibility is considered below in assessing the results of the experiment. Only males were captured and removed. A few female Blackcaps, which were not known to be active in territory defence, were caught incidentally and these were marked and released on the spot. None of these females were seen again once their mates had been removed. Removed birds were held in temporary captivity until the end of the removal period and then released, most of them near Cheltenham, fifty kilometres away. Only one, which escaped in Oxford after the removal period ended, returned to the wood.

Garden Warblers which settled in the removal zone were mist-

netted and colour-ringed as soon as possible. Own-species song playback was also used as a lure. Again, the capture method only caught males, although one female was caught by chance and another was a colour-ringed bird from the 1978 season.

Events throughout the removal zone were studied intensively and daily maps prepared showing the movements of the Garden Warblers, as well as those of any Blackcaps which tried to settle there, during the few hours before the latter were removed. Interspecific and intraspecific interactions were studied as in other parts of the wood (Chapter 5). Removal of Blackcaps continued until June 5th, nineteen days after the arrival of the last Garden Warbler to settle in the area. Some Blackcaps were still trying to settle in the removal zone at that date and these were now permitted to do so. The territories of these Blackcaps, and those of the Garden Warblers, were plotted until the end of June, by when nearly all the Garden Warblers had fledged young and had abandoned their territories.

### 4.3. RESULTS

#### 4.3.1. OBSERVATIONS DURING THE REMOVAL EXPERIMENT

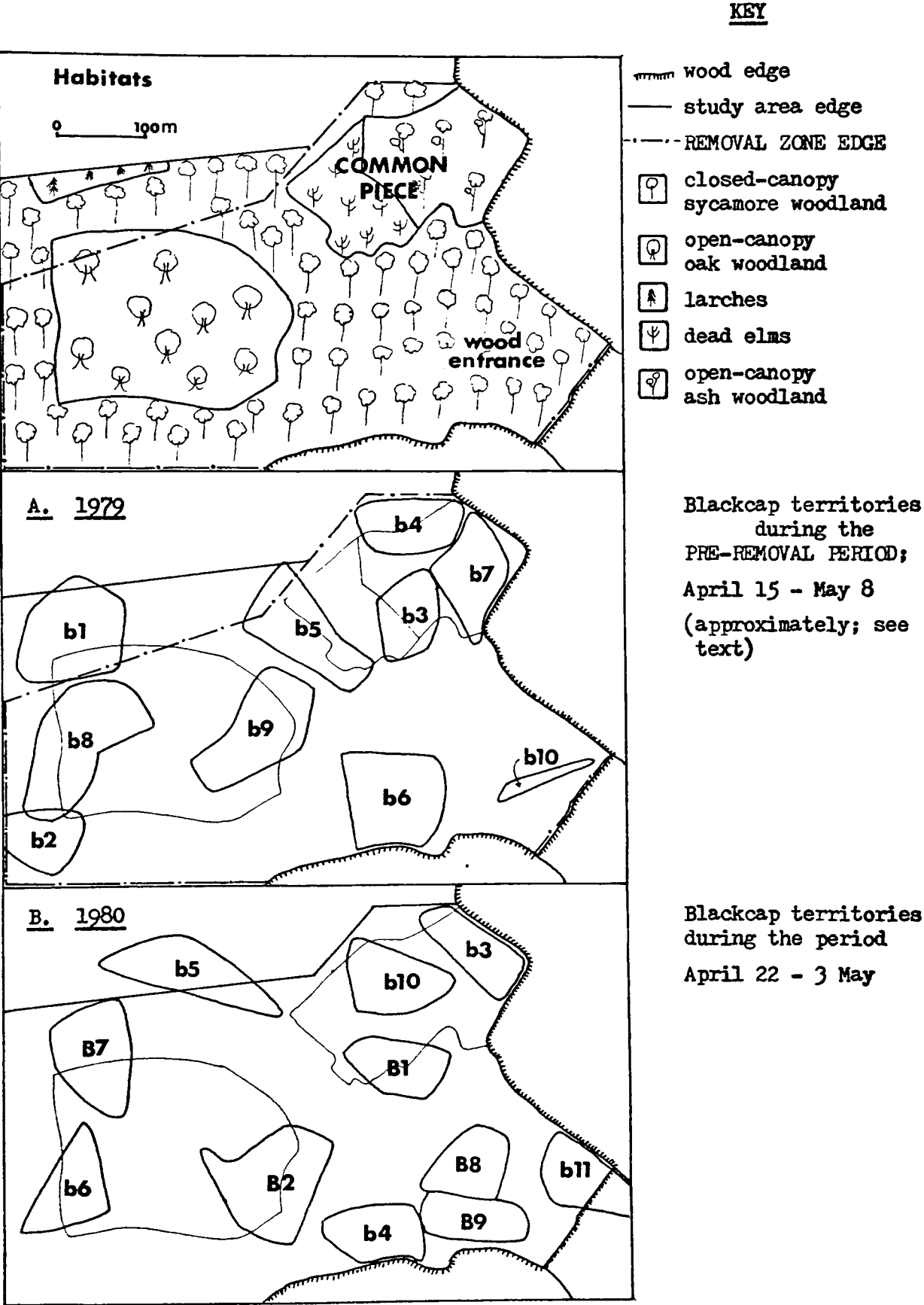
The experiment comprised three phases; the removal period itself and the periods before and after it. These are now considered in turn.

##### A. The pre-removal period. (April 15th - May 8th)

Nine Blackcaps established territories wholly or largely (more than 50%) within the removal zone in advance of the first Garden Warbler arrivals, with a tenth Blackcap (B1) just outside (Figure 4-1A). The first two arrived on April 15th and the rest from April 20th onwards, although two did not arrive until May 7th, the day before the first Garden Warbler appeared. As usual, most of the earlier arrivals wandered extensively before settling on their prospective breeding territories. Figure 4-1A excludes these early wanderings, chiefly by plotting registrations only for the period from April 28th to the date on which each Blackcap was removed.

**FIGURE 4-1. THE POSITIONS OF BLACKCAP TERRITORIES IN THE CENTRAL STUDY AREA BEFORE THE ARRIVALS OF GARDEN WARBLERS IN 1979 AND 1980**

 Blackcap territories  
 Territories are numbered in the order of arrival of the holders. Capitals denote colour-marked birds.



All of the Blackcaps were in areas with dense undergrowth. A comparison with the Blackcap territory positions before Garden Warblers arrived in 1980 (Figure 4-1B) shows that in both years Blackcaps largely skirted the area of open woodland in the centre of the study area (which Garden Warblers used in 1978 and 1980) and occupied much of the Common Piece. Territory positions showed substantial overlap between the two years but there were large areas which were selected by early Blackcaps in only one of the two years (Table 4-1). This could have been due to a certain degree of randomness in the siting of territories or to differences in habitat quality in different parts of the study area between the two years.

#### B. The removal period. (May 9th - June 5th)

Removals began on the Common Piece with the capture of B3, B4 and B7 on May 9th, and were extended to the rest of the removal zone on May 14th, with the capture of B2, B8 and B9. Some of the artificially-vacated areas, especially those on the Common Piece, were immediately claimed by new Blackcaps. These replacement birds probably included new arrivals in the wood but some were believed to be holders of neighbouring territories (presumably inferior ones) since B5, B6 and B10 "disappeared" soon after removals began and before any direct attempt was made to catch them. Replacement Blackcaps were also removed, with two exceptions (B13 and B16 in Figure 4-3) which proved elusive. In all, 24 Blackcaps were removed during the course of the experiment.

Nine Garden Warblers established territories which were wholly or chiefly (more than 50%) within the removal zone (Figure 4-2A). The last of these arrived on May 17th, well before the removal period ended. Five of the Garden Warbler territories were clustered about the Common Piece and adjacent woodland, three were in the central part of the study area and the ninth was at the wood entrance. One of the three centrally-placed birds (G1), which was also the first Garden Warbler to arrive, had held a territory in the same area in 1978 (G4 in Figure 3-11A). Moreover, he was paired in 1979 to the same

TABLE 4-1. THE TOTAL EXTENT OF BLACKCAP TERRITORIES IN THE REMOVAL ZONE IN ADVANCE OF THE GARDEN WARBLER ARRIVALS THERE, COMPARED BETWEEN 1979 (THE EXPERIMENTAL YEAR) AND 1980 (THE CONTROL YEAR)

Data based on Figures 4-1A and 4-1B. The overlaps are derived from their superimposition.

| YEAR | TOTAL AREA USED <sup>1</sup> | TOTAL OVERLAP IN TERRITORY POSITIONS BETWEEN-YEARS | TOTAL BETWEEN-YEAR OVERLAP AS % OF TOTAL AREA USED | MEAN TERRITORY SIZE <sup>2</sup> ( $\pm$ S.D.) |
|------|------------------------------|----------------------------------------------------|----------------------------------------------------|------------------------------------------------|
| 1979 | 6.41 h.                      |                                                    | 42.9 %                                             | 0.84 h. ( $\pm$ 0.27),<br>n = 9                |
|      |                              | 2.75 h.                                            |                                                    |                                                |
| 1980 | 6.21 h.                      |                                                    | 44.3 %                                             | 0.69 h. ( $\pm$ 0.19),<br>n = 11               |

NOTES 1. For territories only partly within the removal zone only that portion within the zone has been included .

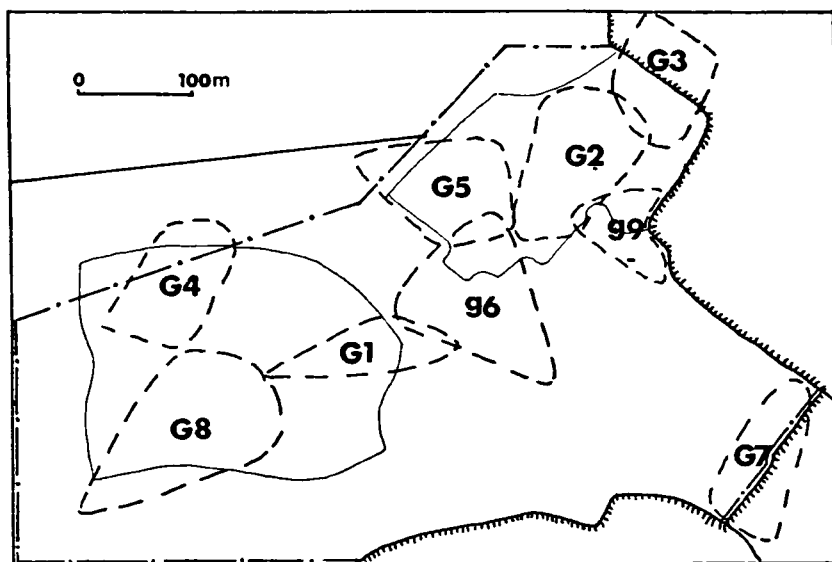
2. Territory sizes were calculated for the central study area as a whole, i.e. including territories which were not entirely within the removal zone. B10 in 1979 is excluded; it arrived the day before removals started and the small area plotted for it is probably incomplete. Territory sizes are not significantly different between the two years (Mann Whitney U-Test, 2-tailed,  $p > 0.05$ ).

**FIGURE 4-2. THE POSITIONS OF GARDEN WARBLER TERRITORIES IN THE CENTRAL STUDY AREA DURING THE REMOVAL PERIOD IN 1979, COMPARED WITH THOSE OF BOTH BLACKCAP AND GARDEN WARBLER TERRITORIES IN THE SAME AREA DURING THE EQUIVALENT PERIOD OF 1980**

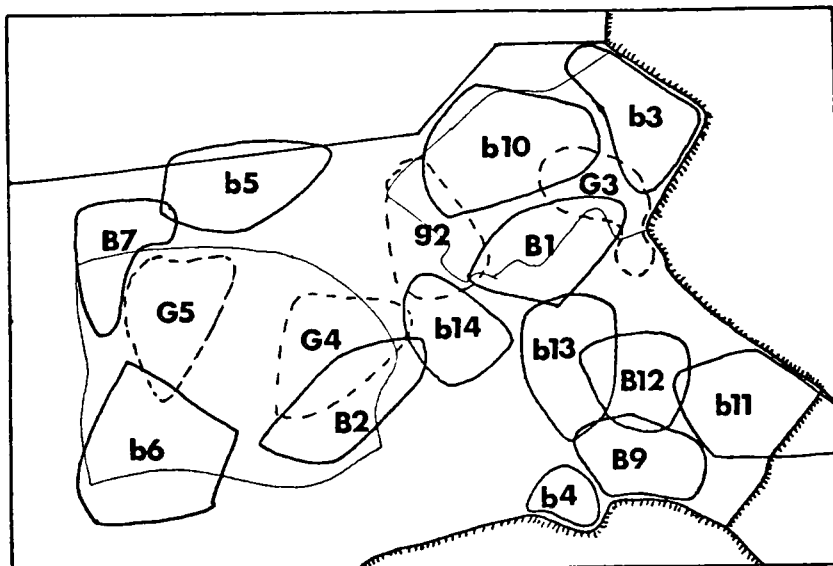
 Blackcap territories    
  Garden Warbler territories

Territories are numbered in the order of arrival of the holders. Capitals denote colour-marked birds. The boundaries of the Removal Zone and the study area, and of the major blocks of different habitats (as shown in Figure 4-1), are indicated.

**A. 1979 GARDEN WARBLER TERRITORIES DURING THE REMOVAL PERIOD,  
MAY 9 - JUNE 5.**



**B. 1980 BLACKCAP AND GARDEN WARBLER TERRITORIES DURING THE PERIOD  
MAY 6 - JUNE 6.**



female as in 1978 (probably an infrequent event for a migrant passerine). He also returned to the same area in 1980 (G<sup>4</sup> in Figure 3-11B). The other Garden Warblers (and all the Blackcaps) which settled in the removal zone did not include any ringed in 1978.

The progressive replacement of Blackcaps by Garden Warblers as the former were removed was striking. It was particularly evident in the vicinity of the Common Piece (Figure 4-3), where most of the area originally claimed by B<sub>3</sub>, B<sub>4</sub>, B<sub>5</sub> and B<sub>7</sub> (and numerous replacement Blackcaps) was taken over by the five Garden Warblers which settled there. As described below, the central part of the removal zone was under much less pressure from replacement Blackcaps than was the Common Piece, and territories were less densely packed there. The effects of the removal of Blackcaps were less pronounced although the three Garden Warblers which settled there also used areas earlier occupied by Blackcaps (Figure 4-4).

A part of the removal area used by Blackcaps, notably B<sub>6</sub> and B<sub>10</sub> in Figure 4-1A, was not taken over by Garden Warblers when the Blackcaps were removed. This could indicate that insufficient Garden Warbler potential-colonists were available or, perhaps more probably, that the habitat there was suitable for Blackcaps only. Evidence for the latter is available from a comparison between Garden Warbler territory positions in 1979 and the positions of both species in 1980 (Figure 4-2). It is conspicuous that much of the area which Garden Warblers left vacant in 1979 was avoided by both species in 1980, and so was presumably unsuitable for either of them. However, the area around the wood entrance was used by Blackcaps in 1980 (and in 1978; Figure 3-11A) but was not occupied by Garden Warblers when the Blackcaps were removed in 1979. That area, of closed-canopy sycamore woodland, was presumably mainly suitable for Blackcaps only, although a Garden Warbler did appear to try and settle in a part of it in 1980 (Figure 3-12) and some Garden Warbler territories (notably G<sub>6</sub> in 1979) included large tracts of apparently-similar habitat.

FIGURE 4-3. THE PROGRESSIVE REPLACEMENT OF BLACKCAPS BY GARDEN  
WARBLERS IN THE COMMON PIECE AREA DURING THE REMOVAL  
PERIOD (MAY 9th - JUNE 5th)

A. May 9th

The positions of Blackcap territories when the first Garden Warbler (G2) arrived in the area. The movements of G2 are indicated (o—→). G2 was first noticed at 0620 hours, when it began to sing. It was immediately pursued by B3 and B7 when it entered their territories. B3, B4 and B7 were removed that evening, and G2 was caught and colour-ringed at the same time.

B. May 10th

G2 had already paired and was seen to have settled in an area which included parts of the former territories of the three Blackcaps removed the previous day. Two new Blackcaps (B11 & B12) were also present; one of these was possibly B5 which had apparently disappeared and might have shifted its territory position. Interspecific contests occurred between G2 and B11 and B12 in turn, but in neither case was the aggressor identified. B11 and B12 were removed at 10.30.

C. May 11th & 12th

Two new Blackcaps (B13 & B14) and another Garden Warbler (G3) arrived on May 11th. G2 and G3 interacted vigorously but eventually settled as shown. B13 settled at the edge of the area, intruding only slightly into the removal zone; it eluded capture and was left to settle there. B14 intruded into the territory of G2, but left when the latter approached it. B14 was removed on May 11th and G3 was colour-ringed the same day. B15 arrived and was removed on May 12th. G5 arrived on May 12th and settled in an area which had originally been largely within the territory of B5. Another Garden Warbler(o) arrived on May 12th within the territory of G2. It was chased out by the holder, and may have been the same bird which occupied the territory marked G6 next day.

D. May 13th - 25th

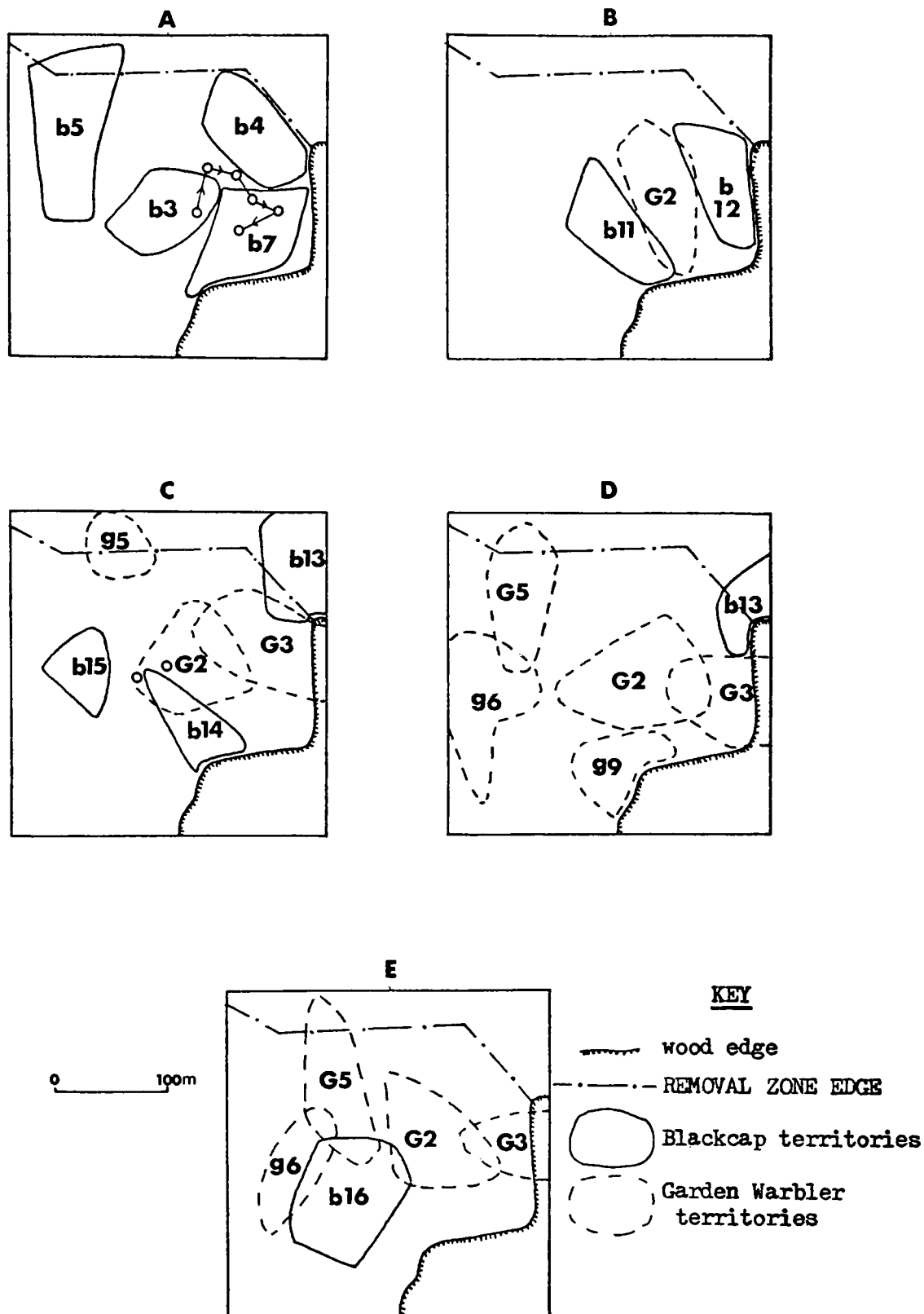
Five Garden Warblers were established in the Common Piece during this period, and a further eight Blackcaps were removed from the area. G6 used most of the area claimed by B15 during its short stay. G5 was colour-ringed on May 19th but G6, and the fifth Garden Warbler (G9) which arrived on May 17th, proved elusive and remained unringed. Occasional contests continued between G2 and G3 and, perhaps as a result of this, G3 extended its territory to hedgerows just outside the wood, where it spent much of its time.

E. May 26th - June 5th

Four Garden Warblers were present. A fifth was seen on several days within the territory of G2, being chased by the latter each time. It was presumed to be G9, although G9 was not seen within its territory, which now appeared vacant of *Sylvia* warblers. B13 was not recorded and may have been removed among a further four Blackcaps. B16 arrived on May 26th; it eluded capture but could still be identified because it had a distinctive voice. It settled largely outside the Garden Warbler territories.



**FIGURE 4-3**



Territories are numbered in the order of arrival of the holders.  
 Capitals denote colour-marked birds.

FIGURE 4-4. THE PROGRESSIVE REPLACEMENT OF BLACKCAPS BY GARDEN  
WARBLERS IN THE CENTRAL PART OF THE REMOVAL ZONE  
DURING THE REMOVAL PERIOD (MAY 9th - June 5th)

A. May 8th

The positions of Blackcap territories when the first Garden Warbler (G1) arrived. The movements of G1 are indicated (o————→). B9 occupied the site of the 1978 territory of G1; G1 was chased by B9, however, when it entered the Blackcap's territory.

B. May 9th - 14th

G4 arrived on May 11th and settled in an area partly claimed by B1 and B8 earlier in the season. It was unclear whether G4 displaced B1 or B8, or whether the Blackcap territories had contracted in any case. G1 settled next to B9, having apparently partly displaced the latter. B2, B8 and B9 were removed on May 14th and G4 was colour-ringed the same day.

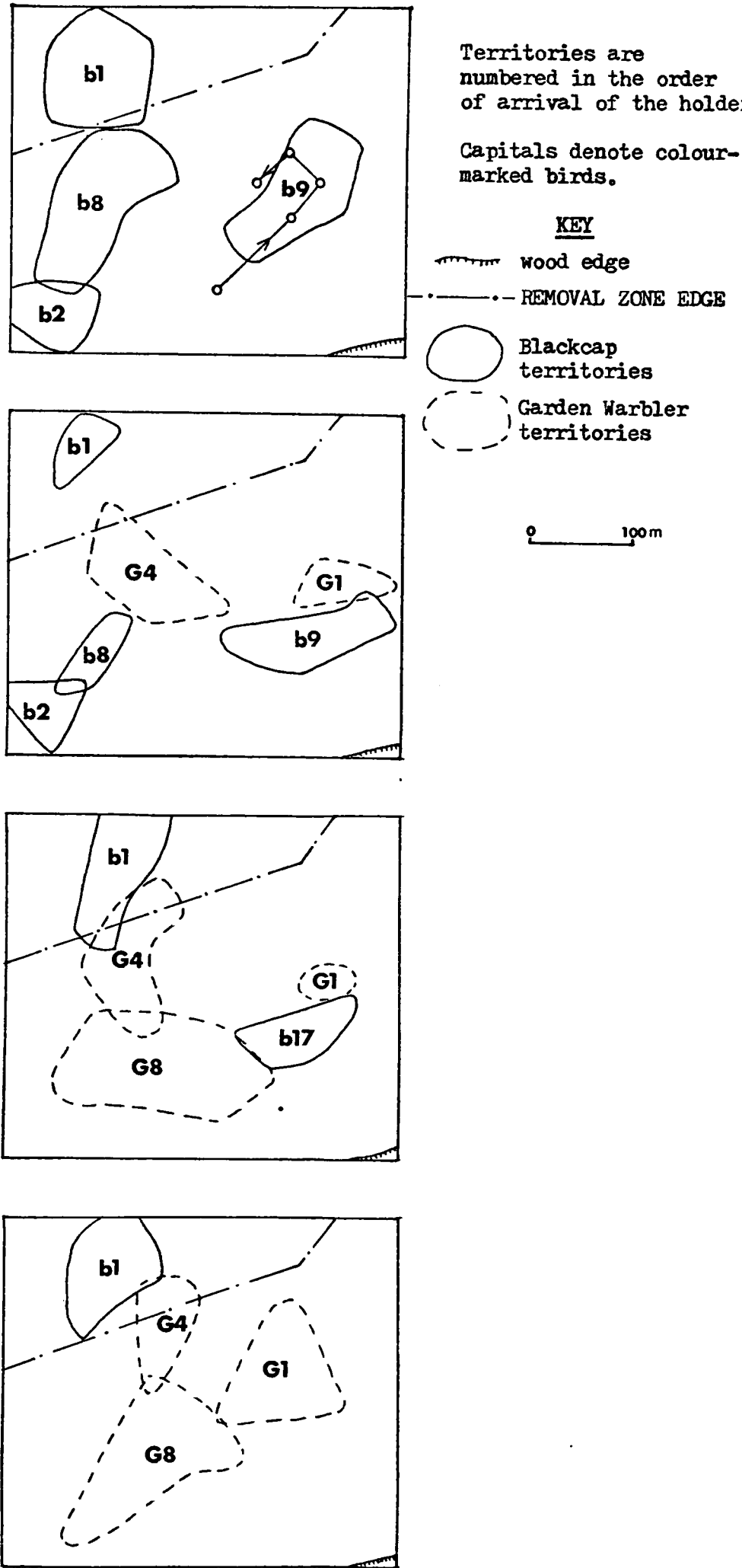
C. May 15th - 24th

G8 arrived on May 15th and settled in an area which included parts of the former territories of B2 and B8. It was colour-ringed next day. G8 partly displaced G4. B17 replaced B9 on May 16th. B17 was seen to expand its territory and G1 became very unobtrusive at the same time and apparently disappeared by May 21st, on which date B17 was seen to take over the entire territory of G1 (not mapped).

D. May 25th - June 5th

G4 and G8 were now well-established. B17 was removed on May 26th, having eluded capture until then. G1 "reappeared" soon after, on May 28th, although it did not avail itself of much of the area used by B9 and B17.

FIGURE 4-4



C. The post-removal period. (June 6th - June 30th)

A normal, albeit belated, pattern of interspecific territoriality between the two species was restored after Blackcap removals ended. A number of new Blackcaps continued to arrive in the area for some time (the last immigrant was noted on June 23rd) and these settled as shown in Figure 4-5. All but two were caught and colour-ringed. The origin of these new Blackcaps can only be conjectured-at. Some perhaps were very late arrivals from winter quarters but at least some seem likely to have been birds from elsewhere in the wood, perhaps failed breeders or birds which were going to attempt a second brood in a new locality. They may even have included some "floaters", birds which had failed to secure a territory earlier in the season but which now happened upon a "surprisingly" vacant area.

The removal zone presented a striking contrast to the rest of the wood, once Blackcaps were permitted to settle there. Elsewhere most Blackcaps and Garden Warblers had already fledged young or were about to do so, and the level of warbler song was low. In the removal zone it was early spring again, at least aurally, as the lately-established Blackcaps noisily proclaimed their territories and, presumably, sought to attract mates. The Garden Warblers too were unusually vocal, some perhaps because they were stimulated by the activity and challenge of their new Blackcap neighbours, but at least two were known to be still at an early stage of the breeding cycle. Of these, G1 was found to have a nest with four eggs, the first laid on or about May 28th (two young fledged on about June 20th), and G2 had a nest with four young, which had been started on about June 20th. G2 had had an earlier nest, which was destroyed by a predator on June 11th, and G1 had probably suffered a similar fate (although no earlier nest was ever found) since it is unlikely to have been present and paired on territory for three weeks without starting nesting.

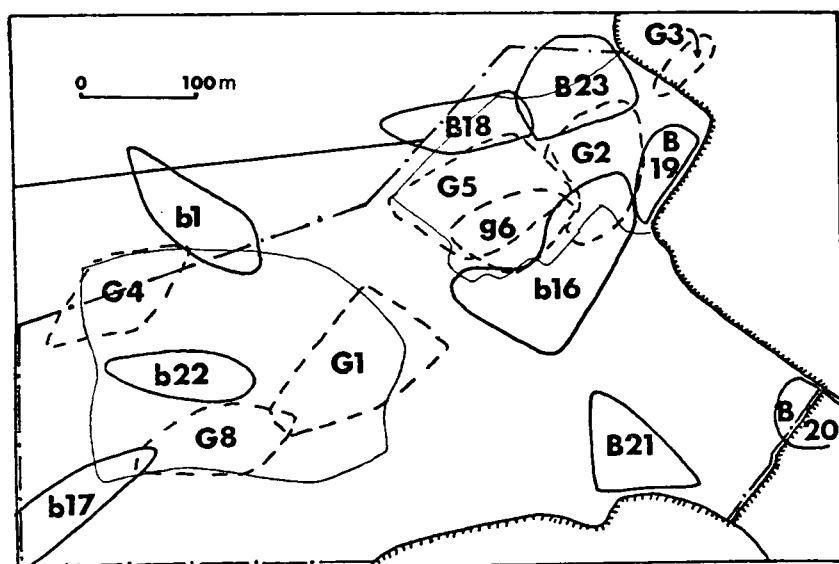
The newly-arrived Blackcaps often intruded into the Garden Warbler territories and, in some cases, took the initiative in seeking-out

FIGURE 4-5. THE POSITIONS OF BLACKCAP AND GARDEN WARBLER TERRITORIES IN THE CENTRAL STUDY AREA DURING THE POST-REMOVAL PERIOD ;

June 6th - 15th 1979

 Blackcap territories 
  Garden Warbler territories

Territories are numbered in the order of arrival of the holders. Capitals denote colour-marked birds. The boundaries of the Removal Zone and the study area, and of the major blocks of different habitats (as shown in Figure 4-1), are indicated.



- NOTES B16 had young in the nest and vigorously defended its territory against newly-arrived Blackcaps, making sorties well outside its territory boundaries to challenge newcomers. It also defended its territory against its neighbour Garden Warblers.
- B19 originally settled in the area later occupied by B21. It was colour-ringed there but moved to the Common Piece afterwards (see text).
- B23 was originally removed from the territory of G2 on June 3rd, the day on which it tried to settle there. It escaped in Oxford city on June 11th and was back in the wood on June 15th, establishing itself where indicated.
- G3 largely stayed outside of the removal zone during this period. G1 was feeding young and extended over a larger area than earlier in the season. Neither G7 nor G9 were definitely identified during the period mapped, although G7 "reappeared" later in June.

and attacking the long-established Garden Warbler holders (Chapter 5). For example, B18, which arrived on June 6th, entered the territory of G5 on June 11th and chased the holder vigorously for half an hour. The Garden Warbler "stood its ground" at first and physical contact resulted. B18, a colour-ringed bird, nevertheless maintained a territory largely outside that of <sup>G5</sup>~~G4~~, so that it appeared that the Garden Warbler was not totally ineffective in defending its territory.

It became more or less impossible to keep track of the Garden Warblers from mid-June onwards. Some had fledged young and were now wandering extensively. In fact, during June, instances of trespassing by Garden Warblers on each other's territories became frequent and led to interactions in which two or three males from separate territories would chase each other about, the dense vegetation generally making it difficult to see who was chasing whom. Some of the new Blackcaps also began to wander as the season continued, quite possibly <sup>because</sup> they all seemed to be unpaired. B19 was seen excitedly-courting a female within his territory on June 20th and, surprisingly, B20 was seen to arrive from his territory 250 metres away and he also started to solicit the female. The two males chased each other but it was never discovered which one, if either, succeeded in pairing with her.

#### 4.3.2. THE EFFECTS OF THE REMOVAL OF BLACKCAPS

##### A. The effect on Garden Warblers

The removal of Blackcaps coincided with the presence in the removal zone of more nesting Garden Warblers than in either 1978 or 1980, and this was not accompanied by an increase in Garden Warbler numbers in the other part of the wood studied (Table 4-2). The woodland C.B.C. index for Garden Warblers was actually lower in 1979 than in either 1978 or 1980, suggesting that Garden Warblers were not generally more abundant during the removal year (see Chapter 7). By its very nature, a removal experiment involving birds is only feasible on a small scale (unless several workers participate), and so the total numbers involved in the present study are

TABLE 4-2. THE NUMBERS OF GARDEN WARBLERS AND BLACKCAPS HOLDING TERRITORIES IN THE REMOVAL ZONE IN 1979 (THE EXPERIMENTAL YEAR) COMPARED WITH THOSE IN 1978 AND 1980, AND WITH THE NUMBERS PRESENT IN THE RIVERSIDE STUDY AREA

| YEAR | REMOVAL ZONE   |                | RIVERSIDE AREA (Control) |          |
|------|----------------|----------------|--------------------------|----------|
|      | GARDEN WARBLER | BLACKCAP       | GARDEN WARBLER           | BLACKCAP |
| 1978 | 5              | 9              | 6                        | 6        |
| 1979 | 9              | 2 <sup>i</sup> | 6                        | 7        |
| 1980 | 4              | 11             | 7                        | 7        |

i. Only present for part of the period. See text.

- NOTES
1. Territories with at least 50% of their area within the zone are included.
  2. Numbers are compared for the period early May - early June in each year, this corresponding to the period of Blackcap removals in 1979.
  3. The use of the Riverside area as a control assumes that any unusual abundance of Garden Warblers in 1979 would have affected both areas similarly. This might not have been the case since the Riverside area is largely scrub and the Removal Zone largely deciduous woodland, but unfortunately no suitable "woodland" control site could be located. However, if Garden Warblers in 1979 were commoner in deciduous woodland only, some might have been expected to occur in woodland tracts from where the species was normally absent, but this was not seen to be the case.

TABLE 4-3. THE AREAS OF GARDEN WARBLER TERRITORIES IN THE REMOVAL ZONE DURING THE REMOVALS PERIOD IN 1979 COMPARED WITH THOSE OF GARDEN WARBLERS AND BLACKCAPS IN THE SAME AREA DURING THE EQUIVALENT PERIODS OF 1978 AND 1980

| TERRITORIES OF ;                             | MEAN TERRITORY AREAS ( $\pm$ S.D.) |
|----------------------------------------------|------------------------------------|
| GARDEN WARBLERS IN 1979<br>(Removal year)    | 0.80 h. ( $\pm$ 0.30), n = 9       |
| GARDEN WARBLERS IN 1978<br>AND 1980 COMBINED | 0.57 h. ( $\pm$ 0.10), n = 9       |
| BLACKCAPS IN 1978<br>AND 1980 COMBINED       | 0.76 h. ( $\pm$ 0.25), n = 21      |

Garden Warbler territories were significantly larger in 1979 than in 1978/80 (Mann-Whitney U Test, 2-tailed,  $p < 0.05$ ).

limited and the numerical changes too small to warrant statistical analysis. However, Garden Warbler territories in the removal zone during the removal period (Figure 4-2A) were significantly larger than those present there at the equivalent stages of the breeding season in 1978 and 1980 (Table 4-3).

An increased number of breeding Garden Warblers could have been achieved by more birds squeezing into the same area used by Garden Warblers in other seasons. This was not the case. The Garden Warblers in the removal zone used not only "their" habitat but also tracts which were normally used by Blackcaps (Table 4-4). Indeed the positions of the Garden Warbler territories around the Common Piece would have been quite incompatible with the presence there, in their original positions, of the previously-established Blackcaps (B3, B4, B5 and B7), given the general observations of the existence of interspecific territoriality between the two species (Figure 4-3). The results presented in Table 4-4 suggest that certain parts of the removal zone were suitable only for one species or the other but that a substantial area was usable by both, but was only settled by Garden Warblers in the year that Blackcaps were removed. For example, 55% of the area used by Garden Warblers in 1979 was used by Blackcaps, to the exclusion of Garden Warblers, in 1980. This suggests that in these areas the presence of Blackcaps prevents the settling of Garden Warblers.

The habitat changes which occurred in the removal zone between 1978 and 1979 (described in Chapter 3) can be discounted as an explanation for the increase in Garden Warbler numbers in 1979. The destruction of tracts of undergrowth in the central area of open woodland probably made the area less attractive to both species in 1979 and 1980, than it was in 1978. The Common Piece area, which was thinned in 1978, was densely settled by Blackcaps before the Garden Warblers arrived in 1979 (and in 1980) and so was clearly attractive to the two species.

#### B. The effect on Blackcaps

The most obvious effect of the removal experiment was the almost



TABLE 4-4. THE TOTAL EXTENT OF GARDEN WARBLER TERRITORIES IN THE REMOVAL ZONE DURING THE REMOVAL PERIOD IN 1979 COMPARED WITH THAT OF GARDEN WARBLERS IN 1980 AND THAT OF BLACKCAPS IN 1979 AND 1980

TOTAL AREA used by Garden Warblers in the Removal Zone in 1979, = 6.05 h.  
the experimental year, after Blackcaps were removed.

TOTAL AREA used by Garden Warblers in the Removal Zone in 1980, = 2.83 h.  
the control year, when Blackcaps were present as usual.

Of the area used by Garden Warblers in 1979 :

- A. Only 1.99 h. (32.9 %) was also used by them in 1980 (This overlap represents 70.3 % of the area used by Garden Warblers in 1980).
- B. 2.45 h. (40.4 %) was previously occupied by Blackcaps in 1979, before their removal. This figure, which is the potential minimum overlap between the two species in 1979, increases to 3.14 h. (51.9 %) when Blackcap territory positions after removals ended are included.
- C. 3.31 h. (54.7 %) was used by Blackcaps in 1980.
- D. A minimum of 1.88 h. (31.1 %) was used by Blackcaps in both 1979 (pre- and post-removals) and 1980, and so appears to have been especially favoured by the latter species. (This is an inevitable underestimate since the Blackcap settling pattern in 1979 was incomplete as a result of the removal experiment)

- NOTES
- 1. Overlaps are based on superimpositions of the maps of territory positions during the removal period in 1979 and during the equivalent period in 1980 (Figures 4-2 A. and B.), with the exception that Blackcap territory positions in 1979 are taken (and are inevitably incomplete) from the observations made before (Figure 4-1) and after (Figure 4-5) the removals occurred.
  - 2. 1978 is excluded from this table since the positions of Blackcap territories especially were possibly not known fully as a result of the late commencement of observations in the area during that season.

total disruption of breeding in the removal zone. Only one Blackcap (B16) was known to have succeeded in nesting there. Female Blackcaps were not seen to linger in the area after their mates had been removed. Presumably they moved elsewhere in search of unattached males. There certainly was no pool of unattached females available for those Blackcaps which settled in the zone once removals ended, none of which was known for certain to have succeeded in pairing.

The replacement Blackcaps which tried to settle in the removal zone did not do so at random (Figure 4-6). The Common Piece attracted a disproportionate number of would-be colonists, even though the area was densely settled by Garden Warblers, and numerous interactions occurred between the latter and the newly-arrived Blackcaps. The fact that new Blackcaps were still attracted to the Common Piece despite the presence there of Garden Warblers suggests that interspecific territoriality between the two species may be asymmetrical in that most Blackcaps appear able to exclude Garden Warblers from their territories but the converse may not apply. This is compatible with observations of the greater aggressiveness of Blackcaps in interspecific interactions, as described in Chapter Five.

Some Blackcaps initially settled elsewhere in the zone but most of these soon "vanished". Their disappearance sometimes coincided with the arrival in the Common Piece area of new Blackcaps, suggesting that perhaps some of the latter had moved from elsewhere in the removal zone (as indeed was suspected to have happened with some of the original Blackcap inhabitants of the zone, which vanished without being captured in situ). Some confirmation that new Blackcaps might have moved about the zone before settling, by preference, in the Common Piece came from observations of B19 (Figure 4-5). This bird arrived on June 8th (shortly after the removals had ended), and settled originally in the area later occupied by B21. It readily responded to playback there and was caught and colour-ringed. It was released on the spot but by June 11th had moved to the Common Piece, where it remained until



at least the end of the month. These observations suggest that the Common Biece, an area used by Blackcaps and settled by Garden Warblers when the former were removed, was particularly attractive to Blackcaps and was not marginal habitat for them.

#### 4.4. DISCUSSION

The removal experiment provides strong evidence that Blackcaps and Garden Warblers are genuinely interspecifically-territorial, and that the limited amount of overlap between their territories can not be fully explained by interspecific differences in habitat-selection. Some of the habitat originally settled by Blackcaps when they first arrive is claimed by Garden Warblers when the Blackcaps are removed, showing that Blackcaps are able to exclude Garden Warblers from certain areas which they would otherwise normally inhabit. On the other hand, a portion of the available habitat, in this case tall, closed-canopy sycamore woodland, is not used by Garden Warblers after the resident Blackcaps have been removed. This suggests that such habitat is acceptable to Blackcaps only, and hence that the two species are segregated by differences in habitat-selection, to some degree.

Once established, Garden Warblers are not displaced by any subsequent Blackcap arrivals. This could mean that Garden Warblers defend their territories against Blackcaps effectively, and hence that interspecific territoriality is mutual between them. This possibility can best be examined by performing a second experiment, to remove established Garden Warblers, to see if they are keeping out any Blackcaps. The same experiment would serve to show whether the areas normally used by Garden Warblers (e.g. the centre of the Central area and the scrub of the Riverside area) would otherwise be used by late Blackcap arrivals, or whether such habitat is acceptable to Garden Warblers only.

The removal of Blackcaps showed the existence of a considerable number of other conspecifics ready to occupy the vacated habitat. When the numbers of Blackcaps removed and the number of post-experiment Blackcap settlers

are added it is found that the removal zone would have housed 32 Blackcap territories, had all the birds which tried to settle there been able to do so. It is clearly improbable that this large number of Blackcaps, about three times the normal Blackcap density for the area, could have settled and bred there. Similarly, the numbers of Garden Warblers which settled in the removal area were about twice the normal density for the area (and perhaps would have been even higher had it been possible to keep the removal zone totally Blackcap-free throughout the experiment). Presumably, these extra birds of both species are normally excluded by intraspecific and interspecific interactions with the previously-established territory holders.

The origin of the replacement birds is not known. Other studies have identified the conspecifics which replace removed territory holders as inhabitants of sub-optimal adjacent habitats (as in Great Tits, Krebs 1971) or as members of a pool of non-territorial birds, unable to breed because the suitable habitat has been filled by territorial individuals (as in Red Grouse, Watson 1967). An additional possibility with migrant birds, such as warblers, is that the replacements are new-arrivals which are still seeking a vacant area in which to establish themselves. The existence of replacement birds is good evidence that (in the area studied) normally all suitable habitat is eventually occupied, by one species or the other, and, conversely, that vacant areas are left empty because they are unsuitable and not because there are not enough birds to fill them.

An important question which the study leaves largely unanswered is whether the additional habitat which Garden Warblers use once Blackcaps have been removed from it, differs in its suitability from that which normally only one species or the other uses. It is not known for certain whether the "shared" habitats are optimal or marginal for both or either species, although the Common Piece area seemed particularly attractive to Blackcaps. It is similarly unknown whether the Garden Warblers which took advantage of the Blackcap removals differed in fitness from those which normally inhabit the removal zone. Were they "inferior" floaters, which would

not otherwise have been able to breed at all, or were they "fit" birds, which readily accepted the opportunity to breed in a suitable habitat from which Blackcaps normally exclude them ? Rice (1978B) found that Red-eyed Vireos enjoyed a higher breeding success in the habitat-type which they shared with Philadelphia Vireos (with which they are interspecifically territorial) than in the habitat-type which only they used. A similar comparison of the breeding success of Blackcaps and Garden Warblers in the "shared" and "exclusive" habitats within the removal zone, which would have helped to answer the above questions, was unfortunately impossible, not only because of the difficulty of finding nests but also because sample sizes would have been very small and hence unreliable.

To conclude, the removal experiment provides evidence that Blackcaps and Garden Warblers compete for space and that, specifically, Blackcaps prevent Garden Warblers from settling and breeding in habitats which they would otherwise inhabit.

CHAPTER FIVE

AGGRESSIVE INTERACTIONS  
AMONG  
TERRITORIAL  
BLACKCAPS AND GARDEN WARBLERS

## CHAPTER FIVE

### AGGRESSIVE INTERACTIONS AMONG TERRITORIAL BLACKCAPS AND GARDEN WARBLERS

#### 5-1. INTRODUCTION

The Territory has often been defined as a "defended area" (Noble 1939, Brown & Orians 1970) and it seems axiomatic to assert that in the absence of aggression, or the threat of attack, territorial behaviour does not exist. Interactions between a territory owner and an intruder may be indirect. For example, songbirds may be dissuaded from trying to settle in a particular area when they hear an established bird already singing there. Krebs (1977) has shown experimentally that Great Tit song serves this purpose (among others). He removed all Great Tits from a copse and then "occupied" parts of the area with loudspeakers periodically broadcasting Great Tit song. Those parts were the last to be recolonised by replacement tits.

Quite possibly the majority of interactions between territorial and non-established birds do not reach the stage of actual intrusions. The widespread occurrence of territorial advertising song among birds suggests that song alone is normally a successful deterrent to intruders, so that many interactions are one-sided, with the potential settlers withdrawing before the owners become aware of their presence. Subtle interactions of this type are normally impossible to detect in the field, although the existence of responses by particular species to the songs of conspecifics and others can readily be tested-for by song playback experiments (Chapter 6).

The term interaction requires definition since it is sometimes applied loosely. Notably Cody (1978) describes interactions between sylviid warblers without referring to having actually seen any close contacts between the birds. He infers instead that interactions occur on the grounds of the presence or absence of particular species-combinations in certain habitats. "Interaction" here refers to the direct encounters which happen when a bird intrudes into, or approaches, the territory of another and is detected by the territory holder. In practice, all the interactions considered here involved the movement of one bird towards another, often culminating in close approaches



and actual chases.

Howard (1920), in his pioneer account on avian territoriality, noticed not only intraspecific fighting but also similar contests between closely-related sympatric species-pairs including the Sedge Warbler and Reed Warbler, Chiffchaff and Willow Warbler, and Blackcap and Garden Warbler. However systematic observations on the course and outcomes of interspecific contests between those species which defend mutually-exclusive territories have seldom been made. An exception is the detailed study of two vireos by Rice (1978a.). Morse (1976) has analysed the intraspecific and interspecific encounters between Dendroica warblers but the four species which he studied were not interspecific-ally territorial.

The Blackcap and the Garden Warbler are described by Howard (1920) as "constant rivals" but there are earlier anecdotal references to hostility between them. Seebohm (1883) states that they "do not get on very well in the same area" and Saunders (1889) comments that the Garden Warbler is "intolerant of rivalry" being scarce where the Blackcap abounds. Lord Grey (in Maynard-Smith 1958) noted a Garden Warbler which permitted Willow Warblers into its territory but excluded Blackcaps. Most accounts, including Howard (1907-1914) refer to the Blackcap as dominant in encounters between the two species. Bannerman (1954) describes the Garden Warbler as shy, "avoiding any kind of unpleasantness from the other more aggressive species". L. Howard (1974) mentions a Blackcap chasing an intruding Garden Warbler. Solonen (1979) records that in Finland interactions occur between Blackcaps and Garden Warblers and the former seems to be the more aggressive species. Only Cody (1978) states categorically that the Garden Warbler is the dominant of the two species, but he gives only circumstantial supporting evidence.

An effort was made to observe natural interactions between Blackcaps and Garden Warblers, not only because such encounters may be good indicators of the relationship between them but also because they could be expected to reveal how both species respond to real intruders, information

valuable in interpreting the results of song-playback experiments.

## 5-2. METHODS

Colour-ringing and the regular plotting of territory boundaries revealed the ownership of particular sites and allowed territory owners to be distinguished from intruders. Interactions for which this information was not known are omitted from the analysis. Most contests were only noticed once they were already in progress, loud singing and rapid changes of position by one or both participants making them conspicuous. They were observed until they ended (at least temporarily) when one or both birds withdrew from the scene. Not infrequently, intruders ousted from territories returned some time later and such contests were often protracted taking several hours and occasionally more than a day to resolve. All contests between the same two individuals observed on the same day are regarded here as one contest, with the exception of a very few instances where the roles of holder and intruder became reversed when a holder followed an intruding neighbour back into the latter's territory. Such cases are treated as two interactions.

Observations were made on the following variables, although some contests produced information on only some of them largely because most interactions took place in dense low vegetation where the birds were often hard to observe.

Closest approaches. The initiator (holder or intruder) of the closest observed separation between the two participants. The distance separating the birds at this point was estimated.

Chases. Their occurrence, and the identity of the pursuer and pursued.

Physical contact. Whether this occurred.

Contest outcomes. The short-term outcome of an interaction. It must be stressed that in this account the terms "win" and "lose" do not imply any changes of ownership of particular sites. The contest outcomes reported are merely short-term events. Losers were birds which terminated contests by withdrawing when approached by the other participants (winners), although if they were territory

holders they did not necessarily abandon the area in which the contest took place. Thus, for example, a bird which retreated to the centre of its own territory from the periphery on the approach of a neighbour is scored as losing that particular interaction.

Vocalisations. Whether the holder or intruder sang during the contest or within the first five minutes after the final separation of the participants. It proved impractical to record anything other than whether a bird sang or not, although a measure of actual song output would have been desirable. The occurrence of tac-tac calls (see Chapter 6) was also noted. No other vocalisations were noticed.

The interactions observed are summarised in Table 5-1. The use of the Chi-squared test in the analysis assumes that each interaction is independent. This assumption would not be justified if any of the birds were involved in a disproportionately-large fraction of the the total number of interactions observed and if such birds were in any way atypical. No Blackcaps were involved in more than three interactions but one Garden Warbler (YR,= yellow red, his colour rings) was involved as territory holder in 10 out of the 24 Garden Warbler - Garden Warbler interactions and in 22 out of the 52 Garden Warbler - Blackcap interactions observed. The possibility that YR was unrepresentative and biased the sample is considered below (5.3.6).

Only males were involved in the interactions. No contests were seen after the end of June. It would have been desirable to have related the occurrence and outcomes of contests to the stage in the breeding cycle reached by the participants but too few nests were discovered to permit this.

### 5.3. RESULTS

#### 5.3.1. Closest approaches in interactions

In intraspecific interactions a large and significant majority of close-approaches were initiated by territory holders, and this was also the case in interactions between Blackcap holders and Garden Warbler intruders. In

TABLE 5-1. THE NUMBERS OF INTERACTIONS INVOLVING BLACKCAPS (BC) AND GARDEN WARBLERS (GW) OBSERVED AT WYTHAM

| TYPE OF INTERACTION. | TOTAL NUMBER OF INTERACTIONS OBSERVED. | TOTAL NUMBERS OF DIFFERENT INDIVIDUALS INVOLVED IN EACH TYPE OF INTERACTION. |           |
|----------------------|----------------------------------------|------------------------------------------------------------------------------|-----------|
|                      |                                        | HOLDERS                                                                      | INTRUDERS |
| HOLDER - INTRUDER    |                                        |                                                                              |           |
| A. BC - - - BC       | 32                                     | 21                                                                           | 17        |
| B. GW - - - GW       | 24                                     | 11                                                                           | 17        |
| C. BC - - - GW       | 28                                     | 21                                                                           | 16        |
| D. GW - - - BC       | 52                                     | 23                                                                           | 46        |

- NOTES
1. The numbers of intruders are not known precisely since many were new, unringed birds, presumably recently-arrived and trying to establish themselves.
  2. Holders outnumber intruders in total in type C interactions because on a few occasions the same Garden Warbler was watched as it was ejected from one Blackcap territory only to go and intrude into territories of other neighbouring Blackcaps (for example see Figure 3-5).
  3. The relatively high number of type D interactions observed is thought to be an effect of the removal experiment. Garden Warblers in the Common Piece, notably YR, were in an area which attracted new Blackcap colonists rapidly when the established Blackcaps were removed. Whereas perhaps normally there would have been initial interactions between these birds and their neighbours resulting in eventual relative stability between them, the artificially-high turnover of Blackcaps made this impossible. All replacement Blackcaps interacted with the Garden Warblers in the course of establishing themselves. (This partly explains why YR was involved in many interactions, as described in the text. Another reason was that he was present and studied in both 1979 and 1980.)
  4. The chapter presents the pooled observations of 1978, 1979 and 1980.

these contests, therefore, holders normally sought-out intruders. This did not apply to interactions between Garden Warbler territory holders and intruding Blackcaps, where the Blackcaps often sought out the territory holders; in such interactions there is no significant difference between the numbers of holder-initiated and intruder-initiated close-approaches (Table 5-2A). The distances separating the birds during close-approaches were similar in all four types of interactions (Table 5-2B).

### 5.3.2. Chases

The frequency of chases was higher in intraspecific than in interspecific interactions (Table 5-3A). The difference is not significant between the two types of contests on Blackcap-held territories but is pronounced on Garden Warbler territories. Chases occurred in a significant majority of Garden Warbler - Garden Warbler interactions but were significantly less frequent in interactions between Garden Warbler holders and intruding Blackcaps. The numbers of contests between Garden Warbler holders and Blackcap intruders involving chases are similarly low in comparison to their frequency in Blackcap - Blackcap interactions, and the difference is again highly significant.

Chases were extended rapid pursuits in flight and it was sometimes uncertain which bird was doing the chasing, particularly in intraspecific contests where plumage colour was no guide. However, in intraspecific chases, and in chases between Blackcap holders and Garden Warbler intruders, the chaser was the holder in virtually all cases where it was possible to establish its status. In contrast, in encounters between Garden Warbler holders and Blackcap intruders, the Blackcap was the chaser in 5 of the 9 contests where the status of the participants was established. This relatively-high occurrence of intruder-initiated chases is significantly different from that observed in all other types of interactions (Table 5-3B).

### 5.3.3. Physical contact

This was rare and only four instances were observed in the entire study period. One involved two Blackcaps and the other three occurred in

TABLE 5-2. CLOSEST-APPROACHES IN BLACKCAP (BG) AND GARDEN WARBLER (GW) INTERACTIONS

A. INITIATORS OF CLOSEST APPROACHES

| CLOSEST-APPROACH<br>INITIATED BY | INTRASPECIFIC INTERACTIONS |                            |                         |                            | INTERSPECIFIC INTERACTIONS |                  |                         |  |
|----------------------------------|----------------------------|----------------------------|-------------------------|----------------------------|----------------------------|------------------|-------------------------|--|
|                                  | 1. BC HOLDER               |                            | 2. GW HOLDER            |                            | 3. BC HOLDER               |                  | 4. GW HOLDER            |  |
|                                  | BC INTRUDER<br>(n = 22)    |                            | GW INTRUDER<br>(n = 19) |                            | GW INTRUDER<br>(n = 27)    |                  | BC INTRUDER<br>(n = 46) |  |
| HOLDER                           | 19                         |                            | 16                      |                            | 25                         |                  | 18                      |  |
| INTRUDER                         | 3                          |                            | 3                       |                            | 2                          |                  | 28                      |  |
| Within-column<br>comparisons     | p<0.01                     |                            | p<0.01                  |                            | p<0.001                    |                  | n.s.                    |  |
| Between-column<br>comparisons    | 1 v 2 <sup>1</sup><br>n.s. | 1 v 3 <sup>1</sup><br>n.s. | 1 v 4<br>p<0.001        | 2 v 3 <sup>1</sup><br>n.s. | 2 v 4<br>p<0.01            | 3 v 4<br>p<0.001 |                         |  |

- NOTES. 1. The table gives the number of occasions on which closest-approaches were holder-initiated or intruder-initiated.
2. Statistical comparisons are by Chi-squared test (d.f. = 1) or Fisher Exact Test (i), the null hypothesis being that there is no significant difference between the numbers of occasions in which closest-approaches were holder-initiated or intruder-initiated.

TABLE 5-2. (continued)

B. THE CLOSEST OBSERVED SEPARATION-DISTANCES BETWEEN PARTICIPANTS IN INTERACTIONS

|                                                                    | INTRASPECIFIC INTERACTIONS              |                                         | INTERSPECIFIC INTERACTIONS              |                                         |
|--------------------------------------------------------------------|-----------------------------------------|-----------------------------------------|-----------------------------------------|-----------------------------------------|
|                                                                    | 1. BC HOLDER<br>BC INTRUDER<br>(n = 22) | 2. GW HOLDER<br>GW INTRUDER<br>(n = 19) | 3. BC HOLDER<br>GW INTRUDER<br>(n = 27) | 4. GW HOLDER<br>BC INTRUDER<br>(n = 46) |
| Mean distance in<br>metres separating<br>the birds ( $\pm 1$ S.E.) | 6.9 ( $\pm 2.0$ )                       | 5.7 ( $\pm 2.4$ )                       | 6.6 ( $\pm 1.3$ )                       | 7.6 ( $\pm 1.3$ )                       |

NOTES 1. All possible pairwise comparisons of the distances were made using the Mann-Whitney U test (2-tailed). No differences are significant.

2. Type 4 interactions were the only ones where many close-approaches were intruder-initiated. In these interactions the mean closest separation distance was 8.4 m ( $\pm 2.3$ ) when the approach was initiated by the holder and 7.4 m ( $\pm 1.9$ ) when the initiator was the intruder; the two sets of distances are not significantly different.

TABLE 5-3. CHASES IN BLACKCAP (BC) AND GARDEN WARBLER (GW) INTERACTIONS

A. THE FREQUENCY OF CHASES

|                            | INTRASPECIFIC INTERACTIONS |          |           |          | INTERSPECIFIC INTERACTIONS |          |           |          |
|----------------------------|----------------------------|----------|-----------|----------|----------------------------|----------|-----------|----------|
|                            | 1. BC                      |          | 2. GW     |          | 3. BC                      |          | 4. GW     |          |
|                            | HOLDER                     | INTRUDER | HOLDER    | INTRUDER | HOLDER                     | INTRUDER | HOLDER    | INTRUDER |
|                            | (n = 32)                   |          | (n = 23)  |          | (n = 25)                   |          | (n = 48)  |          |
| CHASE OCCURRED             | 21                         |          | 17        |          | 9                          |          | 11        |          |
| NO CHASE OCCURRED          | 11                         |          | 6         |          | 16                         |          | 39        |          |
| Within-column comparisons  | n.s.                       |          | p < 0.05  |          | n.s.                       |          | p < 0.001 |          |
| Between-column comparisons | 1 v 2                      | 1 v 3    | 1 v 4     | 2 v 3    | 2 v 4                      | 3 v 4    |           |          |
|                            | n.s.                       | n.s.     | p < 0.001 | p < 0.05 | p < 0.001                  | n.s.     |           |          |

- NOTES.
- The table compares the number of occasions in which chases were seen during each type of interaction. No distinction is made between contests in which only one chase was seen and those were several happened.
  - Statistical comparisons are by the Chi-squared test (d.f. = 1).



TABLE 5-3. (continued)

B. THE IDENTITY OF THE CHASERS

|                            | INTRASPECIFIC INTERACTIONS |          |           |          | INTERSPECIFIC INTERACTIONS |          |                    |          |
|----------------------------|----------------------------|----------|-----------|----------|----------------------------|----------|--------------------|----------|
|                            | 1. BC                      | HOLDER   | 2. GW     | HOLDER   | 3. BC                      | HOLDER   | 4. GW              | HOLDER   |
|                            | BC                         | INTRUDER | GW        | INTRUDER | GW                         | INTRUDER | BC                 | INTRUDER |
| HOLDER CHASER              |                            | 12       |           | 13       |                            | 7        |                    | 4        |
| INTRUDER CHASER            |                            | 1        |           | 0        |                            | 0        |                    | 5        |
| Within-column comparisons  | p < 0.01                   |          | p < 0.001 |          | p < 0.01 <sup>ii</sup>     |          | n.s. <sup>ii</sup> |          |
| Between-column comparisons | 1 v 2 <sup>i</sup>         | 1 v 3    | 1 v 3     | 1 v 4    | 2 v 3                      | 2 v 4    | 3 v 4              |          |
|                            | n.s.                       | n.s.     | n.s.      | p < 0.05 | n.s.                       | p < 0.01 | p < 0.05           |          |

- NOTES. 1. Statistical comparisons are by the Chi-squared test, Fisher Exact test (i) or the Binomial test (ii).
2. In the sole case where a holder Blackcap was seen to be chased by an intruder Blackcap the holder was the immature bird (B4 in Figure 3-9) which was also unusual in that it later apparently lost much of its territory to a Garden Warbler.

interactions between Blackcap intruders and Garden Warbler holders. In the latter, one occurred during an owner-initiated chase and another was probably also owner-initiated but on the third occasion the Garden Warbler was struck by the intruding Blackcap. In all cases physical contact only occurred once and very briefly. It would probably happen more often were it not that birds never stood their ground when approached closely by opponents. Several times a bird was seen to fly straight at another at speed but always the latter flew off just when a collision seemed inevitable, and it was then invariably pursued for some distance. This was seen in all types of interactions.

#### 5.3.4. The short-term outcomes of interactions

The eventual outcome of territorial disputes was detected by repeated observation and updating of territory boundaries on maps (Chapters 3 & 4). The data presented here (Table 5-4) concerns only the immediate outcomes of interactions, scoring birds which terminated contests by withdrawing from the scene of the encounter as "losers".

In general territory holders of both species were successful in repelling conspecific intruders and they won the great majority of such contests. The small proportion of instances where conspecific intruders won encounters does not differ significantly between species. Of the three cases where Blackcap holders withdrew from Blackcap intruders, two were boundary encounters with neighbours, in which the intruder did not penetrate deeply into the owner's territory. The third instance involved the young bird B4 referred-to in Table 5-3. One of the two cases of Garden Warbler holders losing to conspecific intruders was a boundary encounter. The other occurred when a Garden Warbler who had annexed a neighbour's territory the previous day, following the unexplained permanent disappearance of the holder, was successfully challenged over the newly-acquired extra area by a recently-arrived bird.

In interspecific contests the situation was quite different. There was only one instance seen where a Blackcap holder withdrew from a

TABLE 5-4. THE SHORT-TERM OUTCOMES OF BLACKCAP (BC) AND GARDEN WARBLER (GW) INTERACTIONS

| CONTEST<br>OUTCOME                    | INTRASPECIFIC INTERACTIONS |                            |                         | INTERSPECIFIC INTERACTIONS |  |  |
|---------------------------------------|----------------------------|----------------------------|-------------------------|----------------------------|--|--|
|                                       | 1. BC HOLDER               | 2. GW HOLDER               | 3. BC HOLDER            | 4. GW HOLDER               |  |  |
|                                       | BC INTRUDER<br>(n = 22)    | GW INTRUDER<br>(n = 20)    | GW INTRUDER<br>(n = 22) | BC INTRUDER<br>(n = 44)    |  |  |
| HOLDER LEAVES AREA<br>(INTRUDER WINS) | 3                          | 2                          | 1                       | 17                         |  |  |
| INTRUDER LEAVES AREA<br>(HOLDER WINS) | 18                         | 17                         | 20                      | 23                         |  |  |
| BOTH LEAVE AREA                       | 1                          | 1                          | 1                       | 4                          |  |  |
| Within-column<br>comparisons          | p < 0.01                   | p < 0.01                   | p < 0.001               | n.s.                       |  |  |
| Between-column<br>comparisons         | 1 v 2 <sup>1</sup><br>n.s. | 1 v 3 <sup>1</sup><br>n.s. | 2 v 3<br>n.s.           | 3 v 4<br>p < 0.01          |  |  |

- NOTES.
1. Statistical comparisons are of the proportions of holder-wins and intruder-wins in each type of interaction, by Chi-squared test or Fisher Exact test (1).
  2. Contests in which both birds left the area of the interaction are excluded from the comparisons.

Garden Warbler intruder, and this was possibly ambiguous. It happened when a Blackcap flew to the vicinity of a Garden Warbler intruder who was singing some 15 metres within the territory. The latter stopped singing and the Blackcap sang alone for several minutes before withdrawing to a central part of its territory. The Garden Warbler, which did not appear to have been located, did not leave but began to sing again unchallenged in the same spot some minutes later. In contrast, Blackcap intruders won a significant proportion of their encounters with Garden Warbler holders.

#### 5.3.5. Vocalisations

Song was a conspicuous feature of most contests. Singers, both holders and intruders, made up a significant majority during interspecific interactions and in Blackcap - Blackcap contests, but there was no significant difference in the proportion of singers to silent birds in Garden Warbler - Garden Warbler contests (Table 5-5A).

A larger proportion of birds were silent during the first five minutes after interactions had ended. Singers significantly outnumbered silent birds only among territory holders after both types of interspecific contests (Table 5-5B). Both during and after all types of contests the proportions of singer to non-singers did not differ significantly between intruders and holders, nor within holders and intruders compared during and after contests.

There is no clear tendency for silences to be synchronous between holders and intruders; in most cases when one bird was silent the other was singing (Table 5-6). The possible exceptions are the observations following Blackcap - Blackcap interactions, when both were silent on half of the fourteen occasions when one bird was silent, and during Garden Warbler - Garden-Warbler interactions, when dual silences occurred on five out of seven such occasions. However, the sample sizes are too small for meaningful conclusions to be drawn.

Most interactions ended in holder-victories but the cases of

TABLE 5-5. THE OCCURRENCE OF SINGING IN BLACKCAP (BC) AND GARDEN WARBLER (GW) INTERACTIONS

| A. FREQUENCY OF<br>SINGING DURING<br>INTERACTIONS. | INTRASPECIFIC INTERACTIONS |                            | INTERSPECIFIC INTERACTIONS |                                                  |                            |           |
|----------------------------------------------------|----------------------------|----------------------------|----------------------------|--------------------------------------------------|----------------------------|-----------|
|                                                    | 1. BC<br>HOLDER            | 2. GW<br>HOLDER            | 3. BC<br>HOLDER            | 4. GW<br>HOLDER                                  |                            |           |
|                                                    | BC INTRUDER                | GW INTRUDER                | GW INTRUDER                | BC INTRUDER                                      |                            |           |
| 1. HOLDER SINGS                                    | 18                         | 14                         | 27                         | 44                                               |                            |           |
| 2. HOLDER SILENT                                   | 4                          | 5                          | 1                          | 8                                                |                            |           |
| Within-column<br>comparisons                       | p < 0.01                   |                            | n.s.                       | p < 0.001                                        |                            | p < 0.001 |
| Between-column<br>comparisons                      | 1 v 2 <sup>i</sup><br>n.s. | 1 v 3 <sup>i</sup><br>n.s. | 1 v 4<br>p < 0.01          | 2 v 3 <sup>i</sup><br>2 v 4<br>n.s.              | 3 v 4<br>n.s.              |           |
| 3. INTRUDER SINGS                                  | 17                         | 11                         | 24                         | 42                                               |                            |           |
| 4. INTRUDER SILENT                                 | 6                          | 7                          | 4                          | 10                                               |                            |           |
| Within-column<br>comparisons                       | p < 0.05                   |                            | n.s.                       | p < 0.001                                        |                            | p < 0.001 |
| Between-column<br>comparisons                      | 1 v 2<br>n.s.              | 1 v 3<br>n.s.              | 1 v 4<br>n.s.              | 2 v 3 <sup>i</sup><br>2 v 4 <sup>i</sup><br>n.s. | 3 v 4 <sup>i</sup><br>n.s. |           |

Between-row comparisons (Holders v Intruders; rows 1/2 v 3/4) give no significant differences in any of the four types of interactions.

NOTES.

- The table makes all possible comparisons of the number of occasions in which intruders and holders sang or were silent, both within and between each type of interaction. Sample sizes vary within columns since it was not always possible to be certain whether some birds sang or not.
- Statistical comparisons are by the Chi-squared test or Fisher Exact test (i).

**TABLE 5-5. (Continued)**

| B. FREQUENCY OF SINGING<br>IMMEDIATELY AFTER<br>INTERACTIONS | INTRASPECIFIC INTERACTIONS  |                             | INTERSPECIFIC INTERACTIONS  |                             |
|--------------------------------------------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
|                                                              | 1. BC HOLDER<br>BC INTRUDER | 2. GW HOLDER<br>GW INTRUDER | 3. BC HOLDER<br>GW INTRUDER | 4. GW HOLDER<br>BC INTRUDER |
| 5. HOLDER SINGS                                              | 14                          | 10                          | 20                          | 30                          |
| 6. HOLDER SILENT                                             | 9                           | 5                           | 4                           | 15                          |
| Within-column<br>comparisons                                 | n.s.                        | n.s.                        | p < 0.01                    | p < 0.05                    |
| 7. INTRUDER SINGS                                            | 9                           | 6                           | 14                          | 28                          |
| 8. INTRUDER SILENT                                           | 12                          | 9                           | 10                          | 17                          |
| Within-column<br>comparisons                                 | n.s.                        | n.s.                        | n.s.                        | n.s.                        |

All between column comparisons reveal no significant differences. Between-row comparisons (Holders v Intruders; rows 5/6 v 7/8) also give no significant differences in any of the four types of interactions.

Between-row comparisons of the frequency of singers among holders before and after contests (rows 1/2 v 5/6), and similarly for intruders (rows 3/4 v 7/8) show no significant differences.

- NOTES.** 1. The table makes all possible comparisons of the number of occasions in which intruders and holders sang or were silent, both within and between each type of interaction.
2. Statistical comparisons are by the Chi-squared test or Fisher Exact test.

TABLE 5-6. THE NUMBER OF OCCASIONS WHERE BOTH HOLDERS AND INTRUDERS SANG, BOTH WERE SILENT OR ONLY ONE OF THE TWO SANG, IN BLACKCAP (BC) AND GARDEN WARBLER (GW) INTERACTIONS

|                               | INTRASPECIFIC INTERACTIONS |          |       |          | INTERSPECIFIC INTERACTIONS |          |       |          |
|-------------------------------|----------------------------|----------|-------|----------|----------------------------|----------|-------|----------|
|                               | 1. BC                      | HOLDER   | 2. GW | HOLDER   | 3. BC                      | HOLDER   | 4. GW | HOLDER   |
| <u>A. DURING INTERACTIONS</u> | BC                         | INTRUDER | GW    | INTRUDER | GW                         | INTRUDER | BC    | INTRUDER |
| BOTH BIRDS SING               |                            | 14       |       | 11       |                            | 23       |       | 36       |
| ONLY HOLDER SINGS             |                            | 4        |       | 2        |                            | 4        |       | 7        |
| ONLY INTRUDER SINGS           |                            | 2        |       | 0        |                            | 1        |       | 6        |
| BOTH BIRDS SILENT             |                            | 1        |       | 5        |                            | 0        |       | 2        |
| <u>B. AFTER INTERACTIONS</u>  |                            |          |       |          |                            |          |       |          |
| BOTH BIRDS SING               |                            | 7        |       | 4        |                            | 10       |       | 16       |
| ONLY HOLDER SINGS             |                            | 5        |       | 6        |                            | 10       |       | 12       |
| ONLY INTRUDER SINGS           |                            | 2        |       | 2        |                            | 4        |       | 12       |
| BOTH BIRDS SILENT             |                            | 7        |       | 3        |                            | 0        |       | 3        |

NOTE The sample sizes for observations made during interactions sometimes differ from those made after interactions since only partial data was obtained on some contests.

of Blackcap intrusions into Garden Warbler territories are an opportunity to examine whether contest outcomes and singing activity are related (Table 5-7). There are no significant differences between the proportions of singers to non-singers among either holders or intruders both during and immediately after contests, regardless of contest outcomes. There is a tendency for Blackcaps to be silent when Garden Warblers won, as opposed to when they themselves were successful, but the difference falls short of significance. However, when holders (Garden Warblers) won, the numbers of holders which sang after the contests is significantly much higher than the number of those unsuccessful intruders which also sang (Table 5-7).

Only a small minority of birds, usually the holders, gave tac-tac calls but they were heard more frequently in interspecific interactions than in intraspecific ones. Significantly more Blackcap holders "tacked" when confronted by Garden Warblers than by other Blackcaps (Table 5-8). Other differences are not significant.

#### 5.3.6. The contests involving Garden Warbler YR

The summaries of interactions involving Garden Warblers would be unrepresentative if YR was either a particularly aggressive or a particularly meek individual, since he was involved in many of the interactions. However a comparison of the frequency of events observed during interactions involving YR as the territory holder and the total data from interactions involving other Garden Warbler holders reveals no significant differences between the contests involving YR and those involving other holders (Table 5-9). No occasions were observed when YR intruded into any other Garden Warbler's territory but there were a total of five occasions when he intruded into a Blackcap territory. Like other Garden Warblers, he was driven out by the resident Blackcap each time. In general, the data from contests involving YR does not appear to bias the total sample.



**TABLE 5-7. THE SHORT-TERM OUTCOME OF INTERACTIONS BETWEEN GARDEN WARBLER HOLDERS AND BLACKCAP INTRUDERS RELATED TO THE SINGING ACTIVITY OF THE PARTICIPANTS**

| BEHAVIOUR          | A. VOCAL BEHAVIOUR DURING CONTESTS |               |             |               | B. VOCAL BEHAVIOUR AFTER CONTESTS |               |             |               |
|--------------------|------------------------------------|---------------|-------------|---------------|-----------------------------------|---------------|-------------|---------------|
|                    | CONTEST                            |               | OUTCOME     |               | CONTEST                           |               | OUTCOME     |               |
|                    | Holder wins                        | Intruder wins | Holder wins | Intruder wins | Holder wins                       | Intruder wins | Holder wins | Intruder wins |
| 1. Holder sings    | 20                                 | 15            |             |               | 19                                | 12            |             |               |
| 2. Holder silent   | 3                                  | 2             |             |               | 4                                 | 5             |             |               |
| 3. Intruder sings  | 19                                 | 12            |             |               | 9                                 | 11            |             |               |
| 4. Intruder silent | 4                                  | 5             | .           |               | 13                                | 3             |             |               |

- NOTES.**
- The table compares the numbers of singing and silent birds during intruder-victories and holder-victories on Garden Warbler-held territories. Only data from contests which ended in withdrawal of one or other bird are considered, results from interactions where both withdrew thus being among those omitted.
  - After contests won by holders, a significantly high proportion of the holders sang in comparison to the number of singers among the intruder-losers (Table B. Holder wins; rows 1/2 v rows 3/4;  $p < 0.001$ ). There are no other significant differences between the proportions of singers to non-singers between either holders or intruders both during and after contests.
  - Statistical comparisons are by the Chi-squared test or Fisher Exact test.

TABLE 5-8. THE FREQUENCY OF TAC-TAC CALLS DURING BLACKCAP (BC) AND GARDEN WARBLER (GW) INTERACTIONS

| INTRASPECIFIC INTERACTIONS |              | INTERSPECIFIC INTERACTIONS |              |
|----------------------------|--------------|----------------------------|--------------|
| 1. BC HOLDER               | 2. GW HOLDER | 3. BC HOLDER               | 4. GW HOLDER |
| BC INTRUDER                | GW INTRUDER  | GW INTRUDER                | BC INTRUDER  |
| (n = 32)                   | (n = 24)     | (n = 29)                   | (n = 52)     |
| HOLDER CALLS               | 0            | 1                          | 6            |
| INTRUDER CALLS             | 0            | 0                          | 2            |
|                            |              |                            | 1            |

NOTES. 1. The table gives the number of contests in which intruders and holders were heard to call.

2. All possible pairwise comparisons were made between columns of the frequency of occasions in which holders called and those in which intruders called. Significantly more holders called during type 3 interactions than during type 1 interactions. No other differences are significant. (1 p = 0.009)

3. In addition there were single occasions each in type 1 and type 2 interactions in which calls were heard but the identity of the calling bird was not established. In type 3 interactions there was an occasion in which a female mated to the holder called, and another in which a female mated to the intruder was heard to do so.

4. No calls were heard during the five minutes after any of the interactions.

**TABLE 5-9. A COMPARISON OF THE FREQUENCIES OF EVENTS IN INTERACTIONS INVOLVING GARDEN WARBLER YR AS TERRITORY HOLDER WITH THOSE IN INTERACTIONS WHERE OTHER GARDEN WARBLERS WERE THE TERRITORY HOLDERS**

| EVENTS                                    | INTRASPECIFIC INTERACTIONS |              |              | INTERSPECIFIC INTERACTIONS |                |                |
|-------------------------------------------|----------------------------|--------------|--------------|----------------------------|----------------|----------------|
|                                           | 1. YR HOLDER               | 2. GW HOLDER | 3. YR HOLDER | 4. GW HOLDER               | 5. YR INTRUDER | 6. GW INTRUDER |
|                                           | GW INTRUDER                | GW INTRUDER  | " "          | BC INTRUDER                | BC INTRUDER    | BC INTRUDER    |
| Closest approach initiated by holder      | 8                          | 8            |              | 8                          | 10             |                |
| A. Closest approach initiated by intruder | 1                          | 2            |              | 8                          | 20             |                |
| Chase occurs                              | 6                          | 11           |              | 6                          | 5              |                |
| B. No chase occurs                        | 4                          | 2            |              | 16                         | 23             |                |
| Holder chaser                             | 5                          | 8            |              | 2                          | 2              |                |
| C. Intruder chaser                        | 0                          | 0            |              | 1                          | 4              |                |
| Holder leaves area                        | 1                          | 1            |              | 7                          | 10             |                |
| D. Intruder leaves area                   | 7                          | 10           |              | 8                          | 15             |                |
| Both leave area                           | 0                          | 1            |              | 1                          | 3              |                |

(continued)

TABLE 5-2. (continued)

| EVENTS                                     | INTRASPECIFIC INTERACTIONS |          | INTERSPECIFIC INTERACTIONS |                 |       |              |
|--------------------------------------------|----------------------------|----------|----------------------------|-----------------|-------|--------------|
|                                            | 1. YR                      | HOLDER   | 2. GW                      | HOLDER (not YR) | 3. YR | HOLDER 4. GW |
|                                            | GW                         | INTRUDER | GW                         | INTRUDER "      | BC    | INTRUDER BC  |
| <u>E.</u> HOLDER SINGS DURING <sup>i</sup> | 6                          |          | 8                          |                 | 17    | 27           |
| HOLDER SILENT DURING                       | 2                          |          | 3                          |                 | 4     | 4            |
| <u>F.</u> INTRUDER SINGS DURING            | 5                          |          | 6                          |                 | 18    | 24           |
| INTRUDER SILENT DURING                     | 3                          |          | 4                          |                 | 3     | 7            |
| <u>G.</u> HOLDER SINGS AFTER <sup>i</sup>  | 4                          |          | 6                          |                 | 13    | 17           |
| HOLDER SILENT AFTER                        | 3                          |          | 2                          |                 | 5     | 10           |
| <u>H.</u> INTRUDER SINGS AFTER             | 2                          |          | 4                          |                 | 12    | 16           |
| INTRUDER SILENT AFTER                      | 5                          |          | 4                          |                 | 7     | 10           |

- NOTES 1. The table gives the numbers of interactions in which the different events were observed.
2. Comparisons of column 1 v column 2 and of column 3 v column 4 were made for each type of event, by Chi-squared test and Fisher Exact test. No differences are significant.
3. <sup>i</sup>DURING and AFTER refer to whether or not birds sang while interactions were in progress and during the five minutes after the birds had separated.

### 5.3.7. Other interspecific interactions between warblers at Wytham

#### A. Sylvia warblers

Very few interactions were seen involving other Sylvia warblers but these species were very scarce in the study area.

On two separate occasions a singing Whitethroat was closely approached by a Garden Warbler and displaced. A Garden Warbler was seen to chase off a singing Lesser Whitethroat in Wytham and another similar incident was seen at Ivinghoe Beacon, in the Chilterns, on 14 June 1979. All these interactions occurred within Garden Warbler territories but they were very brief unlike many of the Blackcap-Garden Warbler contests. At Wytham several Garden Warbler scrub territories overlapped completely with both whitethroat species.

Blackcap territories did not overlap appreciably with those of Whitethroats. However, Blackcaps have been reported to attack Whitethroats where their territories overlap (Howard 1907-1914). One Lesser Whitethroat territory overlapped extensively with that of a Blackcap but no interactions were seen between the two species.

#### B. Chiffchaffs and Willow Warblers

Fights between Chiffchaffs and Willow Warblers have been reported by Howard (1907-1914) and Jablonski (1967), and both Jablonski and Cody (1978) consider them to be interspecifically territorial in Poland and Yorkshire respectively. At Wytham the two species were certainly not interspecifically territorial and although a special watch was kept for aggressive behaviour between them very few interactions occurred, and always in circumstances suggesting that a mistake in identity had happened. Such mistakes are unsurprising since, unlike Blackcaps and Garden Warblers, the two species look almost identical, although their songs are unmistakably distinct.

Chiffchaffs were seen to chase Willow Warblers on four occasions,

all in early April when the male Willow Warblers first arrived and some settled within pre-established Chiffchaff territories. Each time the Willow Warbler was silent when the Chiffchaff saw it and the chase was immediately (strikingly) discontinued as soon as the Willow Warbler sang, which it did promptly. A similar instance of a Willow Warbler chasing a Chiffchaff was seen once only. In addition, there were several occasions during song playback experiments (Chapter 6) when a Willow Warbler or a Chiffchaff was attracted by a loudspeaker playing its own-species song and saw a bird of the other species foraging nearby. The latter was immediately attacked but the interaction was abruptly curtailed once the chased bird sang, which it did almost at once on each occasion, as if trying to proclaim its species-identity. In contrast to these observations, Willow Warblers and Chiffchaffs were frequently seen foraging and singing simultaneously in the same trees and apparently ignoring each other, although both were most aggressive towards conspecifics.

The peaceful coexistence of Willow Warblers and Chiffchaffs at Wytham does not rule out interspecific territoriality between them in other localities or habitats (or even at Wytham in other years). If this species-pair are genuinely interspecifically-territorial in some areas but not in others then they are ideally suited to a study of the circumstances which give rise to such behaviour.

#### 5.4. DISCUSSION

The observations reported in this chapter are compatible with those described in Chapters 3 and 4. Aggressive interactions normally occur between Blackcaps and Garden Warblers, which are interspecifically-territorial, but not between Chiffchaffs and Willow Warblers, whose territories overlap extensively in some habitats.

Blackcaps and Garden Warblers are effective in holding territories against conspecifics. In addition, newly-arrived Garden Warblers are unable to settle in places already occupied by Blackcaps because the latter are clearly dominant to them in interactions. Established Garden Warblers are

sometimes seen to defend their territories against any later-arriving Blackcaps. However, the relationship between the two species is clearly asymmetrical since although Garden Warbler intruders are virtually always driven-out of Blackcap territories by the holders, new Blackcap arrivals sometimes intrude into Garden Warbler territories and may actually seek-out and chase the Garden Warbler holders.

Garden Warblers appear to maintain territories in the presence of the more-aggressive Blackcaps in either of two ways. They attack and chase out any Blackcaps which intrude into their territories or they simply keep out of the way of the intruders. The latter system may be successful since although the Garden Warblers don't fight the Blackcaps, they don't give up their territories either. Eventually the Blackcaps have to choose between sharing territories with Garden Warblers or moving off elsewhere. The territory maps suggest that they usually adopt the latter option but some of the overlaps between Blackcap and Garden Warbler territories observed during the study may be explicable in terms of the former.

The general finding is that Garden Warblers are less interspecifically aggressive than Blackcaps are. This contrasts with the relationship between Reed and Sedge Warblers, where the later-arriving Reed Warbler is often dominant in interspecific interactions (Brown & Davies 1949, Catchpole 1972). Garden Warblers establish themselves mainly by occupying habitat patches which have not already been filled by Blackcaps.

CHAPTER SIX

SONG PLAYBACK

EXPERIMENTS

WITH

WARBLERS

AT

WYTHAM



## CHAPTER SIX

### SONG PLAYBACK EXPERIMENTS WITH WARBLERS AT WYTHAM

#### 6.1. INTRODUCTION

Song playback experiments have been used to test whether territorial birds are aggressive not only towards conspecifics but also towards other species. The experiments are an attempt to simulate an incursion by a singing male into the territory of another. Qualitative and quantitative observations of the movements and vocalisations of territory holders when presented with song playback enable one to assess not only which songs elicit responses but also how strongly birds respond to different songs.

In general, male songbirds respond aggressively to the sight or sound of conspecifics but they ignore members of other species. This is not the case where a species is interspecifically territorial with another or several species. In such situations song playback experiments have been used to confirm that the observed pattern of largely non-overlapping territories is due to aggressive interactions between territory holders. For example, in Britain Sedge Warblers attempt to defend their territories against Reed Warblers (Brown & Davies 1949, Catchpole 1973) and they react aggressively to playback of Reed Warbler song (Catchpole 1977). Similarly Reed Warblers respond to Marsh Warbler song in Germany, where the two species are sympatric (Catchpole 1978). The Red-eyed and Philadelphia Vireos, which are interspecifically territorial, react to each other's songs (Rice 1978).

All these examples concern congeners. However, not all sympatric congeneric species react to each other's songs. For example, the absence of such a response has been noted between Chiffchaffs and Willow Warblers (Schubert 1971, Helb 1973) and between Goldcrests and Firecrests (Becker 1977). Responses to songs of non-congeneric species have also been demonstrated in a few cases, as between Song Sparrows and Bewick's Wrens (Gorton 1977), between Great Tits and Pied Flycatchers (Jarvi et al. 1978) and between

Great Tits and Chaffinches (T.M.Reed, pers. comm.). In all the examples mentioned, interspecific responses to song playback have involved species known or believed to be in competition during the breeding season.

Properly-controlled playback experiments have not hitherto been performed with Blackcap and Garden Warbler subjects, although there are chiefly-anecdotal reports of Blackcaps responding to Subalpine Warbler song in Sardinia (Cody & Walter 1976), of Garden Warblers responding to Barred Warbler song in Sweden (Cody 1978) and of Blackcaps and Sardinian Warblers responding to each other's songs in Gibraltar (Finlayson 1979). Such experiments could be expected to reveal to what extent male Blackcaps and Garden Warblers react aggressively to each other's presence. Hence they provide an essential supplement to observations of natural encounters (Chapter 5) and relative positions of territory boundaries (Chapter 3). Experiments were also made to test for responses by Blackcaps and Garden Warblers to song playback of Whitethroat and Lesser Whitethroat songs, these two being the other Sylvia warblers with which they are sympatric in Britain. Separate experiments, involving Chiffchaffs and Willow Warblers, were also carried out for comparative purposes, these two species being an example of non-interspecifically territorial congeners.

## 6.2. THE SONGS OF BLACKCAPS AND GARDEN WARBLERS

The songs of the two species are notoriously similar and many British birdwatchers claim to be unable to distinguish them. Nevertheless, I found the two songs to be readily separable in the field; even though some individual Blackcaps and Garden Warblers occasionally sounded like each other, they usually reverted very soon to the song characteristic of their own species. Only a brief general comparison of the songs is given here in anticipation of a more detailed comparison to be based on the large number of songs (12 hours in total) recorded at Wytham.

Examples of songs of the two species are described in Figure 6-1. In both, the songs consist of largely continuous bursts ("songs")

FIGURE 6-1. EXAMPLES OF THE VOCALISATIONS OF THE FOUR SYLVIA  
SPECIES PRESENT AT WYTHAM

- A. Blackcap song      A typical song, ending with a sequence of distinct pure tones.
- B. Garden Warbler song      A typical song, spanning a wider frequency range than the Blackcap song (A) and unlike it in having a buzzy quality and a lack of pure tones.
- C. Blackcap song      The introduction to this song includes some harsh-sounding elements but the song still ends with a series of pure tones, as is characteristic of the species.
- D. Garden Warbler song      A song superficially resembling that of a Blackcap because of the presence of a number of pure tones.

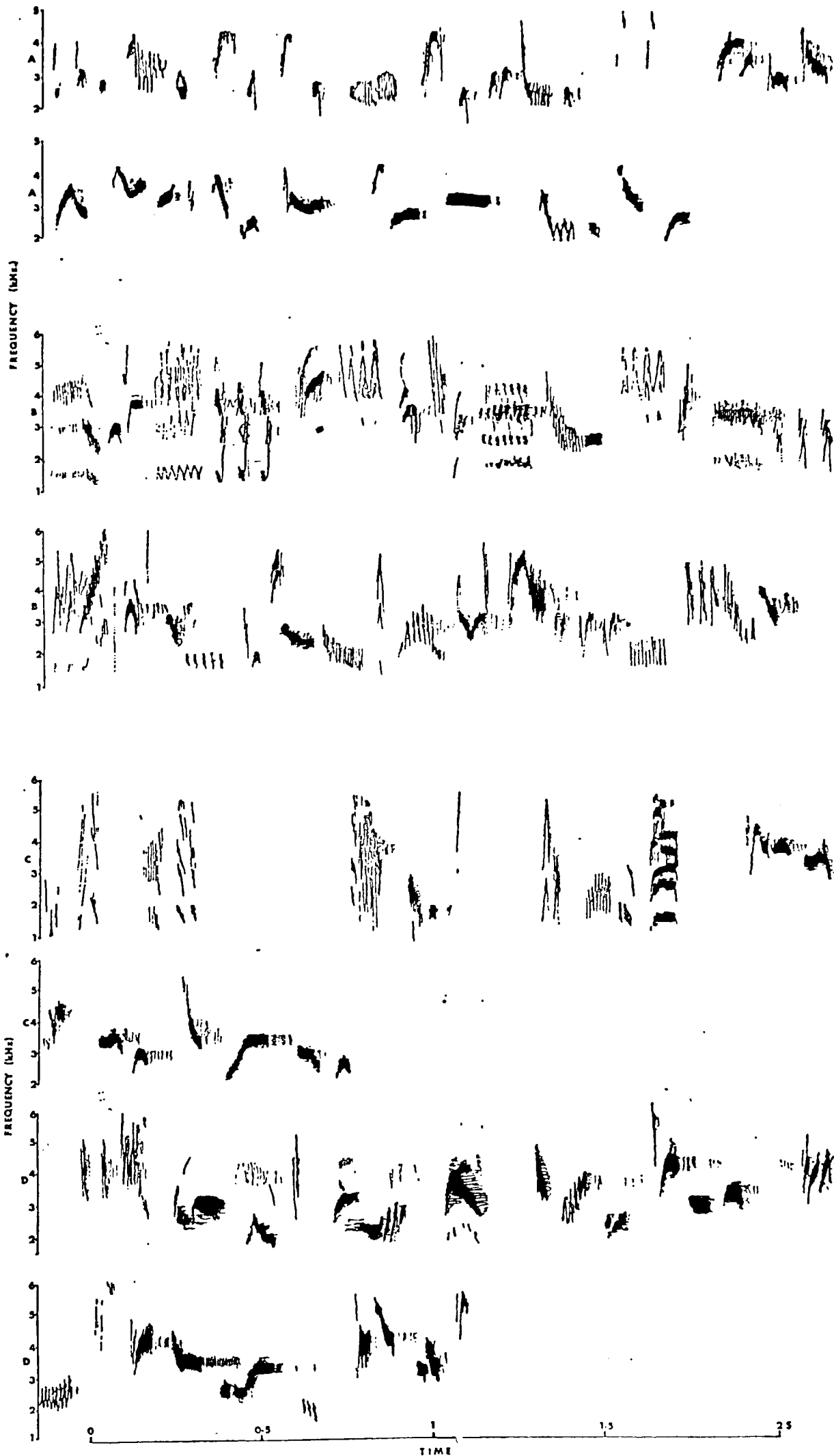
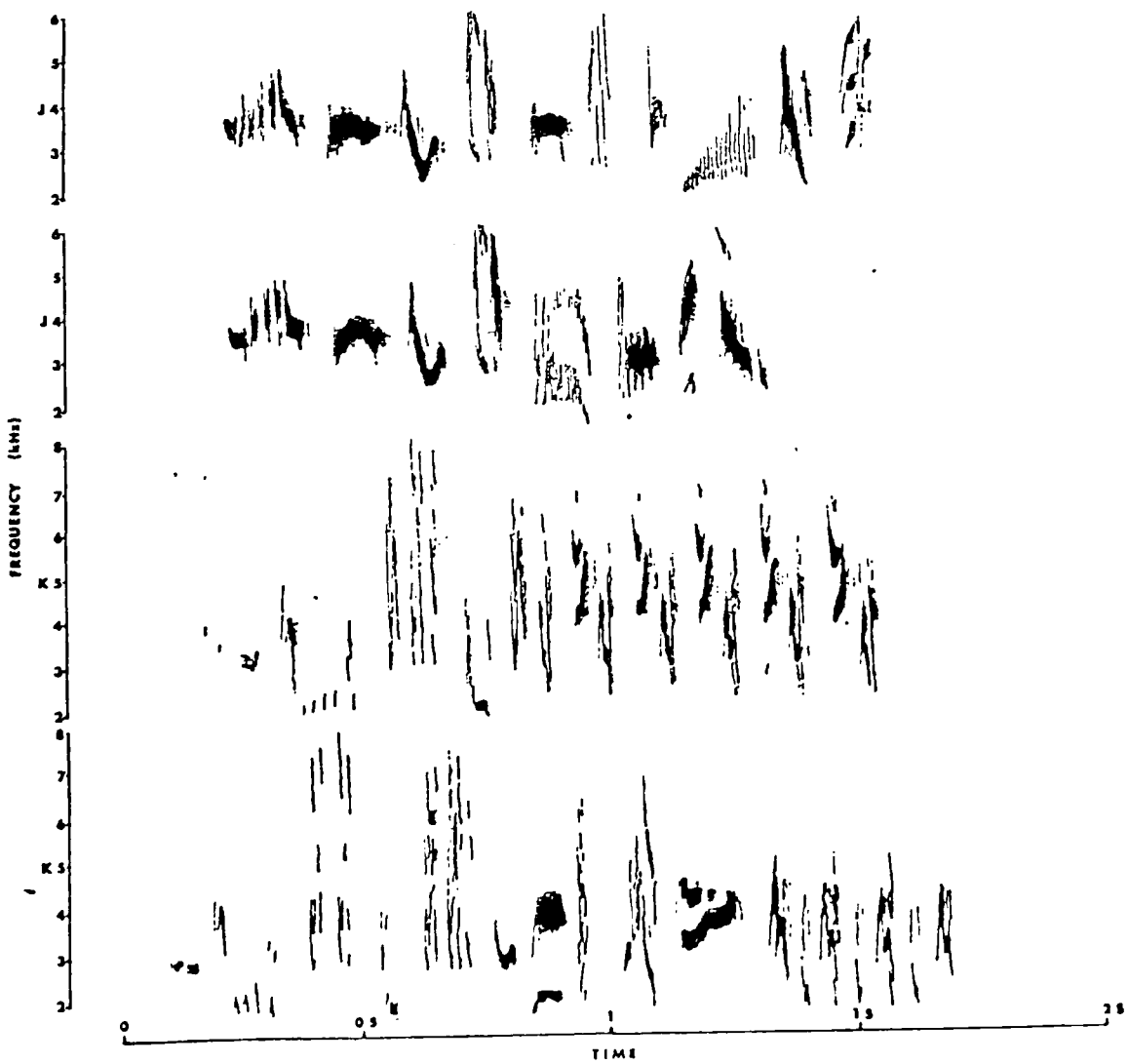
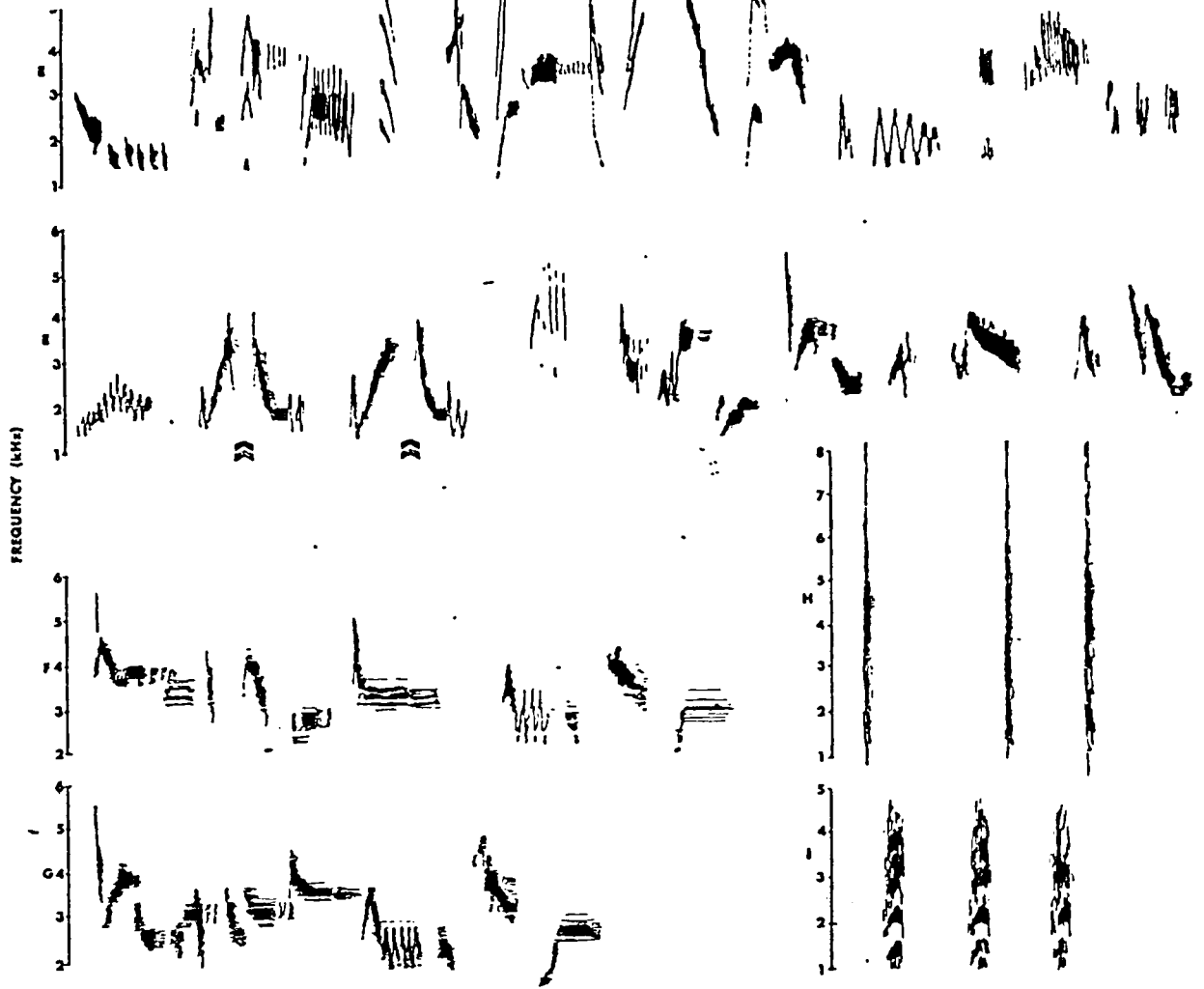


FIGURE 6-1. (continued)

- E. Garden Warbler song A variable song showing a transition from complex introductory elements to relatively pure concluding tones. The repeated elements (arrowed) may be species-specific. They were only heard from Garden Warblers most of which used them occasionally. The sound is a "weeoo-weeoo", suggesting the song of the Golden Oriole.
- F. Blackcap song A typical song-ending.
- G. Garden Warbler song The same ending as (F) but sung by a Garden Warbler. The elements are practically identical but the tempo of the Blackcap song is slower.
- H. Blackcap tacs TAC is a good phonetic rendition.
- I. Garden Warbler tacs These sound quite different from those of Blackcaps. The sound is a "nasal" check-check.
- J. Whitethroat song Two songs by the same bird in one singing bout. The songs are characteristically brief and both are introduced by the same elements. It would be unusual to find this degree of stereotypy in Blackcap or Garden Warbler songs. The elements themselves are very similar to those of Blackcap or Garden Warbler songs.
- K. Lesser Whitethroat song Two songs sung by the same individual. The most stereotyped of the four songs, starting with a variable chatter but ending with a harsh rattle on one note.



comprising complex and variable combinations of an apparently-large number of elements ("notes"). Many elements are shared between the species, although at present it is unknown what proportion are common to the two, or even whether any at all are species-specific. Both species, but especially Blackcaps, are accomplished mimics of the vocalisations of a wide range of bird species (Howard 1907-1914). This imitative tendency makes it more likely that where the two are sympatric their songs may come to resemble each other very closely.

The lengths of songs are highly variable in the two species although mean song lengths are similar (4.07s., s.d. 2.34,  $n = 233$  songs, for Blackcaps and 4.06s., s.d. 2.86,  $n = 1741$  songs, for Garden Warblers). Blackcaps usually have a lower song output because they pause for longer between successive songs than Garden Warblers do (for examples the two species may be compared in Tables 6-7 to 6-10). The mean pause length for Blackcaps is 6.41s (s.d. 2.46,  $n = 192$ ) and for Garden Warblers 3.36s (s.d. 2.13,  $n = 1679$ ). This comparison arbitrarily excludes pauses longer than 15 seconds, taking these as signifying the end of a song bout. The difference in mean pause lengths is highly significant ( $t_{\infty} = 18.48$ ,  $p < 0.001$ , 2-tailed), and is also conspicuous in the field. Both species sing within the frequency range 1,500 - 7,000 Hz., although mainly between 2,000 - 5,000 Hz. Blackcap songs appear to include a higher proportion of pure tones, especially in song endings, but such tones do also occur in Garden Warbler songs (Figure 6-1).

Brief sonagrams, as shown here and in Cody (1978), are poor evidence for assessing song similarity in species with complex songs. It is possible to select highly-similar(or highly-dissimilar)short snatches of song from the large repertoires of element-combinations available, whereas in nature the birds have the opportunity to discriminate each other's songs on the basis of temporal patterning and the sequences in which the elements are arranged, and perhaps by recognition of species-specific elements. It is unknown whether such discrimination occurs but it seems probable that the complexity of the two songs offers features on which discrimination

might be based.

The songs of the two whitethroat species used in song playback experiments contrast with those of Blackcaps and Garden Warblers mainly in being comparatively stereotyped (Figure 6-1, J,K).

### 6.3. METHODS - SONG PLAYBACK EXPERIMENTS WITH BLACKCAP AND GARDEN WARBLER SUBJECTS

#### 6.3.1. Subjects.

All subjects were established males, whose territories had been plotted by observation over several days previous to their first encounter with the experimental tapes. In 1978 about a third of the subjects were mist-netted and colour-ringed on their territories before the experiments began but most subjects in this and later seasons were unringed at the time of the experiments. Since some territories were extensive, capturing the owners was potentially very time-consuming unless song playback was used to lure them into the nets. Experimental subjects were not captured using song playback since it was felt that the experience might later inhibit or diminish their responses during playback experiments. Later results showed this precaution to have been fully justified (Appendix 6-2). However, most experiments with particular individuals were completed within a few days and observation of marked birds suggested that it was unlikely that any large-scale changes in territory ownership occurred once birds were established. In short, most subjects were identified by location but a minority were distinguishable on voice or plumage features or had been colour-ringed during "random" mist-netting.

The first series of experiments was designed to test for the existence of reactions by Blackcaps and Garden Warblers to each other's songs. It was completed between 27 April and 29 May 1978, when 15 Blackcaps and 14 Garden Warblers were tested with Blackcap, Garden Warbler and Great Tit song, the last serving as a control.



A second series of experiments using the same three tapes, was conducted between 27 June and 14 July 1978, to test for responses late in the breeding season. By this time, most subjects of the first series had fledged young and were no longer traceable on their former territories. In the case of Blackcaps some of these territories were occupied now by different males who only settled there during June. Three such new birds were tested in addition to seven others which were also still defending territories. The seven included one bird which had been a subject in the first series of experiments and six which had not been tested previously. The territories of these six had been continuously occupied since May but because the birds were unringed it was impossible to be certain whether the occupants in July were the same birds which were there at the beginning of the breeding season. In all, nine Blackcaps were tested with Blackcap and Garden Warbler song and seven of them also received playback of Great Tit song. Only five Garden Warblers were at all evident on their territories in late June and early July 1978. Three had already been tested earlier in the season and the other two had been present since May but had not been tested previously. All five were tested with Blackcap, Garden Warbler and Great Tit song tapes.

In 1979 playback experiments were only conducted with Blackcap subjects in an experiment designed to test whether they discriminated between two types of Garden Warbler song. Twelve were tested with both songs, between 2 May and 18 June.

In 1980 fifteen Blackcaps received playback of Blackcap and Whitethroat song and twelve of them were also tested with Garden Warbler song, these experiments being completed between 25 April and 19 May. Six Garden Warblers were tested with Blackcap, Garden Warbler and Whitethroat song between 17 May and 2 June and five other birds were tested with one or two of these three tapes. Playback experiments with Lesser Whitethroat song and both Blackcap and Garden Warbler subjects began in mid-May and were completed on 4 June. Six Garden Warblers and eight Blackcaps were tested,

all of them new subjects; i.e. birds which had not previously been tested with any other tapes. New subjects were used since it was felt that to present a fourth tape to a bird could produce artificially-weak responses through habituation to the playback situation, as described in Appendix 6-2. There was insufficient time to present more than two test tapes to these later subjects and so each was tested with Lesser Whitethroat song and Blackcap song (in the case of Garden Warbler subjects) or Garden Warbler song (in the case of Blackcap subjects), to test for the continuing existence of the interspecific reactions to song playback revealed by earlier experiments.

In all, 67 Blackcaps and 31 Garden Warblers were used as subjects during the course of the whole study.

#### 6.3.2. Apparatus.

Songs were recorded using a Uher 4000 Report L tape recorder and a Grampian DF8/M microphone mounted at the focal point of a 24-inch Grampian parabolic reflector. Recordings were at a tape speed of 19 cm. per second and were played back at a fixed normal volume through a 15 watt amplifier and a Model P5 Era Acoustics poly-planar loudspeaker, the latter hung at the end of a 30-metre lead.

#### 6.3.3. Experimental Tapes.

Preliminary inspection showed that some territories were over one hectare in area and there seemed a possibility that distant subjects might not hear the tapes at all. Tapes of five minutes duration were used to give them a fairly good opportunity to do so.

In 1978 the warbler tapes used were made up from recordings supplied by the British Library of Wildlife Sound. The songs concerned had been recorded in Worcestershire in 1963 (Blackcap) and 1965 (Garden Warbler) by A.G. Field. The control Great Tit tape was made up from recordings in Wytham wood by P.K.McGregor. The tapes were made up from bursts of spontaneous steady song of about 100 seconds duration and so required only

three repetitions to achieve the desired five minute output. Continuous recordings spanning the entire five minute period would have been preferred but were not available in the material provided by B.L.O.W.S.

Tapes used in 1979 and 1980, including those of the two whitethroats, were of birds recorded in the study area in 1978 (1980 in the case of the Lesser Whitethroat tape). The tapes of Blackcap and Garden Warbler song were again made up to five minutes duration from 100 second-long recordings. Continuous five minute recordings proved impossible to obtain, birds rarely singing so long without a break or without changing position. Different stretches of song could have been used to avoid repetition in the experimental tapes but this was not done in order to standardise the procedure with that carried out in 1978, when tapes included an element of repetition. The individuals recorded were not used as subjects themselves. The tapes of Whitethroat and Lesser Whitethroat song were made up to five minutes duration from 30 second-long recordings, the longest ones available. They thus included a higher element of repetition than the Blackcap or Garden Warbler song tapes. This difference must be considered when comparing responses of subjects to different songs but it is thought unlikely to have had a serious influence on the results since, as earlier described, both whitethroat songs are highly stereotyped (and hence repetitive) in comparison to Blackcap or Garden Warbler songs.

#### 6.3.4. Experimental Procedure.

The tapes were presented to each subject in random order to control not only for any tendency of response intensity to vary as the season advanced but also for the existence of habituation to playback. Different tapes were usually presented to individual subjects on successive days, although unsuitable weather sometimes delayed particular experiments by up to a week. All experiments were done in the mornings when natural vocal activity was usually high. This is also when most natural intrusions were seen to occur, perhaps because warblers are characteristically night

migrants and new arrivals are generally seeking for territories in the mornings. Nearly all experiments were completed between 05.00 and 10.30 hours B.S.T. but in 1978 poor weather on many May mornings meant that playback was delayed and carried out between 10.30 and 12.00 hours on a few occasions. Ideally territories would have been visited in random order to control further for any time-linked variations in activity and song. However, the wide separation of the territories made this impractical in some parts of the study area. Nevertheless, experiments were not carried out on the same day in territories immediately adjacent to any subject tested, to remove the possibility of a bird having heard the tape when it was played to a neighbour immediately previously.

The substantial size of the territories of both species, combined with the skulking behaviour of the birds and the dense vegetation which they inhabit, raised the difficulty of knowing when a bird was actually present on the territory. It was decided not to attempt any song playback unless the subject was seen or heard during the five minutes preceding each experiment. This helped to distinguish between a nil response and a negative result caused by the subject being out of earshot. The procedure was not foolproof since on several occasions it appeared that a bird moved further away immediately prior to song playback and possibly did not hear the tape during the experiment itself.

The playback procedure was standardised as follows. A territory was visited and the owner located by sight or sound. The loudspeaker was then hung at breast height in a central position in the territory. The same playback position was used for all experiments with each individual subject, principally because nest sites were rarely known and to have varied the playback position might have affected responsiveness if different experiments were conducted at different distances from nests or any parts of territories which holders might have been especially motivated to defend. A compromise had to be found between hanging the speaker in a very

conspicuous position, where any approach to it would be easily detected, and placing it in a less exposed situation, where approaching birds would tend to be concealed by the vegetation. Whereas open sites were desirable since they facilitated observation, it was evident that too exposed a site would have meant a reduced response level if birds were reluctant to stray well out from cover. The speaker was hung so that birds could approach right up to it through the vegetation. The presence of some cover near the speaker was important too in that it avoided setting-up a situation in which a bird could hear a "rival" singing out of an obviously-empty bush. Since warblers often sing from cover, foliage near the speaker presented the possibility that an intruder was singing in concealment there. A number of potential subjects were not tested at all since their territories were too densely and homogeneously vegetated to provide any suitable playback location. In general, it was impossible to standardise the degree of exposure of the loudspeaker position and this is one factor which may partly explain the observed individual differences in response intensity between subjects.

Events were observed from cover 20 to 30 metres away from the speaker. A record of the number and total duration of vocalisations was taken for a five minute period immediately preceding song playback. This established a baseline for the vocal activity of territory holders, for later comparison with their vocal activity during and after hearing the tapes. The tape was switched on immediately after this period and a full record of all acoustic and visible behaviour of the subject was dictated into a portable tape-recorder throughout the test period, for later analysis. A record of vocalisations was again taken for the five minutes following song playback.

Occasionally, just before an experiment a subject was already singing at a neighbour. On these occasions playback was postponed to avoid confronting the bird with several simultaneous stimuli. Playback was also delayed if a bird was within 20 metres of the speaker when the experiment

was due to begin, in order to provide the subject with the opportunity to make a detectable approach to it. Experiments were cancelled during rainy or windy weather.

#### 6.3.5. Categories of Response.

A bird was taken to have responded to a particular song if it moved towards the speaker during the period when that song was broadcast. The responses were quantified using the response-measures utilised by Catchpole (1977) in his study of Sedge Warblers. Unlike Sedge Warblers, Blackcaps and Garden Warblers occupy structurally-complex habitats in which they are often difficult to locate or observe. Thus, the responses noted are in some cases almost certainly an underestimate of the actual response intensity. It sometimes happened that birds were soon attracted by song playback but skulked about in vegetation near the speaker. They could not be identified until they sang or came out into view. In some cases a Blackcap or a Garden Warbler was eventually seen but in a few instances it was impossible to be certain whether the unidentified birds originally observed were the same as the Sylvia later detected. All the results need to be regarded therefore as minimum responses.

Where a response was suspected, but never proved, to occur the result was dropped from the analysis. No experiments were repeated since it was intended to compare subject's reactions to their first encounter with each of the tapes. Hence, the exclusion of results from birds suspected but not proved to respond means that for several subjects only partial results (responses to only one or two of the test tapes) are available. A more important source of such partial results arose where subjects did not meet the criteria for commencement of song playback on dates subsequent to the first or second experiments with them. This happened mainly in 1978 when long periods of wet weather in April and May depressed vocal activity and it became impossible to re-locate a number of subjects.

The response categories were as follows;

### Response latency (LATENCY)

The interval from the start of the test tape to the first observed movement of the bird towards the speaker.

### Nearest distance of approach to the speaker (DISTANCE)

The closest approach to the speaker seen during the playback period. This was estimated visually but was measured in a few doubtful cases.

### Time spent near the speaker (TIME)

The total period spent within a radius of ten metres of the speaker during the time when the tape was being broadcast.

### Number and duration of songs

The number and total duration of songs uttered during song playback and during the five minutes previous and subsequent to each experiment. (In 1978 only the number of songs was recorded).

### Number of calls

The number of Tac-Tac calls (Figure 6-1 H, I) heard during song playback and during the five minutes before and after it. No other calls were heard during the experiments.

Subjects which fail to respond at all are a potential complication in the statistical analysis of response data. The problem arises from the need to assign values to the Latency, Distance and Time variables for non-responders. Other workers (e.g. Catchpole 1977) have assigned such birds a maximum Latency value equal to the full duration of the test tape and a zero Time value. The Distance variable poses the greatest difficulty since the positions of birds which do not approach are rarely known accurately, if at all. Such birds may be assigned an arbitrary Distance score, e.g. equal to the mean territory radius (Catchpole 1977) or may be scored at infinity, statistical calculations then centring on median responses (Pickstock & Krebs 1980). It has been found possible to avoid the problem in the present study. With the exception of control tapes, test

tapes provoked a response from the great majority of Blackcap and Garden Warbler subjects. It is thus justified to compare the response variables of responders only, after examining the proportion of responders to non-responders for each set of experiments.

#### 6.4. METHODS - SONG PLAYBACK EXPERIMENTS WITH CHIFFCHAFF AND WILLOW WARBLER SUBJECTS

Unlike Blackcaps and Garden Warblers, the songs of Chiffchaffs and Willow Warblers are unmistakably distinct, even to human ears (Figure 6-2). Two short series of song playback experiments were conducted to investigate the findings of Schubert (1971) and Helb (1973) that both Chiffchaffs and Willow Warblers do not react aggressively to each other's songs. On 23 April 1978 eight Chiffchaff males received playback of Chiffchaff song, Willow Warbler song and Great Tit song. Four of the Chiffchaff territories overlapped with Willow Warbler territories and the movements of the male Willow Warblers were also noted during the experiments. Six Willow Warbler and six Chiffchaff males received playback of conspecific and each other's songs, between 10 and 22 April 1980.

The equipment used for recording and playback of Sylvia songs was also used with Phylloscopus subjects. Tapes consisted of bursts of spontaneous song of about 45 seconds duration, repeated to make up a three minute-long tape. Both species have smaller territories than some Sylvia warblers and a comparatively short playback time of three minutes was adequate for holders to hear the tapes and respond or otherwise.

The first series of experiments was completed in one morning during which territories were visited in random order with at least 30 minutes elapsing between successive exposures to playback of individual subjects. The order of presentation of the three tapes was also random. The second series of experiments presented one of two test tapes to each subject on consecutive days, half the subjects receiving Willow Warbler song playback before Chiffchaff song playback, and vice-versa. The latency of

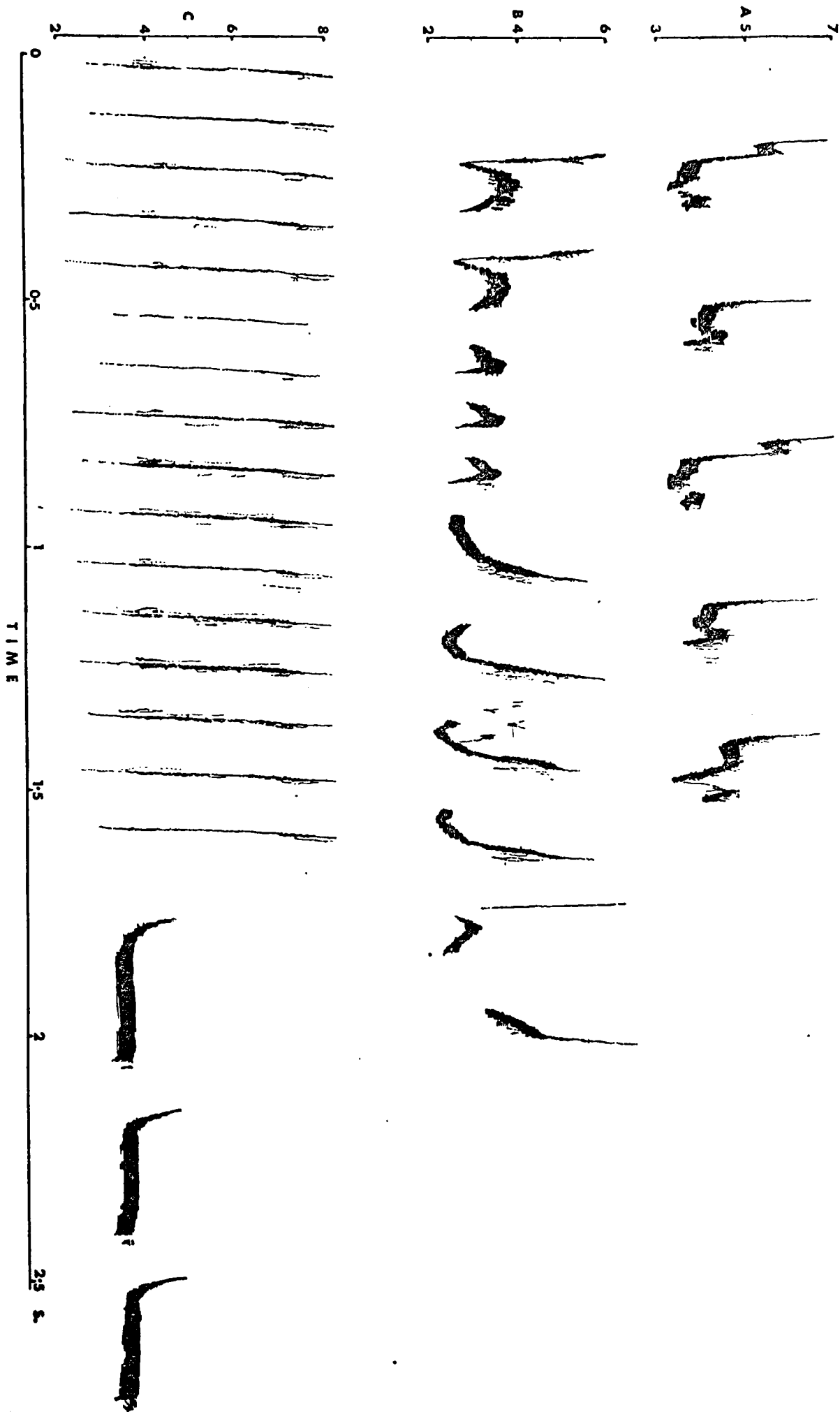


FIGURE 6-2. EXAMPLES OF TYPICAL SONGS OF THE THREE PHYLLOSCOPUS  
SPECIES PRESENT AT WYTHAM

The third species, the Wood Warbler, is included for purposes of comparison. All three songs are unmistakably species-distinctive.

- A. CHIFFCHAFF SONG      A jumble of sibilant, repeated "chiff" and "chaff" elements.
- B. WILLOW WARBLER SONG      A descending cadence of pure notes, typically decelerating at the end.
- C. WOOD WARBLER SONG      A monotonous trill of variable duration, ending sometimes (as here) with several loud, pure whistles.

FREQUENCY (kHz)



response, closest distance of approach to the speaker and time spent within ten metres of the speaker were recorded. The number and duration of vocalisations during song playback, and during the preceding and successive three minutes, were recorded only during the second series of experiments.

## 6.5. RESULTS - SONG PLAYBACK EXPERIMENTS WITH CHIFFCHAFFS AND WILLOW WARBLERS

These results are presented first since they illustrate a situation which may be typical of what normally occurs when sympatric congeneric species hear each other's songs. They provide a baseline for comparison with the very different situation revealed by the playback experiments with Blackcaps and Garden Warblers.

### 6.5.1. Responses to song playback

For both species, only conspecific song produced a significant response (Table 6-1A). All but one Chiffchaff responded rapidly to Chiffchaff song and most approached to within two metres of the speaker (median score one metre) and remained there for some time. Although three Chiffchaffs moved in the direction of the speaker during the Willow Warbler song playback, these movements were slow and not obviously directed at the speaker itself; none of the birds approached it closer than seven metres. Similarly, all Willow Warblers responded strongly to Willow Warbler song, all but one approaching within a metre of the speaker. In contrast, only one bird moved towards the speaker during playback of Chiffchaff song and it did not approach closer than ten metres. No Chiffchaffs or Willow Warblers responded to Great Tit song. The Latency, Distance and Time scores for birds responding to conspecific song do not differ significantly between the two species (Table 6-1B).

Vocal responses of Chiffchaffs show no statistically significant trends (Table 6-2B). Three Chiffchaffs sang more after than before playback of both Chiffchaff and Willow Warbler song and three sang less in both cases. Only one of the birds which sang more after than before Chiffchaff song was among those which sang more after than before Willow Warbler song

TABLE 6-1. RESPONSES TO SONG PLAYBACK BY CHIFFCHAFFS AND WILLOW WARBLERS

A. The numbers of Chiffchaffs and Willow Warblers which responded to Chiffchaff, Willow Warbler and Great Tit song

|                                         | SONG PRESENTED     |                    |               |
|-----------------------------------------|--------------------|--------------------|---------------|
|                                         | 1. Chiffchaff      | 2. Willow Warbler  | 3. Great Tit  |
| CHIFFCHAFF SUBJECTS                     | 13/14              | 3/14               | 0/8           |
| Between-column <sup>i</sup> comparisons | 1 v 2<br>p < 0.001 | 1 v 3<br>p < 0.001 | 2 v 3<br>n.s. |
|                                         | SONG PRESENTED     |                    |               |
|                                         | 1. Willow Warbler  | 2. Chiffchaff      | 3. Great Tit  |
| WILLOW WARBLER SUBJECTS                 | 10/10              | 1/10               | 0/4           |
| Between-column <sup>i</sup> comparisons | 1 v 2<br>p < 0.001 | 1 v 3<br>p < 0.001 | 2 v 3<br>n.s. |

- NOTES 1. The pairwise comparisons are of the relative numbers of responders to non-responders, by Fisher Exact Test.
2. The numbers which responded are given as a fraction of the total number of subjects tested.

B. The response parameters of subjects responding to conspecific songs

Mean responses ( $\pm 1$  S.E.)

|              | Responses of Chiffchaffs<br>to Chiffchaff song<br>(n = 13) | Responses of Willow Warblers<br>to Willow Warbler song<br>(n = 10) |
|--------------|------------------------------------------------------------|--------------------------------------------------------------------|
| LATENCY (s)  | 34.2 ( $\pm 6.9$ )                                         | 30.5 ( $\pm 7.4$ )                                                 |
| DISTANCE (m) | 2.2 ( $\pm 0.7$ )                                          | 0.7 ( $\pm 0.3$ )                                                  |
| TIME (s)     | 106.9 ( $\pm 11.9$ )                                       | 145.5 ( $\pm 7.2$ )                                                |

The Latency, Distance and Time values do not differ significantly between the two species (Mann-Whitney U Test, 2-tailed,  $p > 0.05$ ).

TABLE 6-2. THE TOTAL TIME SPENT SINGING BY CHIFFCHAFFS AND WILLOW WARBLERS DURING PLAYBACK OF CHIFFCHAFF SONG (C) AND WILLOW WARBLER SONG (W)

Mean total song durations in seconds ( $\pm 1$  S.E.). The maximum possible score is 180s.

A. CHIFFCHAFF SUBJECTS (n = 6)

|                 | Playback of<br>C song | Playback of<br>W song | Between-tapes<br>comparison |
|-----------------|-----------------------|-----------------------|-----------------------------|
| Before playback | 61.5 ( $\pm 10.0$ )   | 57.0 ( $\pm 14.5$ )   | n.s.                        |
| During playback | 36.2 ( $\pm 12.5$ )   | 47.7 ( $\pm 12.4$ )   | n.s.                        |
| After playback  | 72.8 ( $\pm 19.8$ )   | 54.3 ( $\pm 16.6$ )   | n.s.                        |

For both tapes comparisons of song output before v during, during v after and after v during playback show no significant differences ( $p > 0.05$  in each case).

B. WILLOW WARBLER SUBJECTS (n = 6)

|                 | Playback of<br>W song | Playback of<br>C song | Between-tapes<br>comparison |
|-----------------|-----------------------|-----------------------|-----------------------------|
| Before playback | 36.0 ( $\pm 7.3$ )    | 30.0 ( $\pm 5.0$ )    | n.s.                        |
| During playback | 5.2 ( $\pm 2.5$ )     | 12.8 ( $\pm 4.4$ )    | n.s.                        |
| After playback  | 63.7 ( $\pm 2.7$ )    | 25.0 ( $\pm 2.7$ )    | n.s.                        |

Comparisons of song output before v during, during v after and after v during playback show birds sang significantly more after than before W song playback, and both after and before than during W song playback ( $p < 0.05$ , in each case). Birds also sang significantly less during playback of C song than before it ( $p < 0.05$ ). Other differences are not significant.

NOTE All statistical comparisons are by the Wilcoxon Test (2-tailed).

playback. Four sang less during Chiffchaff song playback than before the experiment began. Two of these, both of which responded by approaching the speaker closely, stopped singing completely during the song playback and then sang at a very high rate when the tape ended.

Two Willow Warblers sang more after than before Chiffchaff song, three sang less and one sang about the same. In contrast all elevated their song output after playback of Willow Warbler song. All six birds sang less during playback of both Chiffchaff and Willow Warbler song than before the presentation of either song but the effect was most pronounced during playback of Willow Warbler song. These differences are all significant (Table 6-2B).

#### 6.5.2. Further observations of responses to song playback

A total of 32 Chiffchaffs and 25 Willow Warblers were captured using song playback to attract them into mist-nets and an unrecorded number of unsuccessful capture attempts were made. Most captures or attempted-captures were made in areas where territories of the two species overlapped widely and so both songs were played successively at each net-site.

It was always the case that Willow Warblers approached the net and were captured only during Willow Warbler song playback and similarly Chiffchaffs responded only to Chiffchaff song playback. It was extremely unusual for males of both species to fail to respond to own-species song and quite unknown for either to approach the speaker closely during playback of each other's songs. Whereas vocal responses to song playback varied between individuals, as suggested by the results in Table 6-2, often silent birds were stimulated to sing at a high rate by own-species song playback. Both species have a distinctive response to conspecific song playback. In general, Chiffchaffs approach the speaker and make themselves conspicuous by repeatedly quivering their wings. If they sing they frequently intersperse their song bursts with chattering noises. Willow Warblers respond by making frequent glides past the speaker. They perch near it adopting a conspicuous

vertical posture in which the pale belly and wing-linings are displayed, and make themselves even more noticeable by constantly fanning their wings gently. These overt reactions of both species were observed in response to own-species song playback exclusively, suggesting that the few responses observed during playback of each other's songs (Table 6-1A) were weak or perhaps just coincidental, representing the normal wanderings of males about their territories. However, since no subjects approached the speaker at all during Great Tit song playback and since Willow Warblers in particular depressed their song output not only during playback of Willow Warbler song but also during that of Chiffchaff song, it may be that some individuals of both species are not wholly indifferent to each other's songs.

The reduction in song output by both species during song playback may be simply an example of acoustic competition, a phenomenon in which birds sing when competing sounds, including songs of other species, are not prominent and their own vocalisations are most likely to penetrate the acoustic environment and be heard by their intended recipients (Cody & Brown 1969, Wasserman 1977). In this event, Willow Warblers and Chiffchaffs may be sensitive to each other's songs but to no greater extent than they may be to songs of other, unrelated species. Further experiments to observe song output during presentations of control tapes are needed to verify this.

The general results confirm that both Willow Warblers and Chiffchaffs behave aggressively in response to conspecific songs but do not respond to each other's songs.

## 6.6. RESULTS - SONG PLAYBACK EXPERIMENTS WITH BLACKCAPS AND GARDEN WARBLERS

### 6.6.1. Responses of both species to playback of Blackcap and Garden Warbler songs during the principal part of the breeding season

This section considers responses during the part of the breeding season between late April and early June, when territories are established and first clutches are being attended.

A similar proportion, and the great majority, of Blackcap subjects responded to both Blackcap and Garden Warbler songs (Table 6-3A). All Garden Warblers responded to Garden Warbler song and most (74%) also did so to Blackcap song, but here the proportion of non-responders differs significantly between the two tapes (Table 6-3B). Inspection of the table suggests that this difference between Blackcap and Garden Warbler subjects is due to the fact that all Garden Warblers, but not all Blackcaps, responded to conspecific song rather than to fewer Garden Warblers than Blackcaps responding to playback of the non-conspecific song.

Great Tit song evoked no responses at all from Garden Warbler subjects. Two Blackcaps did move in the direction of the speaker during Great Tit song playback. One case appeared to be coincidental and the bird did not approach the speaker at all closely. In the other case, the Blackcap approached the speaker and chased off a male Great Tit which had previously been attracted by the tape. This time it was found later that the speaker had been hung inadvertently four metres away from the Blackcap's nest. In general there were no responses to Great Tit song from either species and hence detailed results are not presented for those experiments.

#### A. Movements of subjects during song playback.

The movements of subjects responding to song playback are represented by the Latency, Distance and Time scores of their responses. The principal question examined here is whether Blackcaps and Garden Warblers react more or less strongly to each other's songs than they do to songs of conspecifics. Results are presented for those subjects which responded to both songs (Table 6-4). This simplifies the analysis by omitting birds which responded to only one or neither of the tapes. The comparison remains valid since responsiveness to both songs is characteristic of the large majority of Blackcap and Garden Warbler subjects (Table 6-3).

For both species there are no significant differences between Latency, Distance or Time scores, i.e. on average both Blackcaps and Garden



TABLE 6-3. THE NUMBERS OF BLACKCAPS AND GARDEN WARBLERS WHICH RESPONDED TO PLAYBACK OF BLACKCAP, GARDEN WARBLER AND GREAT TIT SONG DURING EXPERIMENTS IN THE PRINCIPAL PART OF THE BREEDING SEASON

|                            | SONG PRESENTED             |                    |                    |
|----------------------------|----------------------------|--------------------|--------------------|
| A.                         | 1. Blackcap                | 2. Garden Warbler  | 3. Great Tit       |
| BLACKCAP SUBJECTS          | 25/29                      | 37/40              | 2/13               |
| Between-column comparisons | 1 v 2 <sup>i</sup><br>n.s. | 1 v 3<br>p < 0.001 | 2 v 3<br>p < 0.001 |

|                            | SONG PRESENTED                  |                    |                    |
|----------------------------|---------------------------------|--------------------|--------------------|
| B.                         | 1. Garden Warbler               | 2. Blackcap        | 3. Great Tit       |
| GARDEN WARBLER SUBJECTS    | 23/23                           | 17/23              | 0/13               |
| Between-column comparisons | 1 v 2 <sup>i</sup><br>p = 0.011 | 1 v 3<br>p < 0.001 | 2 v 3<br>p < 0.001 |

- NOTES
1. The pairwise comparisons are of the relative numbers of responders to non-responders, by Chi-squared Test or Fisher Exact Test (i).
  2. The numbers which responded are given as a fraction of the total number of subjects tested.
  3. The combined results from all subjects tested in 1978, 1979 and 1980 are given.

TABLE 6-4. THE RESPONSE PARAMETERS OF SUBJECTS WHICH RESPONDED TO BOTH BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG PLAYBACK DURING THE PRINCIPAL PART OF THE BREEDING SEASON

Mean responses ( $\pm 1$  S.E.).

A. RESPONSES OF BLACKCAP SUBJECTS (n = 15)

|              | Responses to BC song<br>playback | Responses to GW song<br>playback |
|--------------|----------------------------------|----------------------------------|
| LATENCY (s)  | 75.6 ( $\pm 14.4$ )              | 117.1 ( $\pm 62.7$ )             |
| DISTANCE (m) | 2.5 ( $\pm 0.9$ )                | 5.9 ( $\pm 1.1$ )                |
| TIME (s)     | 148.4 ( $\pm 19.7$ )             | 94.3 ( $\pm 21.1$ )              |

B. RESPONSES OF GARDEN WARBLER SUBJECTS (n = 15)

|              | Responses to GW song<br>playback | Responses to BC song<br>playback |
|--------------|----------------------------------|----------------------------------|
| LATENCY (s)  | 94.5 ( $\pm 22.5$ )              | 132.5 ( $\pm 25.7$ )             |
| DISTANCE (m) | 9.9 ( $\pm 2.3$ )                | 8.4 ( $\pm 1.0$ )                |
| TIME (s)     | 90.5 ( $\pm 27.6$ )              | 83.0 ( $\pm 21.5$ )              |

The Latency, Distance and Time values are not significantly different between the two experimental songs for either species (Wilcoxon Test, 2-tailed,  $p > 0.05$ ).

Warblers responded just as quickly to either Blackcap or to Garden Warbler song, approaching the speaker as close and remaining near it for a similar length of time in both cases.

Catchpole (1977) found that the Latency, Distance and Time scores of Sedge Warblers responding to song playback were not correlated, although they showed related trends. However, the corresponding scores for Blackcaps and Garden Warblers do show some significant correlations (Table 6-5). For both species, there is no significant correlation between how quickly birds respond (Latency) and how closely they approach the speaker (Distance). For Blackcap subjects presented with either Blackcap or Garden Warbler song the Distance and Latency scores are significantly negatively correlated with the time spent within ten metres of the speaker (Time), i.e. birds which spent a long period near the speaker tended to be those which approached it closely and those which responded rapidly to the tapes. The same pattern is evident for Garden Warbler subjects but here the correlation between Distance and Time scores of birds responding to Blackcap song is weak and not significant. The existence of these correlations is not unexpected. Subjects which respond rapidly have a greater opportunity to achieve a high Time score than those which respond more slowly, when a larger part of the experimental period has already elapsed. The relationship between Distance and Time scores may be explicable by the fact that those birds which approached the speaker very closely, to within a couple of metres, rarely did so directly. These strongly-responding birds usually arrived in the general area of the speaker and then approached closer by degrees. Once near the speaker they searched the vegetation around it carefully. Some of these birds then withdrew some distance only to return and search the vicinity of the speaker again as the song playback continued. In general, the prolonged searching behaviour of close-approachers may explain why they also achieved high Time scores.

As already noted, different tapes were used in 1978 and in 1980.

TABLE 6-5. CORRELATION COEFFICIENTS (r) FROM PAIRWISE COMPARISONS OF THE LATENCY, DISTANCE AND TIME SCORES OF ALL SUBJECTS TESTED WHICH RESPONDED TO PLAYBACK OF BLACKCAP (BC) OR GARDEN WARBLER (GW) SONG

A. BLACKCAP SUBJECTS

|                    | Responses to BC song<br>playback<br>(n = 24) |           | Responses to GW song<br>playback<br>(n = 37) |           |
|--------------------|----------------------------------------------|-----------|----------------------------------------------|-----------|
| LATENCY v DISTANCE | 0.099                                        | n.s.      | 0.254                                        | n.s.      |
| DISTANCE v TIME    | -0.752                                       | p < 0.001 | -0.607                                       | p < 0.001 |
| LATENCY v TIME     | -0.404                                       | p < 0.05  | -0.543                                       | p < 0.001 |

B. GARDEN WARBLER SUBJECTS

|                    | Responses to GW song<br>playback<br>(n = 23) |           | Responses to BC song<br>playback<br>(n = 17) |          |
|--------------------|----------------------------------------------|-----------|----------------------------------------------|----------|
| LATENCY v DISTANCE | 0.367                                        | n.s.      | -0.161                                       | n.s.     |
| DISTANCE v TIME    | -0.671                                       | p < 0.001 | -0.165                                       | n.s.     |
| LATENCY v TIME     | -0.532                                       | p < 0.01  | -0.615                                       | p < 0.01 |

NOTE Results are included from all birds which responded to song playback during the principal part of the breeding season in all three years of the study.

Garden Warblers approached the speaker significantly more closely in 1980 than in 1978, when responding to Garden Warbler song (Appendix 6-1). No other differences between the responses of either species in either year are significant and hence the results for both years have been pooled in the present analysis.

#### B. Vocal behaviour of subjects during song playback experiments.

For present purposes only birds which moved towards the speaker during playback of a particular song are considered to have responded to it. However, when examining vocal behaviour the possibility must be considered that some individuals may respond (sensu latu) purely vocally to certain tapes without approaching the speaker. Accordingly results are presented below not only for those individuals which approached the speaker but also, in addition, for all individuals tested. Since only a small proportion of subjects did not approach the speaker, insufficient data is available to enable further separate consideration of the vocal behaviour of such birds.

In both species, vocal behaviour during song playback experiments was found to vary greatly between individuals. Some were clearly stimulated to sing by certain tapes and did so for a high rate for some time after the experiment had ended. Others were conspicuously silent even though a number of these approached the speaker closely and spent some time searching the vegetation near it. This variability results in the data showing few overall trends which are significant.

Table 6-6 illustrates the variability of vocal behaviour among the 19 Blackcaps and 19 Garden Warblers which were tested with both Blackcap and Garden Warbler songs. It uses the number of songs sung rather than the total time spent singing in comparing song output between different stages of the experiments since the latter information was only recorded during the 1980 experiments. Song duration is an unequivocal measure of song output, unlike the number of songs sung, since song lengths are variable. However,

TABLE 6-6. THE VOCAL BEHAVIOUR OF BIRDS PRESENTED WITH BOTH BLACKCAP (BC)  
AND GARDEN WARBLER (GW) SONG PLAYBACK

The table gives the number of subjects to which each of the behaviour categories stated applied.

A. BLACKCAP SUBJECTS (n = 19)

| BEHAVIOUR                                      | PLAYBACK<br>OF BC SONG | PLAYBACK<br>OF GW SONG | Number of subjects<br>in common |
|------------------------------------------------|------------------------|------------------------|---------------------------------|
| 1. Silent throughout playback                  | 4                      | 0                      | 0                               |
| 2. Silent before playback                      | 9                      | 6                      | 4                               |
| 3. Silent during playback                      | 6                      | 2                      | 0                               |
| 4. Silent after playback                       | 7                      | 7                      | 3                               |
| 5. Singing more during than<br>before playback | 8                      | 9                      | 4                               |
| 6. Singing more after than<br>during playback  | 10                     | 9                      | 5                               |
| 7. Singing more after than<br>before playback  | 8                      | 9                      | 2                               |

B. GARDEN WARBLER SUBJECTS (n = 19)

| BEHAVIOUR                                      | PLAYBACK<br>OF GW SONG | PLAYBACK<br>OF BC SONG | Number of subjects<br>in common |
|------------------------------------------------|------------------------|------------------------|---------------------------------|
| 1. Silent throughout playback                  | 0                      | 0                      | 0                               |
| 2. Silent before playback                      | 4                      | 3                      | 1                               |
| 3. Silent during playback                      | 2                      | 1                      | 0                               |
| 4. Silent after playback                       | 2                      | 3                      | 0                               |
| 5. Singing more during than<br>before playback | 9                      | 14                     | 7                               |
| 6. Singing more after than<br>during playback  | 11                     | 12                     | 8                               |
| 7. Singing more after than<br>before playback  | 5                      | 12                     | 3                               |

- NOTES
1. For both Blackcap and Garden Warbler subjects between-song comparisons within each of the behaviour categories show no significant differences (Chi-squared Test, Fisher Exact Test). However in Table B line 7 the difference is close to significance ( $\chi^2 = 3.83$ , d.f.=1).
  2. Song output was assessed on the number of songs sung.
  3. "Silent throughout playback" includes birds which did not sing at any time before, during or after the experiments.

for both species, the number of songs is highly significantly correlated with the total time spent singing (for Blackcaps  $r = 0.849$ ,  $p < 0.001$ , for Garden Warblers  $r = 0.883$ ,  $p < 0.001$ ,  $n = 93$  and 49 timed five minute periods respectively).

All Garden Warblers sang at some stage of all experiments. All Blackcaps sang during experiments with Garden Warbler song but when Blackcap song was presented four Blackcaps remained silent throughout the experiments. These four were among those silent during the five minutes before Blackcap song was presented. All four responded to the Blackcap song tape strongly nevertheless, three of them approaching within two metres of the speaker. On average, Blackcaps were not stimulated to sing more by either Blackcap or Garden Warbler song. About half elevated their song rate during presentation of either song (Table 6-6A; lines 5 - 7). The remainder reduced it, except for the four birds which were silent throughout Blackcap song playback. Garden Warbler song may have had a depressive effect on Garden Warblers since only five sang at a higher rate after than before its playback (Table 6-6B; line 7). Playback of Blackcap song elevated the song rate of a majority of Garden Warbler subjects (Table 6-6B; lines 5 - 7), although the difference is not significant.

On average, Blackcaps sang a similar number of songs during, before and after song playback, regardless of whether Blackcap or Garden Warbler song was presented (Table 6-7A). The number of songs sung by Garden Warblers before playback of Blackcap song was significantly lower than the number sung by them before playback of Garden Warbler song, presumably by chance (Table 6-7B). However, once experiments began Garden Warblers sang a similar number of songs on average regardless of whether Blackcap or Garden Warbler song was presented.

In comparison to the number of songs sung before playback began, Blackcaps sang significantly more songs after hearing Garden Warbler song, and Garden Warblers after hearing Blackcap song, but both sang similar

TABLE 6-7. THE NUMBER OF SONGS SUNG BY ALL SUBJECTS TESTED WITH BLACKCAP (BC)  
AND GARDEN WARBLER (GW) SONG PLAYBACK

Mean number of songs ( $\pm 1$  S.E.)

A. BLACKCAP SUBJECTS (n = 19)

|                 | Playback<br>of BC song | Playback<br>of GW song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 7.2 ( $\pm 2.3$ )      | 4.8 ( $\pm 1.4$ )      | n.s.                          |
| During playback | 6.9 ( $\pm 1.6$ )      | 7.1 ( $\pm 1.4$ )      | n.s.                          |
| After playback  | 8.2 ( $\pm 2.1$ )      | 7.9 ( $\pm 1.9$ )      | n.s.                          |

Comparisons of the number of songs sung before v during, during v after and before v after playback of each tape show that significantly more songs were sung after than before playback of Garden Warbler song ( $p < 0.01$ ). No other differences are significant.

B. GARDEN WARBLER SUBJECTS (n = 19)

|                 | Playback<br>of GW song | Playback<br>of BC song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 21.8 ( $\pm 4.0$ )     | 11.4 ( $\pm 3.0$ )     | $p < 0.05$                    |
| During playback | 16.8 ( $\pm 3.1$ )     | 19.3 ( $\pm 2.9$ )     | n.s.                          |
| After playback  | 20.7 ( $\pm 3.9$ )     | 21.6 ( $\pm 4.2$ )     | n.s.                          |

Comparisons of the number of songs sung before v during, during v after and before v after playback of each tape show that significantly more songs were sung after than before playback of Blackcap song ( $p < 0.05$ ). No other differences are significant.

NOTES 1. Statistical comparisons are by the Wilcoxon test (2-tailed).

2. Only results from experiments performed during the main part of the breeding season are included.



numbers in response to songs of conspecifics (Table 6-7). This difference could be due to the fact that the song output of both species before being presented with each other's songs happened to be lower than that on the occasion of experiments with conspecific songs since for both species the the number of songs sung after playback was similar irrespective of whether Blackcap song or Garden Warbler song was presented.

The total time spent singing during, before and after song playback is given in Table 6-8 for those subjects, all in 1980, for which the information was recorded. As with song number, within each of the three periods Blackcaps sang on average for a similar length of time irrespective of whether Blackcap song or Garden Warbler song was presented. The total song duration of Garden Warblers during the five minutes preceding playback of Garden Warbler song was significantly longer than that during the period preceding playback of Blackcap song (as in Table 6-7) but, again, once song playback commenced the song output of Garden Warblers presented with Garden Warbler song was not significantly different from that during presentation of Blackcap song. The total song duration of Blackcaps following playback of Blackcap song was significantly higher than their output during or before playback. Garden Warblers sang significantly more during than before playback of Blackcap song. No other changes in output were significant.

The number of songs sung by those birds which also approached the speaker are presented in Table 6-9, with the time spent singing by the same birds given in Table 6-10. For Blackcaps neither of these variables give significant differences when compared between treatments and between different stages of the experiments. As earlier noted, for Garden Warblers the number of songs sung before Blackcap song was presented was small, and this contrasts significantly with that during and after the encounter with the tape (Table 6-9B). The same trend is present, but not significant, when the total time spent singing by Garden Warblers hearing Blackcap song is considered (Table 6-10B).

TABLE 6-8. THE TOTAL TIME SPENT SINGING BY ALL SUBJECTS TESTED WITH BOTH BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG PLAYBACK

Mean total song durations ( $\pm 1$  S.E.). The maximum possible song output was 300s.

A. BLACKCAP SUBJECTS (n = 12)

|                 | Playback<br>of BC song | Playback<br>of GW song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 33.4 ( $\pm 17.2$ )    | 51.3 ( $\pm 23.5$ )    | n.s.                          |
| During playback | 25.9 ( $\pm 9.6$ )     | 32.6 ( $\pm 9.9$ )     | n.s.                          |
| After playback  | 46.7 ( $\pm 19.2$ )    | 34.1 ( $\pm 18.0$ )    | n.s.                          |

Comparisons of total song output before v during, during v after and before v after each tape show no significant differences when Garden Warbler song was presented but birds sang significantly more after than during Blackcap song playback ( $p < 0.05$ ) and significantly more after than before Blackcap song playback ( $p < 0.01$ ).

B. GARDEN WARBLER SUBJECTS (n = 8)

|                 | Playback<br>of GW song | Playback<br>of BC song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 81.3 ( $\pm 22.4$ )    | 32.3 ( $\pm 21.3$ )    | $p = 0.05$                    |
| During playback | 64.1 ( $\pm 24.8$ )    | 94.3 ( $\pm 26.2$ )    | n.s.                          |
| After playback  | 47.3 ( $\pm 22.2$ )    | 112.9 ( $\pm 32.2$ )   | n.s.                          |

Comparisons of total song output before v during, during v after and before v after each tape show no significant differences when Garden Warbler song was presented. Birds sang significantly more during than before playback of Blackcap song ( $p = 0.05$ ). No other differences are significant (This may seem anomalous when the mean outputs before and after playback of Blackcap song are examined; in this case four birds sang slightly less after than before playback and four sang very much more afterwards).

NOTES 1. Statistical comparisons are by the Wilcoxon test (2-tailed).

2. Only results from experiments performed during the main part of the breeding season in 1980 are included.

TABLE 6-9. THE NUMBER OF SONGS SUNG BY SUBJECTS WHICH RESPONDED TO BOTH BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG PLAYBACK

Mean number of songs ( $\pm 1$  S.E.)

A. RESPONSES OF BLACKCAP SUBJECTS (n = 11)

|                 | Playback<br>of BC song | Playback<br>of GW song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 6.2 ( $\pm 2.7$ )      | 4.6 ( $\pm 1.8$ )      | n.s.                          |
| During playback | 7.4 ( $\pm 2.2$ )      | 7.3 ( $\pm 2.0$ )      | n.s.                          |
| After playback  | 5.7 ( $\pm 2.5$ )      | 9.7 ( $\pm 3.6$ )      | n.s.                          |

Comparisons of the number of songs sung before v during, during v after and before v after playback of each tape show no significant differences.

B. RESPONSES OF GARDEN WARBLER SUBJECTS (n = 14)

|                 | Playback<br>of GW song | Playback<br>of BC song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 26.0 ( $\pm 4.4$ )     | 11.1 ( $\pm 4.0$ )     | $p < 0.01$                    |
| During playback | 18.5 ( $\pm 3.9$ )     | 20.6 ( $\pm 3.5$ )     | n.s.                          |
| After playback  | 21.4 ( $\pm 3.9$ )     | 27.0 ( $\pm 4.8$ )     | n.s.                          |

Comparisons of the number of songs sung before v during, during v after and before v after playback of Garden Warbler song show no significant differences. However subjects sang significantly more during than before ( $p < 0.05$ ), after than during ( $p < 0.01$ ) and after than before ( $p < 0.05$ ) playback when Blackcap song was presented.

NOTES 1. Statistical comparisons are by the Wilcoxon test (2-tailed).

2. Only results from experiments performed during the main part of the breeding season are included.

TABLE 6-10. THE TOTAL TIME SPENT SINGING BY SUBJECTS WHICH RESPONDED TO BOTH BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG PLAYBACK

Mean total song durations in seconds ( $\pm 1$  S.E.). The maximum possible song output was 300s.

A. RESPONSES OF BLACKCAP SUBJECTS (n = 11)

|                 | Playback<br>of BC song | Playback<br>of GW song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 36.5 ( $\pm 18.5$ )    | 55.9 ( $\pm 25.3$ )    | n.s.                          |
| During playback | 20.5 ( $\pm 8.6$ )     | 34.6 ( $\pm 10.6$ )    | n.s.                          |
| After playback  | 48.6 ( $\pm 20.2$ )    | 32.7 ( $\pm 18.2$ )    | n.s.                          |

Comparisons of total song output before v during, during v after and before v after playback show no significant differences when either tape is presented.

B. RESPONSES OF GARDEN WARBLER SUBJECTS (n = 6)

|                 | Playback<br>of BC song | Playback<br>of GW song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 98.7 ( $\pm 27.6$ )    | 36.5 ( $\pm 28.5$ )    | n.s.                          |
| During playback | 79.0 ( $\pm 30.8$ )    | 113.5 ( $\pm 30.0$ )   | n.s.                          |
| After playback  | 62.3 ( $\pm 27.1$ )    | 127.0 ( $\pm 38.7$ )   | n.s.                          |

Comparisons of total song output before v during, during v after and before v after playback show no significant differences when either tape is presented. The sample size is small, however, in comparison to that in Table 6-9B.

NOTES 1. Statistical comparisons are by the Wilcoxon test (2-tailed).

2. Only results from experiments performed during the main part of the breeding season in 1980 are included.

For Garden Warblers, there are no significant correlations between the numbers of songs sung before, during and after playback of Garden Warbler song and the numbers sung in the equivalent periods during presentation of Blackcap song (Table 6-11). Blackcap subjects differ in that those birds which were already singing at a high rate before presentation of one song also had a high song output on the occasions before the other song was presented. Similarly Blackcaps which tended to have a high song output after hearing Blackcap song also tended to have a high song output after hearing Garden Warbler song. As with Garden Warbler subjects, there was no correlation between the number of songs sung by Blackcaps during playback of Blackcap song and their output during playback of Garden Warbler song. These findings apply both to all the subjects tested with both Blackcap and Garden Warbler songs (Table 6-11A) and to that proportion which approached the speaker during presentation of both songs (Table 6-11B).

The numbers of songs sung during playback by those Blackcaps and Garden Warblers which approached the speaker in response to both songs were correlated with the Latency, Time and Distance scores of the same birds (Table 6-12). For Blackcaps, and for Garden Warblers responding to Garden Warbler song, none of these correlations are significant. Garden Warblers responding to Blackcap song show a significant negative correlation between their song outputs and response Latencies, and a significant positive correlation between their song output and Time scores, i.e. rapid responders and birds which spent a long time near the speaker tended to have high song outputs (Table 6-12A). Similar comparisons between Latency, Distance and Time scores and song outputs during the five minutes just after song playback give no significant correlations for either species (Table 6-12B).

In addition to songs, a number of subjects gave Tac-Tac calls during the experiments (Table 6-13). For each species a similar proportion of subjects gave such calls during playback of either song. Garden Warblers never gave more than a few calls; the maximum recorded was 40 given by one

TABLE 6-11. CORRELATIONS BETWEEN THE NUMBER OF SONGS SUNG BY BOTH SPECIES BEFORE, DURING AND AFTER PLAYBACK OF CONSPECIFIC SONG AND THE NUMBER OF SONGS SUNG BY THE SAME INDIVIDUALS BEFORE, DURING AND AFTER PLAYBACK OF EACH OTHER'S SONGS

Values given are of the correlation coefficient  $r$ .

A. RESULTS FROM ALL BIRDS TESTED

| Correlations between the<br>number of songs sung                   | BLACKCAP<br>SUBJECTS<br>$n = 19$ | GARDEN WARBLER<br>SUBJECTS<br>$n = 19$ |
|--------------------------------------------------------------------|----------------------------------|----------------------------------------|
| before Blackcap song and<br>before Garden Warbler song<br>playback | 0.746 $p < 0.001$                | 0.284 n.s.                             |
| during Blackcap song<br>and during Garden Warbler song<br>playback | -0.002 n.s.                      | 0.333 n.s.                             |
| after Blackcap song and<br>after Garden Warbler song<br>playback   | 0.663 $p < 0.01$                 | 0.166 n.s.                             |

B. RESULTS FROM SUBJECTS WHICH RESPONDED TO BOTH TAPES

| Correlations between the<br>number of songs sung                   | BLACKCAP<br>SUBJECTS<br>$n = 11$ | GARDEN WARBLER<br>SUBJECTS<br>$n = 14$ |
|--------------------------------------------------------------------|----------------------------------|----------------------------------------|
| before Blackcap song and<br>before Garden Warbler song<br>playback | 0.691 $p < 0.05$                 | 0.316 n.s.                             |
| during Blackcap song and<br>during Garden Warbler song<br>playback | 0.044 n.s.                       | 0.325 n.s.                             |
| after Blackcap song and<br>after Garden Warbler song<br>playback   | 0.850 $p < 0.001$                | 0.282 n.s.                             |

TABLE 6-12. CORRELATIONS BETWEEN THE LATENCY, DISTANCE AND TIME SCORES OF BLACKCAPS AND GARDEN WARBLERS WHICH RESPONDED TO BOTH BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG PLAYBACK AND THE NUMBER OF SONGS SUNG BY THEM DURING AND AFTER THE EXPERIMENTS

Values given are of the correlation coefficient r.

A. Correlations with song output DURING song playback experiments

| Song numbers<br>correlated with; | BLACKCAP SUBJECTS<br>n = 11 |                     | GARDEN WARBLER SUBJECTS<br>n = 14 |                     |          |
|----------------------------------|-----------------------------|---------------------|-----------------------------------|---------------------|----------|
|                                  | BC song<br>playback         | GW song<br>playback | GW song<br>playback               | BC song<br>playback |          |
| Latency                          | -0.051                      | -0.250              | -0.310                            | -0.761              | p < 0.01 |
| Distance                         | 0.383                       | -0.485              | 0.346                             | 0.293               |          |
| Time                             | -0.524                      | -0.077              | -0.353                            | 0.651               | p < 0.05 |

B. Correlations with song output AFTER song playback experiments

| Song numbers<br>correlated with; | BLACKCAP SUBJECTS<br>n = 11 |                     | GARDEN WARBLER SUBJECTS<br>n = 14 |                     |  |
|----------------------------------|-----------------------------|---------------------|-----------------------------------|---------------------|--|
|                                  | BC song<br>playback         | GW song<br>playback | GW song<br>playback               | BC song<br>playback |  |
| Latency                          | 0.362                       | 0.304               | 0.008                             | -0.397              |  |
| Distance                         | -0.303                      | 0.230               | 0.404                             | 0.230               |  |
| Time                             | -0.042                      | 0.031               | -0.438                            | 0.453               |  |

NOTE With the two exceptions indicated, none of the correlations are significant.

TABLE 6-13. THE NUMBERS OF SUBJECTS WHICH GAVE TAC-TAC CALLS DURING SONG  
PLAYBACK EXPERIMENTS

|                                                                   | BLACKCAP<br>SUBJECTS<br>n = 19 | GARDEN WARBLER<br>SUBJECTS<br>n = 19 |
|-------------------------------------------------------------------|--------------------------------|--------------------------------------|
| The number which called<br>during Blackcap song<br>playback       | 6                              | 5                                    |
| The number which called<br>during Garden Warbler<br>song playback | 11                             | 4                                    |
| The number which called<br>during playback of both<br>songs       | 5                              | 1                                    |

- NOTES
1. Results are given for all the subjects tested, during the main part of the breeding season.
  2. "During" playback is taken here as the period during which the tape was played and the five minute period immediately after its broadcast combined.
  3. For both species the proportion of birds which called does not differ significantly between the presentations of either song. The proportion of birds which called during playback of conspecific song and during that of non-conspecific song does not differ significantly between the two species. (Chi-squared test,  $p > 0.05$  in each case.) .



male in the five minutes following playback of Garden Warbler song. Blackcaps usually gave only a few tacs but one male called over 100 times following playback of Garden Warbler song and three others called at a similar high rate following playback of Blackcap song. For Blackcaps, but not Garden Warblers, those birds which called in response to conspecific song also tended to do so in response to the other tape.

C. The comparative responsiveness to song playback of Blackcaps and Garden Warblers

Are Blackcaps more or less aggressive in their responses to song playback than Garden Warblers are, or is there no difference? On average, the strongest responses to either Blackcap or Garden Warbler song are given by the birds which have not been exposed previously to song playback (see Appendix 6-2). Table 6-14A makes between-species comparisons of responses given by subjects for whom either Blackcap or Garden Warbler song was the very first tape presented. Table 6-14B makes similar comparisons between responses of the larger sample of subjects whose encounter with either Blackcap or Garden Warbler song playback was not preceded by a response to another tape. Table 6-14B thus includes all the subjects of Table 6-14A as well as others which had been tested with tapes such as the Great Tit song, to which they had not responded. These "naive" subjects are considered in making the between-species comparisons since they provide the closest approximations in the available data to "pure responses", uninfluenced at least by past experiences with song playback.

Blackcaps and Garden Warblers respond similarly strongly to the songs of conspecifics. Responses of Blackcaps to Garden Warbler song average stronger than those of Garden Warblers to Blackcap song, and the difference is significant where the closest distances of approach to the speaker are compared. The trend is therefore for Blackcaps to be more interspecifically aggressive than Garden Warblers.

TABLE 6-14. THE COMPARATIVE RESPONSIVENESS TO SONG PLAYBACK OF BLACKCAP (BC)  
AND GARDEN WARBLER (GW) SUBJECTS

A. Comparisons between responses to the first tape encountered by  
subjects, when this was either Blackcap song or Garden Warbler song

|                   | Responses of BC<br>subjects | Responses of GW<br>subjects |
|-------------------|-----------------------------|-----------------------------|
| LATENCY (OWN) s.  | 84.9 ( $\pm$ 18.9), n = 9   | 105.5 ( $\pm$ 31.4), n = 6  |
| DISTANCE (OWN) m. | 1.7 ( $\pm$ 0.3), n = 9     | 2.8 ( $\pm$ 0.9), n = 6     |
| TIME (OWN) s.     | 156.3 ( $\pm$ 21.1), n = 9  | 162.0 ( $\pm$ 40.8), n = 6  |
| LATENCY (OTH) s.  | 127.4 ( $\pm$ 28.1), n = 8  | 121.6 ( $\pm$ 30.4), n = 9  |
| DISTANCE (OTH) m. | 3.0 ( $\pm$ 1.3), n = 8     | 7.8 ( $\pm$ 1.4), n = 9     |
| TIME (OTH) s.     | 123.9 ( $\pm$ 20.6), n = 8  | 102.2 ( $\pm$ 22.7), n = 9  |

B. Comparisons between responses of subjects whose response to Blackcap  
or Garden Warbler song was not preceded by a RESPONSE to another tape

|                   | Responses of BC<br>subjects | Responses of GW<br>subjects |
|-------------------|-----------------------------|-----------------------------|
| LATENCY (OWN) s.  | 92.0 ( $\pm$ 13.7), n = 14  | 88.8 ( $\pm$ 21.6), n = 12  |
| DISTANCE (OWN) m. | 3.0 ( $\pm$ 0.7), n = 14    | 4.2 ( $\pm$ 1.5), n = 12    |
| TIME (OWN) s.     | 145.2 ( $\pm$ 19.7), n = 14 | 139.9 ( $\pm$ 30.9), n = 12 |
| LATENCY (OTH) s.  | 112.6 ( $\pm$ 20.1), n = 14 | 107.9 ( $\pm$ 26.3), n = 11 |
| DISTANCE (OTH) m. | 2.5 ( $\pm$ 0.8), n = 14    | 7.5 ( $\pm$ 1.3), n = 11    |
| TIME (OTH) s.     | 141.5 ( $\pm$ 18.6), n = 14 | 128.7 ( $\pm$ 25.6), n = 11 |

NOTES. 1. Mean responses ( $\pm$  1 S.E.) are given.

2. Latency (own) and Latency (oth) are latency to own-species song playback and latency to the song of the other species, etc.

3. Only Distance (oth) values are significantly different between Blackcap and Garden Warbler subjects (Mann-Whitney U test, 2-tailed,  $p < 0.02$ , in both tables A & B).

D. Responses by Blackcaps to two different types of Garden Warbler song.

In 1979 twelve Blackcaps were presented with two different five minute tapes of Garden Warbler song. The tapes represented extremes of the normal territorial advertising songs of Garden Warblers. One tape (Long song) consisted of long songs with only short intervening pauses, the total singing time being 250 seconds (out of the possible 300). The other tape (Short song) included brief, well-separated songs, the total singing time being 147 seconds. Both were made up from 100 second long bursts of spontaneous singing with natural intervals between songs, each burst repeated three times to achieve the required tape duration. The experiment tested whether Blackcaps discriminate between two very different Garden Warbler songs. Half the subjects received long song and half short song on their first exposure to song playback. The second tape was usually presented the following morning, although in some cases bad weather caused a delay of several days.

Both songs evoked strong responses but these were not significantly different between the two sets of data (Table 6-15). Two subjects did not respond to long song and three did not do so to short song. The individuals were different in both sets of cases i.e. all subjects responded to at least one of the two tapes. In every case the non-responders were birds who were being presented with their second exposure to song playback. All responded to a Garden Warbler song, irrespective of whether it was long or short, if it was the first song they heard. This finding prompted an analysis of the effect of sequence of presentation of tapes on the magnitude of the responses observed (Appendix 6-2). The number of songs sung (Table 6-16) and their duration (Table 6-17) during and after exposure of birds to either tape were not significantly different between the two treatments. Once again, as with other playback experiments, some subjects responded by singing long and vigorously, others equally-strikingly ceased singing and various intermediate responses were noted. Three birds gave tac-tac calls during playback of long song and two during playback of short song.

TABLE 6-15. THE RESPONSE PARAMETERS OF BLACKCAPS WHICH RESPONDED TO  
PLAYBACK OF LONG AND SHORT GARDEN WARBLER SONGS

Mean responses ( $\pm 1$  S.E.).

|              | Responses to<br>LONG song<br>n = 9 | Responses to<br>SHORT song<br>n = 10 |
|--------------|------------------------------------|--------------------------------------|
| LATENCY (s)  | 69.8 ( $\pm 27.4$ )                | 89.2 ( $\pm 23.3$ )                  |
| DISTANCE (m) | 12.0 ( $\pm 3.9$ )                 | 8.3 ( $\pm 3.7$ )                    |
| TIME (s)     | 111.0 ( $\pm 34.5$ )               | 131.3 ( $\pm 39.5$ )                 |

The Latency, Distance and Time values are not significantly different between the two experimental songs (Mann-Whitney U test, 2-tailed,  $p > 0.05$ ).

TABLE 6-16. THE NUMBER OF SONGS SUNG BY BLACKCAPS TESTED WITH  
PLAYBACK OF LONG AND SHORT GARDEN WARBLER SONGS

Mean number of songs ( $\pm 1$  S.E.).

A. RESULTS FROM ALL BIRDS TESTED     $n = 12$

|                 | Playback of<br>LONG song | Playback of<br>SHORT song | Comparisons<br>within periods |
|-----------------|--------------------------|---------------------------|-------------------------------|
| Before playback | 6.6 ( $\pm 2.3$ )        | 10.5 ( $\pm 2.9$ )        | n.s.                          |
| During playback | 10.0 ( $\pm 3.1$ )       | 9.2 ( $\pm 2.7$ )         | n.s.                          |
| After playback  | 8.9 ( $\pm 3.0$ )        | 9.4 ( $\pm 3.2$ )         | n.s.                          |

B. RESULTS ONLY FROM SUBJECTS WHICH RESPONDED

|                 | Playback of<br>LONG song<br>$n = 10$ | Playback of<br>SHORT song<br>$n = 9$ | Comparisons<br>within periods |
|-----------------|--------------------------------------|--------------------------------------|-------------------------------|
| Before playback | 7.0 ( $\pm 2.7$ )                    | 10.2 ( $\pm 3.3$ )                   | n.s.                          |
| During playback | 11.8 ( $\pm 3.4$ )                   | 10.0 ( $\pm 3.1$ )                   | n.s.                          |
| After playback  | 10.3 ( $\pm 3.5$ )                   | 12.2 ( $\pm 3.9$ )                   | n.s.                          |

In both tables A & B comparisons of the number of songs sung before v during, during v after and before v after playback show no significant differences either when long song or short song was presented.

NOTE Statistical comparisons are by the Wilcoxon test (2-tailed) except for the within-period comparisons in Table B, where the Mann-Whitney U test was used since the two sample sizes were different.

TABLE 6-17. THE TOTAL TIME SPENT SINGING BY BLACKCAPS TESTED WITH  
PLAYBACK OF LONG AND SHORT GARDEN WARBLER SONGS

Mean total song durations in seconds ( $\pm 1$  S.E.). The maximum possible song output was 300s.

A. RESULTS FROM ALL BIRDS TESTED     $n = 12$

|                 | Playback of<br>LONG song | Playback of<br>SHORT song | Comparisons<br>within periods |
|-----------------|--------------------------|---------------------------|-------------------------------|
| Before playback | 30.1 ( $\pm 11.9$ )      | 46.8 ( $\pm 15.1$ )       | n.s.                          |
| During playback | 38.7 ( $\pm 15.1$ )      | 30.0 ( $\pm 10.3$ )       | n.s.                          |
| After playback  | 36.1 ( $\pm 13.6$ )      | 41.9 ( $\pm 16.1$ )       | n.s.                          |

B. RESULTS ONLY FROM SUBJECTS WHICH RESPONDED

|                 | Playback of<br>LONG song<br>$n = 10$ | Playback of<br>SHORT song<br>$n = 9$ | Comparisons<br>within periods |
|-----------------|--------------------------------------|--------------------------------------|-------------------------------|
| Before playback | 33.7 ( $\pm 13.9$ )                  | 46.2 ( $\pm 17.0$ )                  | n.s.                          |
| During playback | 45.6 ( $\pm 17.3$ )                  | 33.6 ( $\pm 12.6$ )                  | n.s.                          |
| After playback  | 42.6 ( $\pm 15.6$ )                  | 55.1 ( $\pm 19.7$ )                  | n.s.                          |

In both Tables A & B comparisons of total song output before v during, during v after and before v after playback show no significant differences either when long song or short song was presented.

NOTE Statistical comparisons are by the Wilcoxon test (2-tailed) except for the within-period comparisons in Table B, where the Mann-Whitney U test was used since the two sample sizes were different.

### 6.6.2. Responses to song playback late in the breeding season

The numbers of subjects which approached the speaker during experiments conducted in late June and July 1978 are given in Table 6-18. No birds responded to the Great Tit control tapes.

A similar proportion of Blackcap subjects responded to both Blackcap and Garden Warbler tapes but in comparison to the results of experiments performed at the height of the breeding season the proportion of non-responders was high. The difference in the proportion of responders to non-responders is not significant between the late-season and early-season experiments for Blackcaps responding to Blackcap song but significantly fewer Blackcaps responded to Garden Warbler song late in the season. The subject which had been tested earlier in the season responded to neither song (it had only responded to Blackcap song during the earlier experiments). The other non-responders consisted of two believed long-established but hitherto untested birds, which responded to neither song, and one recent arrival which responded only to Blackcap song.

Of the five Garden Warblers tested, four responded to neither Blackcap nor Garden Warbler song. Three of these four had responded to both songs during the earlier experiments so their failure to respond can be explained by habituation or a seasonal decline in responsiveness, although the latter seems more likely. The fifth subject responded strongly to Garden Warbler song playback only, although no songs were heard and it was not definitely established that the responder was the territory holder. The responsiveness of Garden Warblers to both Blackcap and Garden Warbler songs was significantly very much weaker during the late-season experiments than earlier in the year. Clearly little territorial defence was being practised by Garden Warblers at the time; most had already fledged their young, although one subject (which gave no responses) still had pulli in the nest. The greater responsiveness of Blackcap subjects, and the observation that more Blackcaps than Garden Warblers were defending

TABLE 6-18. THE NUMBERS OF BLACKCAPS AND GARDEN WARBLERS WHICH RESPONDED TO PLAYBACK OF BLACKCAP, GARDEN WARBLER AND GREAT TIT SONG DURING EXPERIMENTS IN LATE JUNE AND EARLY JULY 1978

|                            | SONG PRESENTED |                   |                   |
|----------------------------|----------------|-------------------|-------------------|
|                            | 1. Blackcap    | 2. Garden Warbler | 3. Great Tit      |
| BLACKCAP SUBJECTS          | 6/9            | 5/9               | 0/7               |
| Between-column comparisons | 1 v 2<br>n.s.  | 1 v 3<br>p < 0.05 | 2 v 3<br>p < 0.05 |

|                            | SONG PRESENTED |                   |               |
|----------------------------|----------------|-------------------|---------------|
|                            | 1. Blackcap    | 2. Garden Warbler | 3. Great Tit  |
| GARDEN WARBLER SUBJECTS    | 0/5            | 1/5               | 0/5           |
| Between-column comparisons | 1 v 2<br>n.s.  | 1 v 3<br>n.s.     | 2 v 3<br>n.s. |

Comparisons with Table 6-3 show that for Blackcap subjects the proportions of responders to non-responders do not differ significantly between late-season and earlier experiments with Blackcap song but late-season experiments with Garden Warbler song produced significantly fewer responses than the earlier experiments ( $p < 0.05$ ). Significantly more Garden Warbler subjects responded to both Garden Warbler song ( $p < 0.001$ ) and Blackcap song ( $p < 0.01$ ) during the experiments conducted earlier in the season than in the later series.

- NOTES
1. Statistical comparisons are by the Fisher Exact test.
  2. The numbers which responded are given as a fraction of the total number of subjects tested.



territories in late June and July, reflects the fact that Blackcaps have a longer breeding season than Garden Warblers, with a higher proportion of the former raising two broods (Chapter 2).

#### A. Movements of late-season subjects during song playback.

This data (and that on vocal behaviour) is presented for Blackcap subjects only (since only they included a high proportion of responders) and is compared with that for Blackcaps tested earlier in the same season (Table 6-19). Although fewer subjects responded late in the season, the responses to Blackcap song of those which did so were as strong as those obtained from birds responding earlier in the season. However, in response to Garden Warbler song birds did not approach the speaker so closely nor for so long a period as they did in the earlier experiments. Latencies of response to Garden Warbler song were not significantly different between the early and late-season experiments.

#### B. Vocal behaviour of late-season subjects.

The total time spent singing by the Blackcaps tested with Blackcap song and Garden Warbler song during June and July 1978 did not differ significantly between presentations of either song or between the three stages of the experiments (Table 6-20A). The average song output of all birds tested was much lower than occurred earlier in the season (c.f. Table 6-8A) and this was conspicuous in the field. As in the earlier experiments, subjects had to be seen or heard before playback was presented but locating birds was comparatively difficult since many were only singing sporadically.

The song outputs of those late-season subjects which did respond to playback (Table 6-20B) were similar to those of responsive early-season subjects (Table 6-10A) once song playback started, although the sample is too small to warrant statistical analysis. Song outputs of responsive late-season Blackcaps were low before playback started; all

TABLE 6-19. THE RESPONSE PARAMETERS OF BLACKCAPS WHICH RESPONDED TO BOTH BLACKCAP AND GARDEN WARBLER SONG PLAYBACK DURING LATE JUNE/JULY 1978 COMPARED WITH THOSE OF BLACKCAPS TESTED WITH THE SAME SONGS EARLIER IN THE SEASON Mean responses ( $\pm 1$  S.E.).

A. RESPONSES TO BLACKCAP SONG

|              | During<br>27 APR - 29 MAY<br>n = 9 | During<br>27 JUN - 14 JUL<br>n = 6 | Between-period<br>comparisons |
|--------------|------------------------------------|------------------------------------|-------------------------------|
| LATENCY (s)  | 94.8 ( $\pm 17.6$ )                | 103.7 ( $\pm 20.7$ )               | n.s.                          |
| DISTANCE (m) | 4.1 ( $\pm 1.3$ )                  | 1.3 ( $\pm 0.3$ )                  | n.s.                          |
| TIME (s)     | 123.8 ( $\pm 26.1$ )               | 133.8 ( $\pm 28.4$ )               | n.s.                          |

B. RESPONSES TO GARDEN WARBLER SONG

|              | During<br>27 APR - 29 MAY<br>n = 8 | During<br>27 JUN - 14 JUL<br>n = 5 | Between-period<br>comparisons |
|--------------|------------------------------------|------------------------------------|-------------------------------|
| LATENCY (s)  | 157.9 ( $\pm 35.8$ )               | 156.0 ( $\pm 40.4$ )               | n.s.                          |
| DISTANCE (m) | 5.9 ( $\pm 1.2$ )                  | 20.4 ( $\pm 5.0$ )                 | p = 0.01                      |
| TIME (s)     | 91.5 ( $\pm 29.9$ )                | 37.2 ( $\pm 37.2$ )                | p < 0.01                      |

NOTE Statistical comparisons are by the Mann-Whitney U test.

TABLE 6-20. THE TOTAL TIME SPENT SINGING BY BLACKCAPS TESTED WITH BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG PLAYBACK DURING LATE JUNE/ JULY 1978

Mean total song durations in seconds ( $\pm 1$  S.E.). The maximum possible song output was 300s.

A. RESULTS FROM ALL BIRDS TESTED (n = 9)

|                 | Playback<br>of BC song | Playback<br>of GW song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 8.9 ( $\pm 6.5$ )      | 10.6 ( $\pm 4.8$ )     | n.s.                          |
| During playback | 19.0 ( $\pm 7.3$ )     | 15.9 ( $\pm 6.2$ )     | n.s.                          |
| After playback  | 25.1 ( $\pm 10.1$ )    | 19.4 ( $\pm 8.6$ )     | n.s.                          |

Comparisons of total song output before v during, during v after and before v after each tape show no significant differences when either Blackcap song or Garden Warbler song was presented.

NOTE Statistical comparisons are by the Wilcoxon test (2-tailed).

B. RESULTS ONLY FROM SUBJECTS WHICH RESPONDED (n = 5)

|                 | Playback<br>of BC song | Playback<br>of GW song |
|-----------------|------------------------|------------------------|
| Before playback | 11.2 ( $\pm 5.0$ )     | 17.4 ( $\pm 7.2$ )     |
| During playback | 32.4 ( $\pm 9.6$ )     | 27.2 ( $\pm 8.1$ )     |
| After playback  | 35.6 ( $\pm 15.5$ )    | 33.6 ( $\pm 12.2$ )    |

of the five increased their song output (four of them from zero) in response to Blackcap song and three of them did so (two of them from zero) in response to Garden Warbler song. This suggests that provided natural song output is low, song playback has a stimulatory effect on song of Blackcap subjects. Early in the season, when natural vocal activity is high, there is not the same opportunity to detect whether or not song playback stimulates vocal behaviour and this probably partly explains why no such trend is visible in the results from the early-season experiments (Tables 6-7 to 6-10).

#### 6.6.3. Responses to Lesser Whitethroat and Whitethroat song.

With the exception of Blackcaps tested with Whitethroat song, few subjects were tested with these two tapes and so the results must be regarded as preliminary. The available data does not warrant as full an analysis as in the preceding sections.

Seven Blackcaps were tested with Lesser Whitethroat song but only one responded. It approached closely and was present near the speaker for 173 seconds, in company with its presumed mate. However, the birds spent most of this time foraging, raising the possibility that their presence near the speaker was a coincidence. The seven were tested with Garden Warbler song and six responded very strongly, approaching within two metres of the speaker. The seventh male did not respond to Garden Warbler song (or Lesser Whitethroat song) but its mate approached the speaker very closely. It was later found that this seventh male was engaged in fighting a neighbouring Blackcap at the time that Garden Warbler song was presented, so it is possible that it would otherwise have accompanied its mate. Similarly, of six Garden Warblers tested with Lesser Whitethroat song, five gave no response. The sixth responded briefly, spending only five seconds at a point four metres from the speaker, and then withdrawing completely. Five of the six were also tested with Garden Warbler song and four of them with Blackcap song as well; all responded to both songs. In general, Lesser

Whitethroat song does not appear to provoke a response from either Blackcaps or Garden Warblers.

Six Garden Warblers were tested with Whitethroat song and five did not respond. The sixth responded so rapidly (latency seven seconds) that it clearly must have approached the vicinity of the speaker before playback began. Five of the six were also tested with Garden Warbler song and four of them with Blackcap song. All of them responded to Garden Warbler song but two did not do so to Blackcap song. The lack of response by Garden Warblers to Lesser Whitethroat or Whitethroat song, and of Blackcaps to Lesser Whitethroat song, contrasts with the results obtained when Whitethroat song was presented to Blackcaps. Eleven out of fifteen Blackcaps tested responded to Whitethroat song and all responded to Blackcap song. Twelve of the same subjects were also tested with Garden Warbler song and eleven of them responded, including three of the four which gave no response to Whitethroat song (the fourth responded to neither Garden Warbler nor Whitethroat song and only very weakly to Blackcap song). These results are summarised in Table 6-21.

Blackcaps responded to Whitethroat song just as rapidly as to Blackcap song but the latter attracted birds significantly closer to the speaker and they stayed near it significantly longer than for presentations of Whitethroat song (Table 6-22A). This contrasts with the results in Table 6-4A, which show that when Garden Warbler song is presented to Blackcaps the responses obtained do not differ significantly in any respects from those given to Blackcap song.

The comparative responsiveness of Blackcaps to Garden Warbler song and to Whitethroat song is best examined using results from individuals tested with both. Eight of the birds which responded to Whitethroat song also responded to Garden Warbler song (and to Blackcap song). Their latency scores are similar in response to all three tapes but otherwise the responses to Garden Warbler and Whitethroat song are weaker than those

TABLE 6-21. THE NUMBERS OF BLACKCAPS AND GARDEN WARBLERS WHICH RESPONDED TO PLAYBACK OF THE FOUR DIFFERENT SYLVIA SONGS

A. BLACKCAP SUBJECTS

| SONG PRESENTED             |                   |                    |                       |
|----------------------------|-------------------|--------------------|-----------------------|
| 1. Blackcap                | 2. Garden Warbler | 3. Whitethroat     | 4. Lesser Whitethroat |
| 15/15                      | 17/19             | 11/15              | 1/7                   |
| Between-column comparisons | 1 v 2<br>n.s.     | 1 v 3<br>p < 0.05  | 1 v 4<br>p < 0.001    |
|                            | 2 v 3<br>n.s.     | 2 v 4<br>p < 0.001 | 3 v 4<br>p = 0.016    |

B. GARDEN WARBLER SUBJECTS

| SONG PRESENTED             |               |                    |                       |
|----------------------------|---------------|--------------------|-----------------------|
| 1. Garden Warbler          | 2. Blackcap   | 3. Whitethroat     | 4. Lesser Whitethroat |
| 11/11                      | 7/10          | 1/6                | 1/6                   |
| Between-column comparisons | 1 v 2<br>n.s. | 1 v 3<br>p < 0.001 | 1 v 4<br>p < 0.001    |
|                            | 2 v 3<br>n.s. | 2 v 4<br>n.s.      | 3 v 4<br>n.s.         |

- NOTES
1. The pairwise comparisons are of the relative numbers of responders to non-responders, by Fisher Exact test.
  2. The numbers which responded are given as a fraction of the total number of subjects tested.
  3. The results presented are all from experiments carried out in 1980, since the two whitethroat songs were only presented in that year.

TABLE 6-22. THE RESPONSE PARAMETERS OF BLACKCAPS WHICH RESPONDED TO  
PLAYBACK OF WHITETHROAT SONG

Mean responses ( $\pm 1$  S.E.).

A. The responses of subjects which responded to both Blackcap (BC)  
and Whitethroat (WH) song playback (n = 11)

|              | Playback<br>of BC song | Playback<br>of WH song | Comparisons<br>within periods |
|--------------|------------------------|------------------------|-------------------------------|
| LATENCY (s)  | 86.8 ( $\pm 18.3$ )    | 90.6 ( $\pm 24.2$ )    | n.s.                          |
| DISTANCE (m) | 1.2 ( $\pm 0.2$ )      | 5.5 ( $\pm 0.8$ )      | $p < 0.01$                    |
| TIME (s)     | 169.4 ( $\pm 24.0$ )   | 87.7 ( $\pm 16.4$ )    | $p < 0.01$                    |

B. The responses of subjects which responded to Blackcap (BC),  
Garden Warbler (GW) and Whitethroat song playback (n = 8)

|              | Playback<br>of BC song | Playback<br>of GW song | Playback<br>of WH song |
|--------------|------------------------|------------------------|------------------------|
| LATENCY (s)  | 89.5 ( $\pm 22.5$ )    | 91.0 ( $\pm 21.5$ )    | 79.4 ( $\pm 26.4$ )    |
| DISTANCE (m) | 1.0 ( $\pm 0.2$ )      | 6.0 ( $\pm 1.6$ )      | 4.8 ( $\pm 0.8$ )      |
| TIME (s)     | 164.4 ( $\pm 23.4$ )   | 93.4 ( $\pm 31.6$ )    | 83.5 ( $\pm 16.2$ )    |

All possible pairwise comparisons of the data in Table B were made. Latencies of response to all three songs do not differ significantly. Birds approached the speaker significantly more closely in response to Blackcap song than in response to either Garden Warbler song ( $p < 0.01$ ) or Whitethroat song ( $p < 0.01$ ) and they spent significantly longer near the speaker when Blackcap song was presented than when either Garden Warbler song ( $p < 0.05$ ) or Whitethroat song ( $p < 0.01$ ) was presented. None of the three response parameters differs significantly between responses to Garden Warbler and Whitethroat songs.

NOTE Statistical comparisons are by the Wilcoxon test (2-tailed).

to Blackcap song (Table 6-22B). However, Table 6-22B can not be used to assert that Blackcap responses to Whitethroat song and Garden Warbler song are of similar intensity, and weaker than those to Blackcap song, because presentation of Garden Warbler song was not originally a planned feature of the playback experiments which tested Blackcaps with Blackcap and Whitethroat song. As a result, as many as seven of the twelve birds tested with Garden Warbler song received that song as a third presentation, after those of Blackcap song and Whitethroat song. The sequence of presentation of tapes may affect the results obtained (Appendix 6-2) and so there are grounds for believing that the response to Garden Warbler song of the eight Blackcaps which responded to all three songs may average weaker than would have been the case had the order of presentation of the three tapes been properly balanced, as in all the other song playback experiments performed. In an attempt to establish whether the responses to Garden Warbler song summarised in Table 6-22B were comparatively weak as a result of the deficiency in experimental design, the responses of Blackcaps receiving their first encounter with song playback in 1980 were compared (Table 6-23). Blackcap song was encountered first by five birds and Garden Warbler song by six birds, all of which responded to the respective songs. Whitethroat song was encountered first by six birds, three of which did not respond to it. As expected, the responses to Blackcap and to Garden Warbler song (and to Whitethroat song by the three birds which did respond) do not differ significantly.

To summarise, most Blackcaps respond to Whitethroat song, although significantly fewer do so than is the case with Garden Warbler song. The response Latencies to all three songs do not differ significantly but responses to Whitethroat song are significantly weaker than those to Blackcap song when Distance and Time scores are considered. In contrast, responses to Garden Warbler song do not differ significantly from those to Blackcap song.



TABLE 6-23. THE RESPONSES OF BLACKCAP SUBJECTS TO THE FIRST EXPERIMENTAL TAPES WHICH THEY ENCOUNTERED, IN 1980

A. The number of subjects which responded

| SONG PRESENTED |                |             |
|----------------|----------------|-------------|
| Blackcap       | Garden Warbler | Whitethroat |
| 5/5            | 6/6            | 3/6         |

The numbers which responded are given as a fraction of the total number of subjects tested.

B. The response parameters of those Blackcaps which responded to Blackcap (BC), Garden Warbler (GW) or Whitethroat (WH) song playback      Mean responses ( $\pm 1$  S.E.).

|              | Playback<br>of BC song | Playback<br>of GW song | Playback<br>of WH song |
|--------------|------------------------|------------------------|------------------------|
| LATENCY (s)  | 84.8 ( $\pm 26.1$ )    | 117.7 ( $\pm 23.8$ )   | 122.3 ( $\pm 61.6$ )   |
| DISTANCE (m) | 1.7 ( $\pm 0.4$ )      | 2.4 ( $\pm 1.6$ )      | 7.7 ( $\pm 1.5$ )      |
| TIME (s)     | 147.6 ( $\pm 34.3$ )   | 148.3 ( $\pm 28.3$ )   | 122.3 ( $\pm 27.4$ )   |

Blackcaps responding to Blackcap song approached the speaker significantly more closely than those responding to Whitethroat song ( $p < 0.05$ ). None of the other possible pairwise comparisons reveals significant differences.

NOTE Statistical comparisons are by the Mann-Whitney U test (2-tailed)

Vocal responses of Blackcaps to Whitethroat song and to Blackcap song are compared in Table 6-24. The mean song output after Blackcap song playback was high in comparison to that after Whitethroat song playback and the two sets of data are significantly different, but only when all the subjects tested are considered. Playback of Whitethroat song had no effect on the mean song output of subjects but Blackcap song caused subjects to sing significantly more after playback than either before or during it. All subjects sang during presentation of Whitethroat song but five remained silent when Blackcap song was presented, although all of the latter approached the speaker closely and otherwise responded strongly to the tape.

Tac-Tac calls occurred more frequently during experiments with Whitethroat song than with Blackcap song. Seven birds called during or immediately after playback of Whitethroat song and four did so when Blackcap song was presented. The difference in proportions is not significant ( $\chi^2 = 0.5$ ,  $p > 0.05$ , 1 d.f.).

#### 6.6.4. Responsiveness to song playback of Blackcaps and Garden Warblers holding territories in different habitats

The territories in the study areas can be divided into two main categories, scrub and woodland (Chapter 2). Table 6-25 compares the numbers of subjects which responded to song playback in woodland and in scrub. The Blackcaps which did not respond to Blackcap and/or Garden Warbler song were all holders of woodland territories. All Garden Warblers responded to Garden Warbler song but all six which did not respond to Blackcap song were holders of scrub territories. The proportions of responders to non-responders do not differ significantly in any of the comparisons made but the numbers of scrub Blackcaps and woodland Garden Warblers tested were small. Possibly Blackcaps and Garden Warblers in the two types of habitats differ in responsiveness to song playback and further experiments are needed to establish this.

All Blackcaps tested with Lesser Whitethroat song were in

TABLE 6-24. THE TOTAL TIME SPENT SINGING BY BLACKCAPS TESTED WITH BOTH BLACKCAP (BC) AND WHITETHROAT (WH) SONG PLAYBACK

Mean total song durations in seconds ( $\pm 1$  S.E.). The maximum possible song output was 300s.

A. RESULTS FROM ALL BIRDS TESTED (n = 15)

|                 | Playback<br>of BC song | Playback<br>of WH song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 27.0 ( $\pm 14.0$ )    | 11.5 ( $\pm 4.6$ )     | n.s.                          |
| During playback | 24.2 ( $\pm 7.7$ )     | 18.5 ( $\pm 3.9$ )     | n.s.                          |
| After playback  | 55.7 ( $\pm 16.7$ )    | 17.7 ( $\pm 3.9$ )     | p = 0.05                      |

Comparisons of total song output before v during, during v after and before v after each tape show that birds sang significantly more after playback of Blackcap song than both during and before playback ( $p < 0.01$  in both cases). On average, song output was uniform during all stages of the experiments with Whitethroat song playback.

B. RESULTS ONLY FROM SUBJECTS WHICH RESPONDED TO BOTH SONGS (n = 11)

|                 | Playback<br>of BC song | Playback<br>of WH song | Comparisons<br>within periods |
|-----------------|------------------------|------------------------|-------------------------------|
| Before playback | 35.6 ( $\pm 18.6$ )    | 10.5 ( $\pm 5.5$ )     | n.s.                          |
| During playback | 19.9 ( $\pm 7.5$ )     | 21.2 ( $\pm 9.8$ )     | n.s.                          |
| After playback  | 57.5 ( $\pm 20.3$ )    | 17.7 ( $\pm 9.1$ )     | n.s.                          |

Comparisons of total song output before v during, during v after and before v after each tape show that birds sang significantly more after playback of Blackcap song than both during playback ( $p < 0.05$ ) and after playback ( $p < 0.02$ ). On average, song output was uniform during all stages of the experiments with Whitethroat song playback.

TABLE 6-25. THE NUMBERS OF BLACKCAPS AND GARDEN WARBLERS WHICH RESPONDED TO PLAYBACK OF BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG COMPARED BETWEEN HOLDERS OF WOODLAND AND SCRUB TERRITORIES

A. BLACKCAP SUBJECTS

| Playback<br>of BC song |         | Playback<br>of GW song |         |
|------------------------|---------|------------------------|---------|
| Woodland               | Scrub   | Woodland               | Scrub   |
| 17/<br>21              | 8/<br>8 | 32/<br>34              | 6/<br>6 |

B. GARDEN WARBLER SUBJECTS

| Playback<br>of GW song |           | Playback<br>of BC song |           |
|------------------------|-----------|------------------------|-----------|
| Woodland               | Scrub     | Woodland               | Scrub     |
| 8/<br>8                | 15/<br>15 | 6/<br>6                | 11/<br>17 |

For both species the proportions of responders to non-responders do not differ significantly between holders of woodland territories and holders of scrub territories, during presentation of either song (Fisher Exact test,  $p > 0.05$  in all four cases).

- NOTES
1. The numbers which responded are given as a fraction of the total number of subjects tested.
  2. Results are given for all subjects tested during the main part of the breeding season.

woodland and all Garden Warblers tested with the same song were in scrub. Five out of six Garden Warblers tested with Whitethroat song, including the sole responder to it, were in scrub. Six of the Blackcaps tested with Whitethroat song were in scrub and one of them did not respond to the song. Nine woodland Blackcaps were tested with Whitethroat song and three of them did not respond to it. The proportion of responders to non-responders does not differ significantly between woodland and scrub Blackcaps tested with Whitethroat song (Fisher Exact Probability test,  $p = 0.46$ ).

#### 6.6.5. Responses to song playback by female and juvenile Blackcaps and Garden Warblers

All the preceding analyses have described the responses of males to song playback. Territory defence by both species was only seen to involve males but possibly females do sometimes participate since there were instances when both sexes responded to song playback.

Female Blackcaps responded during a similar small minority of playback experiments involving all four Sylvia song tapes, but none responded to Great Tit song (Table 6-26A). In general, females arrived with males and stayed near the speaker until their mates withdrew. However, there were two instances where female Blackcaps arrived in response to Garden Warbler song but their mates did not respond.

Female Garden Warblers were harder to detect than female Blackcaps since they could not be distinguished from males visually. However, pairs of Garden Warblers arrived in response to several instances of playback of Blackcap or Garden Warbler song (Table 6-26B). In each of these cases only one bird was heard to sing and this individual showed no hostility towards the other, so that it is highly probable that the second member of each pair was a female and mated to the territory holder.

Table 6-26 excludes the late-season experiments of 1978. During the latter a juvenile Blackcap and a juvenile/female Blackcap were recorded responding to Blackcap song and a juvenile Blackcap responded to

Garden Warbler song. A juvenile Garden Warbler responded to Garden Warbler song and there was also an instance of a (colour-ringed) female Garden Warbler responding strongly to Blackcap song playback; her mate was neither seen nor heard. All these responses involved birds coming into view within three metres of the speaker. The juveniles were identified as such since they still retained conspicuous gape-flanges and were obviously fresh-plumaged.

During the second half of July and throughout August 1978 an attempt was made to catch and colour-ring as many Blackcaps and Garden Warblers as possible in the (fruitless) hope of establishing a pool of marked birds for observation during 1979. By this time territory boundaries had disappeared and hardly any birds were singing. Mist-nets were erected in parts of the wood known to be frequented by both species, particularly near fruiting elder bushes where warblers were feeding. Both Blackcap and Garden Warbler songs were broadcast successively at each net site to see whether birds would be attracted to the vicinity. It was hoped that some birds would be attracted and that these would sometimes wander into the nets. Instead it was found that definite responses occurred to both songs, most responders being juveniles. These birds flew straight towards the vicinity of the speaker and were often caught in the intervening nets.

Blackcaps were only seen to respond and were caught only during playback of Blackcap song and Garden Warblers similarly only during playback of Garden Warbler song (Table 6-27). More Blackcaps than Garden Warblers were caught, this probably reflecting not only their relative abundance in the wood but also the fact that many Garden Warblers leave Britain in August while many Blackcaps remain into September.

It is difficult to see why any responses to song playback should occur once territory boundaries have disappeared and, in particular, why juveniles and females should respond at all at this season. Possibly, it is adaptive for birds to investigate situations where conspecifics are

TABLE 6-26. THE NUMBERS OF FEMALE BLACKCAPS (BC) AND FEMALE GARDEN WARBLERS (GW) WHICH RESPONDED DURING SONG PLAYBACK EXPERIMENTS INVOLVING THEIR MATES

A. BLACKCAP FEMALES

| SONG PRESENTED |                |             |                    |           |
|----------------|----------------|-------------|--------------------|-----------|
| Blackcap       | Garden Warbler | Whitethroat | Lesser Whitethroat | Great Tit |
| 3/29           | 9/40           | 2/15        | 1/7                | 0/13      |

B. GARDEN WARBLER FEMALES

| Blackcap | Garden Warbler | Whitethroat | Lesser Whitethroat | Great Tit |
|----------|----------------|-------------|--------------------|-----------|
| 3/23     | 3/23           | 0/6         | 0/6                | 0/13      |

For both species, all possible pairwise comparisons of relative numbers of responders to non-responders were made, by Fisher Exact test and Chi-squared test. No differences are significant, either within or between-species.

- NOTES
1. The numbers which responded are given as a fraction of the total number of subjects (mates) tested.
  2. In all cases, the number of non-responders is based on the assumption that all the territory holders were paired at the time when they were tested with song playback.

TABLE 6-27. THE NUMBERS OF BIRDS CAPTURED USING SONG PLAYBACK AS A LURE DURING JULY AND AUGUST 1978

|                      | Playback of<br>BC song | Playback of<br>GW song |
|----------------------|------------------------|------------------------|
| Ad. male Blackcaps   | 2                      | 0                      |
| Ad. female Blackcaps | 3                      | 0                      |
| Juv. Blackcaps       | 15                     | 0                      |
| Ad. Garden Warblers  | 0                      | 1                      |
| Juv. Garden Warblers | 0                      | 6                      |
| TOTAL                | 20                     | 7                      |

(Ad. = adult, Juv. = juvenile. Sexes of adult Garden Warblers were not distinguishable)

NOTE Song playback was used as a lure on 12 dates between 18 July and 28 August. The number of unsuccessful capture attempts was not recorded nor was the number of times that playback was presented at each net-site standardised in any way.

behaving unusually, in this case singing when "other" males have long ceased to do so. Also recently-fledged birds of both species are fed by their parents and the fathers still sing during this period. Possibly some juveniles associate song with food and respond in the hope of finding a meal. However, this does not explain why occasional adult birds respond to song playback out of season.

## 6.7. DISCUSSION

The song playback experiments with Chiffchaffs and Willow Warblers show that they do not respond aggressively to each other's songs, which is compatible with the earlier observations (Chapter 5) that fights between the two species are rare at Wytham. Blackcaps and Garden Warblers are quite different; they respond both to conspecific songs and to each other's songs.

Blackcaps react just as aggressively to Garden Warbler song as to Blackcap song. The responses of Garden Warblers to Blackcap and Garden Warbler song are also mainly similar but they do not approach the speaker so closely in response to Blackcap song as they do to their own song. This difference emerges when responses of birds during their first encounters with song playback are examined. For such birds, it is also found that Garden Warblers do not approach the speaker so closely in response to Blackcap song as Blackcaps do in response to Garden Warbler song, i.e. the interspecific response of Garden Warblers is weaker than that of Blackcaps.

The general finding that Blackcaps are similarly aggressive to both songs is noteworthy since, in nearly all cases examined, where a bird responds to songs other than those of its own species the interspecific responses are clearly weaker than those given to conspecific song playback. Among widely-sympatric species such cases include the responses of Sedge Warblers to Reed Warbler song (Catchpole 1977), of Reed Warblers to Marsh Warbler song (Catchpole 1978), of Song Sparrows to Bewick's Wren song (& vice-versa, Gorton 1977), of Pied Flycatchers to Great Tit or Marsh Tit



song (Jarvi et al. 1978) and of Philadelphia Vireos to Red-eyed Vireo song (Rice 1978), and the results of experiments with Blue-winged Warblers (Gill & Lanyon 1964) and Passerina buntings (Thompson 1969). Red-eyed Vireos, which do not discriminate between conspecific song and Philadelphia Vireo song (Rice 1978), provide an example of a situation similar to that found in this study.

The high variability of vocal behaviour, both between different subjects and for the same subjects responding to different songs, must be stressed. Whereas playback of either Blackcap or Garden Warbler song may be confidently predicted to result in an approach to the speaker by the great majority of Blackcaps and Garden Warblers, no definite predictions are possible where vocal responses are concerned. This difference is also apparent in the results of song playback experiments with Acrocephalus warblers. Sedge Warblers tested with Sedge Warbler and Reed Warbler song included some birds which were silent throughout the experiment and others which were highly vocal; some of the silent birds nevertheless approached the speaker closely (Catchpole 1977, Figures 3 & 5). Similarly, Reed Warblers tested with Reed Warbler and Marsh Warbler song included several birds which had high song outputs and others which sang little or not at all; again some close approachers were silent and others sang at a high rate (Catchpole 1978, Figure 2b, d).

The unpredictability of vocal responses to song playback may be explicable in terms of the function which song is believed to have in territorial defence. Krebs (1977), working with Great Tits, has shown convincingly that birds are deterred from establishing territories in areas of suitable habitat from which territorial males have been removed but replaced by loudspeakers broadcasting Great Tit song. This demonstration is strong evidence in favour of the long-established viewpoint that a common function of song is to act as a "keep-out" signal to other birds seeking to establish their own territories.

If song has a similar function in Sylvia warblers, it is not too surprising that subjects often fall silent in response to song playback within their territories. A "keep out" signal has clearly failed when an "intruder" is singing persistently within the territory boundaries. Territorial defence should then involve an approach to the intruder and a fight if he will not withdraw. Most subjects of song playback experiments approach the speaker, and hence can be given Latency, Distance and Time scores, but since they fail to find an intruder their subsequent responses, including whether or not they sing, are liable to vary from their normal responses to real intruders. The variability of responses (of all kinds) may thus be simply a reflection of the novelty of song playback.

The question arises whether the strong responses to Blackcap and Garden Warbler song by both species are due to an inability of subjects to discriminate between the two songs. The songs have been described as sounding similar to the human ear but even a superficial examination of their temporal organisation and structure has revealed features on which discrimination might be based. This is in apparent contrast to the songs of Red-eyed and Philadelphia Vireos (Rice 1978), both of which sing short and similar songs. Since under certain circumstances Garden Warblers approach the speaker less closely when Blackcap song is broadcast than when Garden Warbler song is broadcast, this suggests that they distinguish between the two songs. The main body of results does not show whether Blackcaps can discriminate between the two songs because they respond as strongly to both. However, since Blackcaps respond more strongly to Blackcap song than to Garden Warbler song during late-season experiments, and since tape lures in July and August caught birds of both species responding to conspecific song only, there are grounds for believing that both species can discriminate each other's songs.

Song discrimination is not necessarily equivalent to species-discrimination. It has been pointed out (J.C. Rice, pers.comm.) that perhaps

during the main part of the breeding season birds respond to any songs which fall within a certain broad span of similarity. At this time, for both species, the songs which elicit responses include even each other's songs. For Blackcap subjects, even two very different Garden Warbler songs have been found to elicit similarly strong responses from the same birds. Later in the season, birds are less aggressive and respond only to a narrower range of songs, all of which then fall within the span of variation of conspecific songs. The point is that whereas it can be shown that discrimination of different songs occurs it does not necessarily follow that the responding birds perceive that certain songs belong to another species and others to conspecifics. It is unlikely to be of functional significance, however, whether birds respond to songs or to species.

A confident interpretation of the responses to the two whitethroat song tapes will require results from more extensive series of song playback experiments. An investigation into the relationships of Blackcaps and Garden Warblers with the two whitethroats is also required, to see if they interact in any ways. Both whitethroats are smaller than either Blackcaps or Garden Warblers (Table 1-3). Both are segregated by habitat from most Blackcaps but both occur in the scrub habitats inhabited by many Garden Warblers (Table 2-1).

The song of the Lesser Whitethroat is completely distinct from that of the Blackcap or the Garden Warbler. Whitethroat song is more stereotyped than Blackcap or Garden Warbler song but its elements resemble some of those used by Blackcaps and Garden Warblers. It appears that most Blackcaps respond to Whitethroat song but that most Garden Warblers do not, and that neither species responds to Lesser Whitethroat song. Possibly Blackcaps respond to Whitethroat song because they are unfamiliar with the species and its song is more closely similar to Garden Warbler song (to which they respond more strongly) than to that of any other British woodland species. It may also be that Blackcaps, being more aggressive than Garden

Warblers, investigate any songs even slightly similar to their own. Lesser Whitethroat song, being so distinctive, is ignored but Whitethroat song elicits responses. If this is the case the matter could be tested by observing whether British Blackcaps respond to songs of certain allopatric Sylvia species, such as the Orphean and Barred Warblers, which are also partly reminiscent of Blackcap and Garden Warbler songs. Garden Warblers, on the other hand, respond to neither whitethroat song, perhaps because they are less aggressive than Blackcaps and hence are more selective regarding the characteristics of the songs to which they respond, or perhaps because they have encountered both whitethroat species and have learnt to respond to neither. The latter point presumes that Garden Warblers are not interspecifically territorial with either whitethroat species. If the lack of aggression of Garden Warblers towards either whitethroat song is learned, the matter might be revealed by testing Garden Warblers with the songs in areas where they coexist with whitethroats and in areas where they do not.

To conclude, song playback experiments with Blackcap and Garden Warbler subjects have shown the existence of strong interspecific responses, particularly to each other's songs. The implications of this in relating the territorial behaviour of both species to current theories of the significance and mechanisms of interspecific territoriality are examined in the concluding chapter.

CHAPTER SEVEN

RECENT TRENDS  
IN THE POPULATION SIZES  
OF THE BLACKCAP AND  
THE GARDEN WARBLER  
IN BRITAIN

CHAPTER SEVENRECENT TRENDS IN THE POPULATION SIZES OF THE BLACKCAP AND THE GARDEN WARBLER  
IN BRITAIN

The finding that Blackcaps can apparently exclude Garden Warblers from suitable nesting habitat raises the possibility that changes in the numbers of Blackcaps may affect the population size of Garden Warblers. The observations reported in Chapter 4 are a good indication that such effects may occur on a local scale but it would be interesting to know whether there is any evidence that Garden Warbler numbers and Blackcap numbers are negatively-interrelated, taking the British populations as a whole. More specifically, the question asked is whether the abundance of one species is a factor influencing the numbers of the other during the breeding season.

A variety of published anecdotes suggest that this may be so. A number of authors have commented that Garden Warblers tend to be more numerous where Blackcaps are scarce and vice-versa (Bolan 1912, Cohen & Taverner 1972, Harthan 1946, Saunders 1889, Seebohm 1883, Simms 1971, Shrubbs 1979, Ticehurst 1932). For example, Seebohm remarks

"It would appear that the Garden-Warbler and the Blackcap do not get on very well in the same area. Rarely indeed do the two species occur in any great numbers in the same district; and where the Garden-Warbler is abundant the Blackcap always seems to be rare, and vice-versa."

These observations could simply reflect differences in habitat selection between the two species but several other authors rule out this possibility and comment that the numbers of the two species seem to be interrelated, Garden Warblers being scarce when Blackcaps are abundant and vice-versa (Chislett 1953, Glegg 1929, Harrison 1953, Ticehurst 1909, Walpole-Bond 1938). For example, Ticehurst says (of the Blackcap in Kent)

"its numbers vary locally from year to year and seem to bear some relationship to the local abundance or otherwise of the Garden Warbler. In any given locality the Blackcap will be plentiful and the Garden Warbler scarce, while the next year the positions may be reversed."

Similarly, Chislett says of Yorkshire

"in some woods only Garden Warblers may be found, in others only Blackcaps, but experiences in the same wood may vary in following years".

These observations of numerical "interactions" are of great interest since, if correct, they could represent a natural consequence of interspecific territoriality. Verifying such observations requires data from long-term studies in a number of localities. However, Britain is fortunate in that the activities of its thousands of birdwatchers and ornithologists have generated a number of bodies of information which, taken together, have the potential of testing whether Blackcap and Garden Warbler numbers are interrelated. Five such sources of information were examined. They are the results of the National Breeding Bird Survey, regional assessments of the relative abundance of the two species given in county avifaunas, results of the Common Birds Census scheme, the relative numbers of Nest Record Cards of the two species submitted, and the annual ringing totals of both species for Britain and some nearby countries.

#### 7.1. THE NATIONAL BREEDING BIRD SURVEY

This is better known as the B.T.O./I.W.C. Atlas (Sharrock 1976). Participants recorded the presence or absence of breeding birds of all species in ten-kilometre squares covering the whole of Britain and Ireland during the period 1968 - 1972. The resulting maps, taken together with average densities of both species on C.B.C. plots during the same period, enable a rough estimate to be made of the absolute numbers of breeding pairs of both species in Britain at that time (Sharrock 1976: 368, 370).

Garden Warblers were recorded in 49% of squares and Blackcaps in 57% of squares, and nesting was proved or thought probable in the great majority of these squares in both cases. The two species proved to be equally widely distributed over much of England and Wales, but Garden Warblers were scarce in the English fens, west Cornwall and south-west Lancashire. Both were similarly scarce in Scotland and neither widespread in Ireland, although Garden Warblers were much the rarer species there. The average densities on C.B.C. plots in 1972, extrapolated over the number of squares in which the species were recorded, give a total British-Irish population of about 200,000 Blackcap pairs and 75,000 Garden Warbler pairs (Sharrock 1976). The Atlas thus shows that in the early 1970s breeding Blackcaps greatly outnumbered breeding Garden Warblers in Britain as a whole.

## 7.2. COUNTY CHECKLISTS AND REGIONAL GUIDES

A succession of authors have written descriptions of the avifauna of the various British counties. Most counties have had at least one such guide produced and many have had several, some dating back to the previous century. The comprehensive collection of such guides in the Alexander Library of the Edward Grey Institute was examined in search of local assessments of the abundance of Blackcaps and Garden Warblers.

Many authors actually give their own impressions of the relative abundance of the two species. These assessments are largely subjective but since many writers were long-term residents in their respective counties their remarks are as reliable as can be expected in the absence of actual censuses. The authors often made it clear whether they thought that Blackcaps or Garden Warblers were the commoner of the two species in their counties so that it is possible to draw up a good picture of the relative abundance of the two species in different parts of Britain not only recently but also at about the turn of the century (Table 7-1).



TABLE 7-1. THE SUBJECTIVE ASSESSMENTS OF THE RELATIVE ABUNDANCE OF BLACKCAPS AND GARDEN WARBLERS IN THE ENGLISH COUNTIES.  
AS AVAILABLE IN THE COUNTY AVIFAUNAS AND REGIONAL GUIDES

Counties are listed in approximately geographical order, running from south to north. Sources which did not assess the relative abundance of the two species are not included. Sources are cited fully in the Bibliography.

SOURCES SUGGESTING THAT IN THEIR RESPECTIVE COUNTIES AT THE TIME OF WRITING : -

| <u>COUNTY</u>   | : | THE BLACKCAP WAS COMMONER          | : | NEITHER WAS PREPONDERANT      | : | THE GARDEN WARBLER WAS COMMONER | : |
|-----------------|---|------------------------------------|---|-------------------------------|---|---------------------------------|---|
| Cornwall        | : | Rodd 1880, Penhallurick 1978       | : |                               | : |                                 | : |
| Devon           | : | D'urban & Mathew 1895, Moore 1969: | : |                               | : |                                 | : |
| Dorset          | : | Boys 1978                          | : | Mansell-Pleydell 1888         | : | Blathwayt 1934                  | : |
| Somerset        | : |                                    | : | Palmer & Ballance 1968        | : |                                 | : |
| Wiltshire       | : |                                    | : | Smith 1887                    | : |                                 | : |
| Hampshire       | : | Kelsall & Munn 1905                | : | Cohen & Taverner 1972         | : |                                 | : |
| Sussex          | : | Knox 1855                          | : | Shrubb 1979                   | : |                                 | : |
| Surrey          | : | Bucknill 1900, Parr 1972           | : |                               | : |                                 | : |
| Kent            | : |                                    | : | Ticehurst 1909, Harrison 1953 | : |                                 | : |
| Essex           | : | Glegg 1929, Hudson & Pyman 1968    | : |                               | : |                                 | : |
| Hertfordshire   | : | Sage 1959                          | : |                               | : |                                 | : |
| Middlesex       | : | Montier 1977                       | : | Glegg 1935                    | : |                                 | : |
| Buckinghamshire | : | Clark Kennedy 1868                 | : | Radford 1966                  | : |                                 | : |
| Berkshire       | : | Clark Kennedy 1868                 | : | Radford 1966                  | : |                                 | : |
| Oxfordshire     | : |                                    | : | Aplin 1889, Radford 1966      | : |                                 | : |
| Gloucestershire | : | Witchell & Bishop Strugnell 1892:  | : |                               | : |                                 | : |

continued.

continued.

| <u>COUNTY</u>     | THE BLACKCAP WAS COMMONER | NEITHER WAS PREPONDERANT          | THE GARDEN WARELER WAS COMMONER |
|-------------------|---------------------------|-----------------------------------|---------------------------------|
| Herefordshire     | :                         | : Walker & Smith 1975             | : Gilbert & Walker 1941, 1954   |
| Worcestershire    | :                         | : Hartham 1946, Lord & Munns 1970 | :                               |
| Warwickshire      | :                         | : Hartham 1946, Lord & Munns 1970 | :                               |
| Northamptonshire: | Lilford 1880              | :                                 | :                               |
| Cambridgeshire    | : Lack 1934               | : Marr & Shipley 1904             | :                               |
| Norfolk           | : Riviere 1930            | : Ticehurst 1932, Tate 1977       | :                               |
| Suffolk           | : Payn 1978               | : Ticehurst 1932, Tate 1977       | :                               |
| Leicestershire    | : Withers 1978            | :                                 | : Brown 1889, Otter 1965        |
| Lincolnshire      | :                         | :                                 | : Blathwayt 1914, Smith 1955    |
| Nottinghamshire   | : Dobbs 1975              | : Whitaker 1907                   | :                               |
| Derbyshire        | : Frost 1978              | :                                 | : Whitlock 1893                 |
| Staffordshire     | :                         | : Lords & Munns 1970              | : Smith 1931                    |
| Shropshire        | : Rutter et al. 1964      | :                                 | :                               |
| Cheshire          | :                         | : Coward & Oldham 1900, Bell 1962 | :                               |
| Lancashire        | : Spencer 1973            | :                                 | : Mitchell 1892, Oakes 1953     |
| Yorkshire         | :                         | :                                 | : Nelson 1907                   |
| Durham            | :                         | :                                 | : Temperley 1951                |
| Cumberland        | :                         | : Macpherson & Duckworth 1886     | : { Armitt 1897, Stokoe 1962    |
| Westmoreland      | :                         | :                                 | : { Mitchell & Robson 1974      |
| Northumberland    | :                         | : Bolan 1912                      | :                               |

A pattern emerges from the statements in the literature. In counties south of, and including, Worcestershire, Warwickshire, Northamptonshire, Cambridgeshire and East Anglia, where one species predominates it is always the Blackcap. The situation has not changed within the recorded past, with the apparent exception of Herefordshire, where the Garden Warbler predominated (Gilbert & Walker 1941, 1954) but more recently neither is predominant (Walker & Smith 1975). In some of these southern counties (e.g. Worcestershire, Wiltshire, Kent, Oxfordshire and Hampshire) the literature describes both species as locally common but in different areas and the authors of the local guides do not state that either predominates overall. In counties north of, and including, Yorkshire, the predominant species is the Garden Warbler and this has also been the case throughout the recorded past.

There is evidence of change during the present century in most of the intervening counties. The Garden Warbler was formerly the commoner species in Leicestershire (Brown 1889), Lincolnshire (Blathwayt 1914), Derbyshire (Whitlock 1893), Staffordshire (Smith 1931), and Lancashire (Mitchell 1892, Oakes 1953). More recent statements are that Blackcaps clearly predominate in Leicestershire (Withers 1978), Derbyshire (Frost 1978) and Lancashire (Spencer 1973), and are at least as common as Garden Warblers in Staffordshire (Lords & Munns 1970). The recent situation in Lincolnshire is unclear, although the Garden Warbler was still described as the commoner species by Smith (1955). In Nottinghamshire the two species were apparently similarly abundant early in the century (Whitaker 1907), since when the Blackcap now clearly predominates there (Dobbs 1975).

There are comparatively few statements of the relative abundance of the two species in Wales, and those available suggest that both species are locally common. In North Wales the Blackcap was the commoner species early in the century (Forrest 1910) and this was also the case in at least some of the southern counties; Glamorgan (Heathcote 1967),

Cardiganshire (Ingram et al. 1966) and Breconshire (Massey 1976). Since then Garden Warblers have reportedly increased and outnumber Blackcaps in Cardiganshire and Breconshire but Blackcaps are the commoner species in Flintshire (Flintshire Ornithological Society 1968), Glamorgan (Heathcote 1967), Gwent (Humphreys 1963, Gwent Ornithological Society 1977) and Caernarvonshire (Hope Jones & Dare 1976).

In Scotland, as in northernmost England, the Garden Warbler is the commoner species. Baxter & Rintoul (1953) describe Blackcaps as less numerous and more locally distributed than Garden Warblers. Regarding distribution, the B.T.O./I.W.C. Atlas suggests that Blackcaps have become more widespread in Scotland since then and the Scottish ranges of the two species have become quite similar.

Parslow (1968) examined regional guides, among other material, in a review of changes in status among all British breeding bird species. He noted changes in Blackcap and Garden Warbler abundances at a local level but concluded that there was no evidence of any widespread alteration in the numbers of either species. However, most of the large-scale changes reported above are mentioned in guides published during the 1970s, after Parslow's review.

The general situation suggests a northward spread of Blackcaps in mainland Britain during the present century, so that they are now the commoner of the two species in a wide belt of counties across northern England where Garden Warblers predominated before. Blackcaps have certainly not become scarcer in southern Britain during this period, according to other data presented here, and so the spread north is not suspected to have been at the expense of southerly populations. In particular, there is no evidence that the amount of suitable Blackcap habitat available in north and south Britain has drastically altered between the two areas. In fact, in 1949 the proportion of Britain covered by woodland was higher than at any time since 1871, and probably higher than at any time since the

sixteenth century (Yapp 1962). Of this woodland, most of the broad-leaved trees favoured by Blackcaps are concentrated in southern Britain, which accordingly can probably now accommodate more Blackcaps than hitherto.

### 7.3. THE COMMON BIRDS CENSUS SCHEME (C.B.C.)

The C.B.C. generates an index of population sizes which enables changes in the numbers of birds breeding on the census plots to be monitored. Such indices are available for each year since 1962, for farmland census plots, and since 1964, for woodland plots (in Batten & Marchant 1976, 1977a, b, Marchant 1978, Marchant & Hyde 1980 and Marchant & Taylor 1981). The index is defined as "an estimate of the abundance of a species relative to that in a year arbitrarily chosen as datum" (Bailey 1967). The year chosen was 1966 and the index values are calculated from the percentage year to year changes taking an arbitrary level of 100 for every species in 1966.

The censusing procedure is discussed by Taylor (1965) who concludes that the system is valid as a means of assessing population changes in different species. The indices represent year to year changes in numbers on the census plots (and hence plots are not included in the first year in which they are worked). Some plots are lost and others added to the scheme each year as some participants drop-out and others join. It is necessary that the characteristics of the plots (mean area, vegetation-types etc.) lost from and added to the scheme should be similar if comparisons in population levels relative to 1966 are to be made.

The C.B.C. indices for both species (Appendix 7-1) are considered below. In addition, results from some individual census plots were examined to see if there are any indications of reciprocal fluctuations between the numbers of Blackcaps and Garden Warblers nesting there, i.e. do few Garden Warblers breed in years when there are many Blackcap territories, and vice-versa.

#### 7.3.1. C.B.C. Indices.

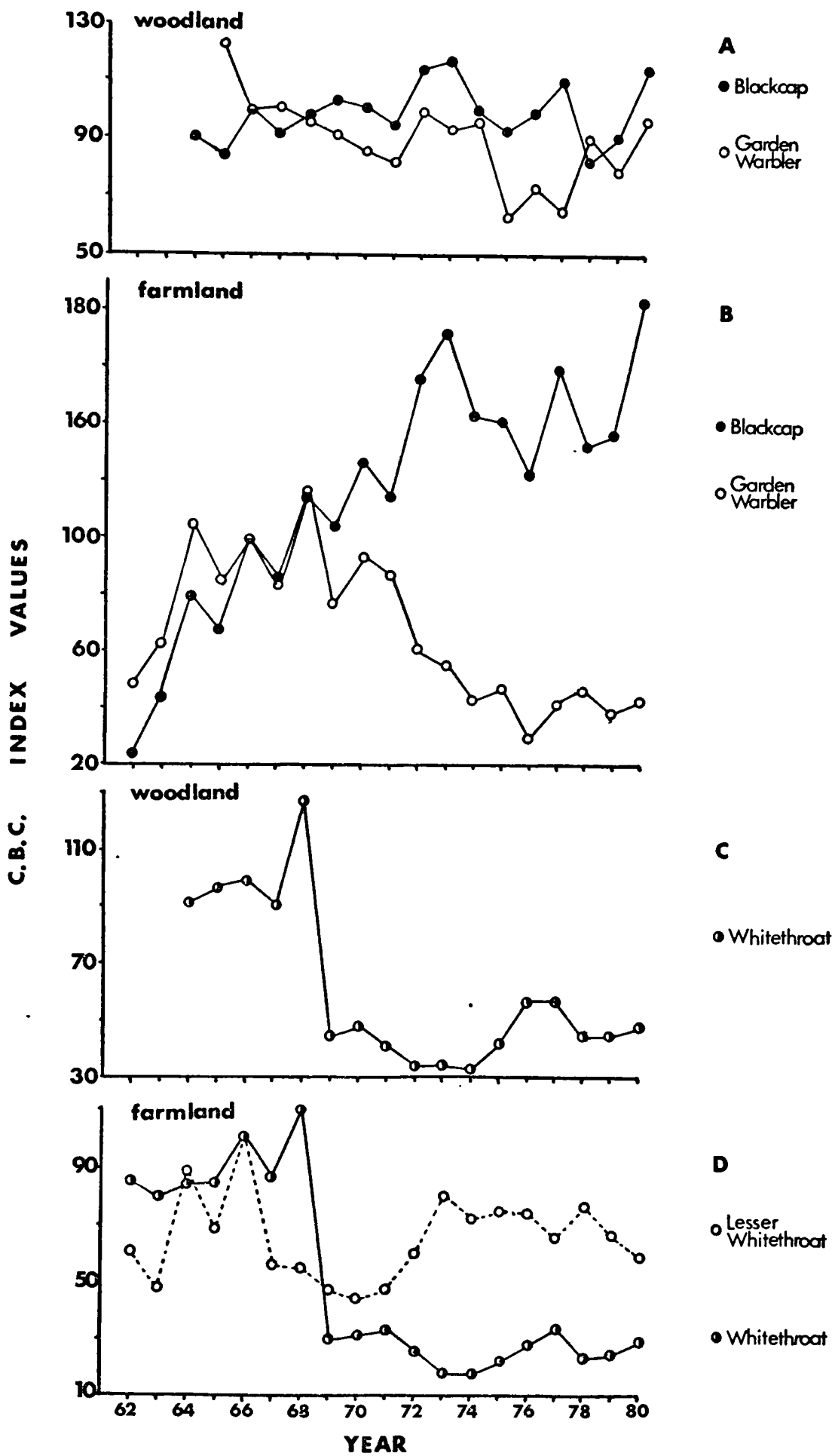
### 7.3.1. C.B.C. Indices.

The woodland indices (Figure 7-1A) for Blackcaps suggest no overall change in population and show no significant correlation with time ( $r_s = 0.268$ ,  $p > 0.05$ , 15 d.f.). The Garden Warbler woodland indices show a significant negative correlation with time ( $r_s = -0.567$ ,  $p < 0.05$ , 14 d.f.). This is mainly due to a sharp fall in the Garden Warbler index in 1975, since when there has been some recovery in numbers. Before 1975 the Garden Warbler woodland indices showed no significant pattern of change with time ( $r_s = -0.521$ ,  $p > 0.05$ , 8 d.f.). Overall the indices suggest a slow decline in Garden Warbler numbers in woodland but the species recently seems to be recovering there from the low population levels of the mid-1970s.

Farmland indices for both species (Figure 7-1B) provide evidence of more-dramatic changes. The Blackcap has become increasingly prominent on farmland plots since the inception of the index. The Blackcap indices show a highly significant correlation with time over this period ( $r_s = 0.867$ ,  $p < 0.001$ , 17 d.f.). Garden Warbler index values show a significant decrease over the same period ( $r_s = -0.721$ ,  $p < 0.001$ , 17 d.f.). Initially both species increased together but, after a population high in 1968, the Garden Warbler has exhibited a pronounced significant decline in the subsequent twelve years (1968 - 1980,  $r_s = -0.846$ ,  $p < 0.001$ , 11 d.f.). (Note: correlation is used instead of regression in examining the trends of changes in the indices over time since a linear model seems inappropriate for the data presented.)

In general, the C.B.C. indices point to a recent increase in Blackcaps and a decrease in Garden Warblers. The changes are only conspicuous on farmland, suggesting that when birds are scarce woodland is filled before farmland habitats, which are mainly tall hedges and patches of scrub. The Garden Warbler indices in particular suggest such a buffer effect. Garden Warbler numbers in woodland were fairly stable between 1962 and 1975, during which period the numbers on farmland plots first increased

FIGURE 7-1. THE ANNUAL COMMON BIRDS CENSUS INDEX VALUES FOR SYLVIA  
WARBLERS DURING THE PERIOD 1962 - 1980



and then progressively declined. The decline of Garden Warblers on farmland was not paralleled by a similar decline in woodland until in 1975, suggesting that by then Garden Warbler numbers were so low that neither habitat could be filled. The recovery in Garden Warbler numbers in woodland following their low point in 1975 corresponds in time with an apparent stabilisation of their numbers on the farmland plots.

The C.B.C. indices for the Whitethroat and the Lesser Whitethroat (Figure 7-1C,D) serve as a comparison. The catastrophic decline of the Whitethroat in 1968/69 (Berthold 1973, Winstanley et al. 1974) was clearly evident on both woodland and farmland plots. It is interesting to note that the initial decline of the Garden Warbler on farmland corresponds in time with the more dramatic decline of the Whitethroat. Both Whitethroat and Garden Warbler are trans-Saharan migrants, unlike the Blackcap and the Lesser Whitethroat, many of which winter in the Mediterranean area and the Middle East respectively. The Lesser Whitethroat only figures on farmland plots since very few nest in woodland. Its indices show no long-term trends of population-size change and there is no suggestion that the demise of the Whitethroat has been accompanied by a compensatory increase in Lesser Whitethroats.

### 7.3.2. Blackcap and Garden Warbler densities on C.B.C. plots.

#### A. Overall densities.

The C.B.C. indices are intended to enable comparisons of population changes to be made within species but not between them. However, since the original data takes the form of the number of territories within plots of known area it is possible to compare directly the densities of Blackcaps and Garden Warblers within each habitat each year. Some warblers have been shown to be harder to census than many other bird species. In a study which combined C.B.C. censusing methods with a meticulous search for nests, a total of fifteen censusing visits still seriously underestimated the numbers of established Blackcaps and Garden Warblers present (Snow 1965).



Blackcaps are just as hard to census as Garden Warblers are (pers.obs.) and hence, for any given visit, both are likely to be underestimated to a similar extent. However, many Garden Warblers arrive later in the spring than Blackcaps, and Garden Warblers are not likely to figure at all in the earlier visits (before early May) to census plots. Hence if a plot is visited on a number of occasions uniformly distributed over the spring there will be more opportunities to record Blackcaps than Garden Warblers and this may exaggerate any differences in the actual abundance of the two species.

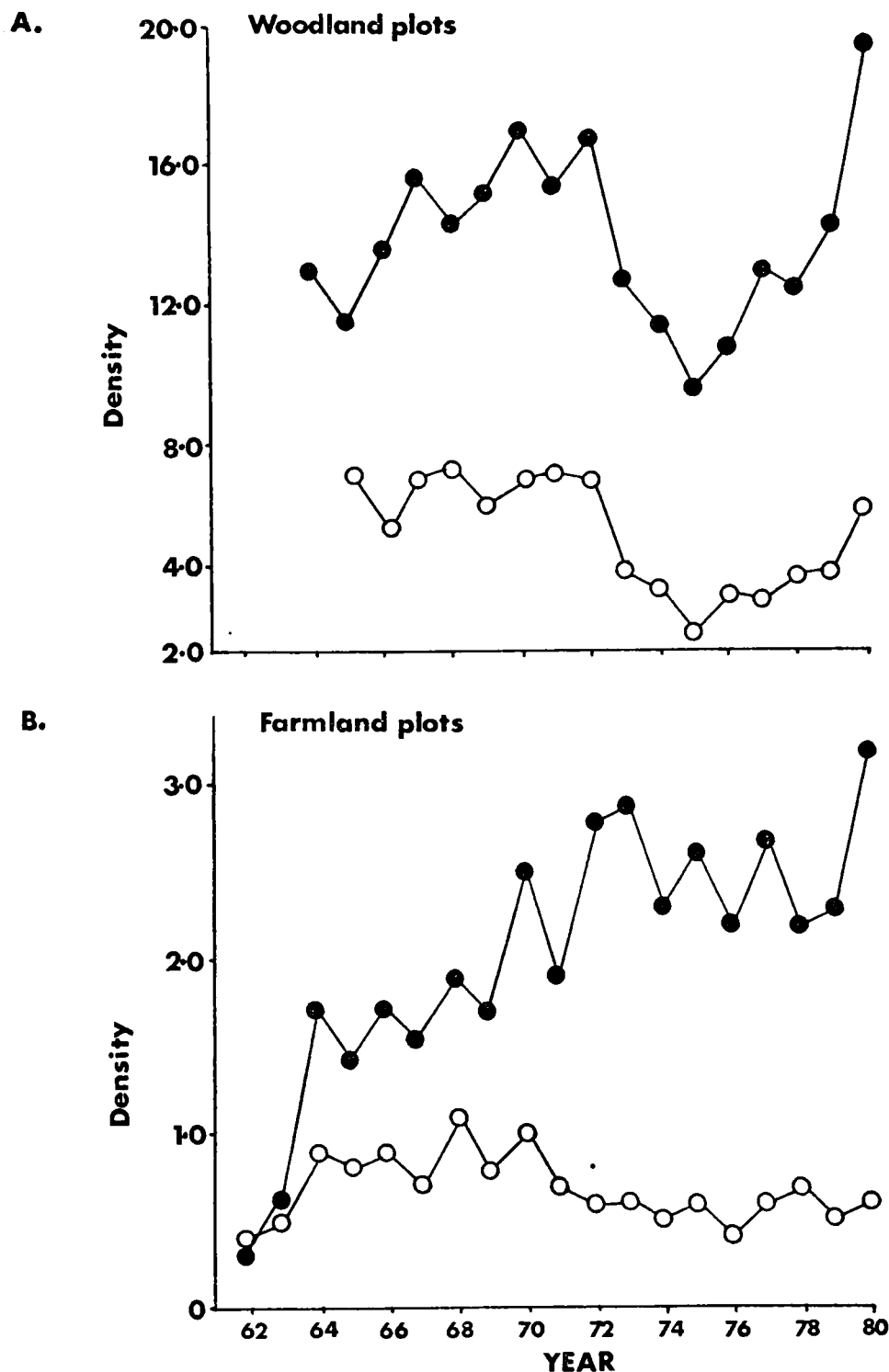
Any differences in the ease of recording of the two species will affect the absolute densities detected but if the discrepancies are fairly constant from year to year they would not prevent the detection of progressive changes in relative abundances. Also between-year changes in plot characteristics, such as habitat composition and plot area (occurring because some plots are added-to and others lost from the scheme each year), would probably affect both species similarly since they share similar habitats, and again would not be expected to conceal changes in relative abundance, although they could account for some year to year differences in densities of both species.

The actual densities of Blackcaps and Garden Warblers on woodland and farmland plots are given in Figure 7-2 (and Appendix 7-2). For both, woodland densities are higher than farmland densities by an average factor of about six, this being due no doubt to the fact that whereas much of woodland is suitable for warblers, farmland includes large areas of arable land where none occur.

The densities of both species correlate with time in the same way as do the C.B.C. indices (unsurprisingly since the latter are derived from the density data). Hence, the patterns of density-changes were compared between species, and between farmland and woodland plots, by using Kendall's partial rank correlation coefficient ( $r_{xy.z}$ ), to partial-out the effects of

**FIGURE 7-2. THE DENSITIES OF BLACKCAPS AND GARDEN WARBLERS ON COMMON BIRDS CENSUS PLOTS**

Densities are given as the number of territories/km<sup>2</sup> each year.



The densities given are based on the total number of territories of each species found each year within the combined area of all the census plots.

● Blackcap densities

○ Garden Warbler densities

time. There is no test of significance of the magnitude of  $r_{xy.z}$  (Siegel 1956) but the critical values of  $r_p$  (Pearson's product-moment correlation coefficient), with  $N - 3$  degrees of freedom, have been used as a guide.

The densities of the two species on both woodland and farmland plots show no signs of any reciprocal fluctuations. On the contrary, Blackcap and Garden Warbler densities on both woodland and farmland are significantly positively correlated with each other (woodland;  $r_{xy.z} = 0.514$ ,  $p < 0.05$ , 13 d.f., farmland;  $r_{xy.z} = 0.533$ ,  $p < 0.05$ , 16 d.f.). There is no significant correlation between Blackcap densities on farmland and those in woodland ( $r_{xy.z} = 0.123$ , n.s., 13 d.f.) nor between Garden Warbler densities on farmland and in woodland ( $r_{xy.z} = 0.319$ , n.s., 13 d.f.).

#### B. Comparisons of Blackcap and Garden Warbler densities on individual C.B.C. plots.

Twelve of the C.B.C. woodland plots examined during the investigation of the distribution of territories in different habitats (Chapter 2) included surveys extending over five years or more. The numbers of Blackcap and Garden Warbler territories present each year in each of these were compared within plots in order to see if they were interrelated. The numbers were significantly negatively correlated on one plot and significantly positively correlated on another, the remaining correlations not being significant (Table 7-2). In fact, only three of the twelve correlations were negative, which is contrary to the prediction of the competition for space hypothesis.

The data examined may be inadequate for the purpose of examining the idea that Blackcap and Garden Warbler numbers show reciprocal fluctuations. Since observers were trying to census all the species present they presumably gave no particular attention to Blackcaps and Garden Warblers and small inaccuracies quite probably occurred, particularly if they found it difficult to distinguish between the songs of the two species. These inaccuracies (hopefully) are not large enough to mask the overall trends

TABLE 7-2. THE ANNUAL COUNTS OF BLACKCAP AND GARDEN WARBLER TERRITORIES  
ON TWELVE WOODLAND C.B.C. PLOTS

n BC, n GW = the number of Blackcap and Garden Warbler territories censused respectively each year. Census plots are identified by the numbers given to them by the British Trust for Ornithology (see Appendix 2-1).  $r_s$  = values of the Spearman rank correlation coefficient for the correlations between the annual totals of Blackcap and Garden Warbler territories on each plot.

|      |     | YEAR (19--) |    |    |    |    |    |    |    |    |    |    |    |    |                   |
|------|-----|-------------|----|----|----|----|----|----|----|----|----|----|----|----|-------------------|
| PLOT |     | 64          | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | $r_s$             |
| 033  | nBC |             |    | 16 | 9  | 5  |    | 8  | 4  |    | 9  | 4  |    | 6  | 0.65, $p < 0.05$  |
|      | nGW |             |    | 3  | 5  | 2  |    | 1  | 1  |    | 2  | 1  |    | 0  |                   |
| 085  | nBC | 4           | 4  | 4  | 4  | 6  |    |    |    |    |    |    |    |    | 0.79, n.s.        |
|      | nGW | 4           | 2  | 2  | 2  | 5  |    |    |    |    |    |    |    |    |                   |
| 906  | nBC |             |    |    |    | 3  | 8  | 6  | 6  | 9  |    |    |    |    | 0.06, n.s.        |
|      | nGW |             |    |    |    | 2  | 3  | 2  | 4  | 2  |    |    |    |    |                   |
| 141  | nBC |             |    | 6  | 2  | 2  |    | 3  | 6  |    |    |    |    |    | 0                 |
|      | nGW |             |    | 2  | 1  | 1  |    | 1  | 0  |    |    |    |    |    |                   |
| 385  | nBC |             | 2  | 4  | 6  | 10 | 7  | 6  | 8  |    |    |    |    |    | -0.71, $p < 0.05$ |
|      | nGW |             | 2  | 1  | 4  | 0  | 0  | 0  | 0  |    |    |    |    |    |                   |
| 641  | nBC |             |    | 3  | 3  | 3  | 5  | 5  | 5  |    |    |    |    |    | 0.45, n.s.        |
|      | nGW |             |    | 1  | 1  | 1  | 1  | 3  | 1  |    |    |    |    |    |                   |
| 642  | nBC |             |    | 8  | 3  | 4  | 3  | 4  |    |    |    |    |    |    | -0.03, n.s.       |
|      | nGW |             |    | 4  | 6  | 4  | 1  | 1  |    |    |    |    |    |    |                   |
| 737  | nBC |             | 2  | 3  |    | 1  |    | 0  | 3  |    |    |    |    |    | 0.34, n.s.        |
|      | nGW |             | 0  | 3  |    | 1  |    | 1  | 1  |    |    |    |    |    |                   |
| 736  | nBC | 1           | 1  | 2  |    | 1  |    | 2  | 3  |    |    |    |    |    | 0.73, n.s.        |
|      | nGW | 1           | 2  | 1  |    | 0  |    | 1  | 2  |    |    |    |    |    |                   |
| 851  | nBC |             | 0  | 1  | 1  | 0  |    | 1  | 2  | 1  | 0  | 0  | 0  |    | 0.12, n.s.        |
|      | nGW |             | 2  | 5  | 3  | 4  |    | 1  | 1  | 5  | 1  | 1  | 2  |    |                   |
| 853  | nBC |             |    | 8  | 4  | 5  |    |    | 7  |    | 7  |    |    |    | 0.15, n.s.        |
|      | nGW |             |    | 11 | 9  | 10 |    |    | 7  |    | 6  |    |    |    |                   |
| 865  | nBC |             |    |    |    | 5  | 3  | 2  | 3  | 9  | 8  | 9  | 12 |    | -0.11, n.s.       |
|      | nGW |             |    |    |    | 4  | 5  | 4  | 3  | 5  | 3  | 5  | 2  |    |                   |

summarised by the C.B.C. indices but they could have a noticeable effect on the small samples examined here. No similar inspection of numbers on farmland plots was made, although this could prove to be a more profitable area for examination since the recent apparent changes in relative abundances have been pronounced on farmland and not in woodland.

In general, the C.B.C. data, while indicating a large increase of Blackcaps and a decrease of Garden Warblers on farmland plots (only) provides no grounds for believing that high densities of one species occur in years when the other species is scarce. However, the question of whether Blackcap and Garden Warbler numbers are interrelated in any habitat can not be answered satisfactorily in the absence of a long-term specific investigation, involving larger sample sizes and more intensive censusing, including searches for nests, than is usual under the C.B.C. procedures.

#### 7.4. THE NEST RECORD CARD SCHEME (N.R.C.)

The scheme has been described in Chapter 2. The number of cards submitted was examined to see if any trends in the relative abundance of the two species could be detected. The analysis was restricted to the thirty-year period 1949-1978, since only occasional cards were available from earlier years. It may be expected that large numbers of cards would be submitted in years when breeding populations were high and, conversely, that fewer nests would be found if breeding numbers were low. The actual number of cards submitted would also vary with year to year differences in observer effort. However, since Blackcap and Garden Warbler nests are probably equally difficult to find, there may be some justification in believing that the numbers of cards submitted for each species are related to the relative frequency of nests in a particular year.

The cards were examined too for evidence to confirm the suggestion that Blackcaps have recently become commoner in relation to Garden Warblers in northern Britain, by comparing the relative abundance of northern and southern nests between the first and second halves of the

period analysed. They were also used to consider whether there have been any changes during the period in the use which either species makes of different habitats.

#### 7.4.1. The numbers of nest record cards submitted.

The numbers of nest record cards submitted annually fluctuate considerably between years (Appendix 7-3) but are generally small for both species. The mean numbers of cards ( $\pm 1$  S.E.) submitted each year during the period 1949-1978 were 43.4 ( $\pm 4.6$ ) for Blackcaps and 25.1 ( $\pm 2.1$ ) for Garden Warblers. More cards were submitted during the second half of the period than during the first half for both species, but the increase was significantly much larger for Blackcaps than for Garden Warblers (Table 7-3).

The pattern of increase in the numbers of cards submitted was far from uniform for either species (Figure 7-3). The numbers submitted for both remained fairly stable for most of the first half of the period examined. However, a relatively sudden increase in the number of submissions occurred between the years 1961 and 1966. The increase affected both species but was more pronounced in the case of Blackcaps than of Garden Warblers, as has already been noted. The peak number of cards submitted in any one year occurred in 1966 for both species; 101 Blackcap cards and 52 Garden Warbler cards. Thereafter, the numbers of cards submitted show a decline, particularly evident in the case of Garden Warblers.

The overall trend towards an increase in the number of cards submitted over the whole thirty-year period is highly significant for both species (Table 7-4). However, when the trend is examined for the two halves of the period separately it is seen that during 1949-1963 the increase in the numbers of Garden Warbler cards received annually was significant but not that in numbers of Blackcap cards. After the substantial increases in the numbers of cards received for both species during the mid-1960s, the numbers of submissions declined, to a significant extent in the case of Garden Warbler but not Blackcap nests.

TABLE 7-3. THE NUMBERS OF BLACKCAP AND GARDEN WARBLER NEST RECORD CARDS  
SUBMITTED DURING THE FIRST AND SECOND HALVES OF THE PERIOD  
1949 - 1978

|                   | Number submitted during<br>1949 - 1963 | Number submitted during<br>1964 - 1978 | %<br>Increase |
|-------------------|----------------------------------------|----------------------------------------|---------------|
| BLACKCAP          | 349                                    | 953                                    | 273 %         |
| GARDEN<br>WARBLER | 264                                    | 488                                    | 185 %         |

The increase during the second period is significantly greater for Blackcaps than for Garden Warblers;  $\chi^2 = 15.30$ ,  $p < 0.001$ , 1 d.f.

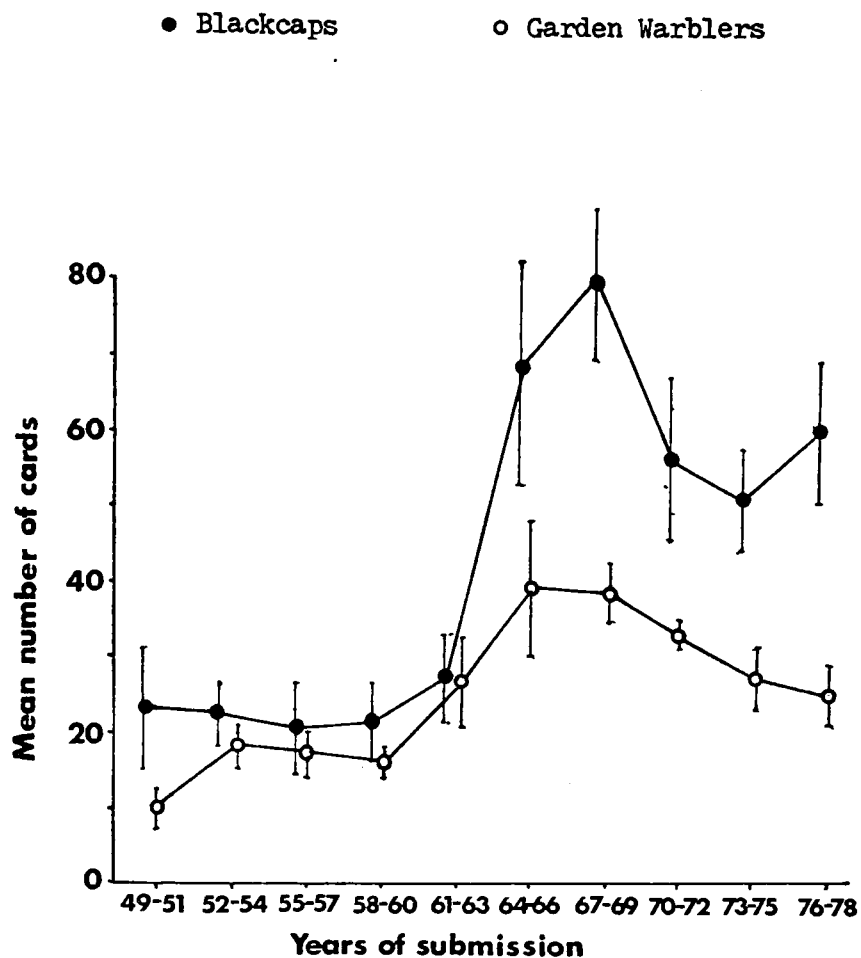
TABLE 7-4. THE RELATIONSHIP BETWEEN THE NUMBERS OF NEST RECORD CARDS  
SUBMITTED AND THE YEAR OF SUBMISSION

Values of the Kendall rank correlation coefficient ( $r_{\text{tau}}$ ) for the correlations between the numbers of cards received each year and time, ascending from 1949.

| <u>PERIOD CONSIDERED</u> | <u>BLACKCAP CARDS</u> | <u>GARDEN WARBLER CARDS</u> |
|--------------------------|-----------------------|-----------------------------|
| 1949 - 1978              | 0.483, $p < 0.001$    | 0.446, $p < 0.001$          |
| 1949 - 1963, (1st half)  | 0.077, n.s.           | 0.539, $p < 0.01$           |
| 1964 - 1978, (2nd half)  | -0.306, n.s.          | -0.452, $p < 0.05$          |

**FIGURE 7-3. THE NUMBERS OF NEST RECORD CARDS SUBMITTED DURING THE PERIOD 1949 - 1978**

The numbers of cards are shown as means for three-year intervals ( $\pm 1$  S.E.).





The numbers of Blackcap and Garden Warbler cards received each year over the whole thirty-year period are positively correlated, even when the effect of time is partialled-out ( $r_{xy.z} = 0.413$ ,  $p < 0.05$ , 27 d.f.). This could indicate that not only is there no inverse relationship between the numbers of breeding pairs of the two species but rather that a good nesting year for Blackcaps is also a good year for Garden Warblers. However, the correlation may simply mean that a good year for finding nests of one species is also a good year for finding nests of the other. For example, a spring with more than the usual number of fine weekends might be expected to enable extra activity on the part of nest-searchers, whereas a wet spring would have the opposite effect.

It must also be considered that the N.R.C. sample is drawn from the whole of Britain and reciprocal fluctuations in nesting populations, if they occur, may not be distributed uniformly over such a large area. For example, an area might have a lower than usual Blackcap population in one season for a variety of reasons; possibilities include a poor breeding season resulting in fewer philopatric first year birds returning to their natal area to breed the next year or unusually-late harsh weather decimating early arrivals. Such events might well not affect the whole country and since the number of cards submitted is small and submissions cover a wide area it may be impossible to pinpoint "good" and "bad" years for either species from the numbers of cards sent. Too few cards are sent from any individual county to enable any numerical fluctuations in smaller areas to be examined. Finally, it is certain that the N.R.C. sample is not a record of nests encountered during random searching. Many observers sent in cards for the two species every year from the same localities, which they presumably searched traditionally. In these circumstances it is easy to imagine an observer whose area experiences a sudden dearth of one of the species noting the fact and making an extra effort to find nests of that species. Any such bias would act to conceal numerical fluctuations in the breeding population.

In general, the numbers of cards submitted provide further evidence of a recent increase in Blackcaps relative to Garden Warblers in that proportionately more Blackcap nests have been found in recent years than earlier. However, it is probably impossible to use the cards to detect whether the breeding populations of the two species show reciprocal fluctuations.

#### 7.4.2. Changes in the numbers of nest record cards submitted from northern and southern Britain.

During the period 1949-1978, the southern sector contained 83.7% of Blackcap nests and 81.8% of Garden Warbler nests, a similar proportion of both ( $\chi^2 = 1.13$ ,  $p > 0.05$ , 1 d.f.). However, when the proportions are examined for the two halves of the period separately it is evident that a higher proportion of Blackcap nests have been found in northern Britain during the latter fifteen years than during the former, and the change is highly significant (Table 7-5). On the other hand, the proportion of Garden Warbler nests found in the north has not altered appreciably between the two periods. It is unlikely that a possible increase in interest in the N.R.C. scheme by persons living in northern Britain would bring about an increase in the number of Blackcap nests found without a corresponding increase in the number of Garden Warbler nests found as well. Hence it is probable that the Blackcap has become more abundant in the north of Britain during the period 1964-1978 than it was there during 1949-1963, a finding which supports the subjective impressions given in the regional guides.

#### 7.4.3. Recent changes in habitat utilisation by Blackcaps and Garden Warblers.

The distribution of nests in different habitats, as revealed by the cards, has been described in Chapter 2. The data is now examined to see whether the proportions of nests of each species found in the different habitat types have altered between the periods 1949-1963 and 1964-1978.

**TABLE 7-5. THE NUMBERS OF BLACKCAP AND GARDEN WARBLER NEST RECORD CARDS SUBMITTED FROM SOUTH AND FROM NORTH BRITAIN DURING THE TWO HALVES OF THE PERIOD 1949 - 1978**

| PERIOD      | NUMBER OF<br>BLACKCAP |         |          | NUMBER OF<br>GARDEN WARBLER |         |          | % | NORTHERN<br>NESTS |
|-------------|-----------------------|---------|----------|-----------------------------|---------|----------|---|-------------------|
|             | CARDS SUBMITTED       |         |          | CARDS SUBMITTED             |         |          |   |                   |
|             | SOUTH                 | NORTH   | NORTHERN | SOUTH                       | NORTH   | NORTHERN |   |                   |
|             | BRITAIN               | BRITAIN | NESTS    | BRITAIN                     | BRITAIN | NESTS    |   |                   |
| 1949 - 1963 | 318                   | 31      | 8.9 %    | 219                         | 45      | 17.1 %   |   |                   |
| 1964 - 1978 | 772                   | 181     | 19.0 %   | 396                         | 92      | 18.9 %   |   |                   |

The proportion of northern Blackcap nests is significantly greater in the second half of the period examined than in the first half;  $\chi^2 = 18.42$ ,  $p < 0.001$ , 1 d.f.

The proportion of northern Garden Warbler nests is not significantly different between the two halves of the period examined;  $\chi^2 = 0.27$ ,  $p > 0.05$ , 1 d.f.

**Note:** For present purposes, south Britain is defined as including all Wales, and England north to and including Shropshire, Staffordshire, Derbyshire, Nottinghamshire and Lincolnshire, counties where the relative abundance of Blackcaps and Garden Warblers has apparently altered recently in favour of Blackcaps. North Britain, as now defined, consists of all those counties, including Scottish ones, where the Garden Warbler is described as the predominant species, as well as Cheshire (where apparently neither predominates - Bell 1962) and Lancashire (where apparently the Garden Warbler predominated until very recently - Spencer 1973). The division between north and south Britain is thus somewhat further north than that used by Mason (1976), in a survey of the regional distribution of card submissions in Britain.

For both species there is a highly significant difference in the distribution of nests by habitat type (Table 7-6). For Blackcaps the difference arises mainly because significantly fewer nests were found in deciduous woodland and significantly more in scrub during the second period than during the first. These changes could be interpreted as the result of an increasing Blackcap population filling all available woodland sites and expanding into scrub. If this has occurred the evidence is that it has not affected the proportionate use by Garden Warblers of these two major habitats, although it remains possible that the numbers of Garden Warblers found in both habitats, and in others, have been reduced as a result. The proportions of Garden Warbler nests found in deciduous woodland have scarcely altered between the two periods. Proportionately more Garden Warbler nests were found in scrub during the second period, but the difference is not significant.

For Garden Warblers, the only significant difference between the two periods is that there has been a recent decline in the number of nests found in parks and gardens. This is an interesting finding in view of the fact that modern books often remark on the ineptitude of the Garden Warbler's vernacular name. It may be that Garden Warblers were formerly more familiar inhabitants of gardens than they are now and that the English name was once not wholly inappropriate. The decline of Garden Warblers nesting in gardens has not been matched by a similar change in the numbers of Blackcap nests found there. The reason for this difference is unknown but one may speculate that the tendency of Garden Warblers to nest significantly lower down in undergrowth than Blackcaps do (Mason 1976) may have adversely affected their ability to survive in any other than the wildest and least-disturbed gardens and parks, of which there are possibly fewer today.

#### 7.5. THE NATIONAL RINGING TOTALS FOR BRITAIN AND SOME ADJACENT COUNTRIES

It might be expected that large numbers of Blackcaps and Garden Warblers would be ringed in years when populations were high and

**TABLE 7-6. THE DISTRIBUTION OF NESTS OF BLACKCAPS AND GARDEN WARBLERS IN DIFFERENT HABITATS COMPARED BETWEEN THE TWO HALVES OF THE PERIOD 1949 - 1978: DATA FROM NEST RECORD CARDS**

| <u>HABITAT</u>      | <u>BLACKCAP NESTS</u>    |       |      | <u>GARDEN WARBLER NESTS</u> |       |                          |
|---------------------|--------------------------|-------|------|-----------------------------|-------|--------------------------|
|                     | 1949 - 1963<br>(N = 301) | %     | (n)  | 1949 - 1963<br>(N = 225)    | %     | (n)                      |
|                     |                          |       |      |                             |       | 1964 - 1978<br>(N = 436) |
| Deciduous woodland  | 74.4                     | (224) | 60.1 | 62.6                        | (141) | 61.0 (266)               |
| Coniferous woodland | 1.3                      | (4)   | 2.6  | 1.3                         | (3)   | 2.5 (11)                 |
| Scrub               | 6.0                      | (18)  | 14.7 | 14.7                        | (33)  | 20.2 (88)                |
| Hedgerows           | 4.3                      | (13)  | 6.6  | 6.7                         | (15)  | 7.8 (34)                 |
| Gardens             | 12.3                     | (37)  | 11.8 | 12.9                        | (29)  | 4.4 (19)                 |
| Other habitats      | 1.7                      | (5)   | 4.2  | 1.8                         | (4)   | 4.1 (18)                 |

- NOTES. 1. The distributions of nests by habitats are significantly different between the two periods for Blackcaps ( $\chi^2 = 28.55$ ,  $p < 0.001$ , 5 d.f.) and for Garden Warblers ( $\chi^2 = 21.29$ ,  $p < 0.001$ , 5 d.f.).
2. For Blackcaps, the numbers of nests found in deciduous woodland v in all other habitats combined, and in scrub v in all other habitats combined, are significantly different between the two periods ( $\chi^2 = 19.36$ , 1 d.f. respectively,  $p < 0.001$  in both cases). For Garden Warblers, the numbers of nests found in gardens v in all other habitats combined are significantly different between the two periods ( $\chi^2 = 14.80$ ,  $p < 0.001$ , 1 d.f.). No other changes in the proportions of nests found in other habitats are significant, for either species.

fewer if birds were scarce. Nevertheless, the greatest caution is necessary in attaching any significance to year to year changes in the numbers of birds captured since ringing totals are prone to a number of biases (reviewed by Ginn 1969) whose magnitude may or may not be known.

The absolute numbers of birds caught chiefly reflect the intensity of the trapping effort. In Britain this has increased greatly during the past thirty years; the total of all species ringed in 1949 was 57,461 and rose more than tenfold by 1978, to 651,657. Nevertheless, the relative numbers of Blackcaps and Garden Warblers caught are not necessarily affected by the increases in the amount of trapping. The similarity in ecology, habitat selection and national distribution of Blackcaps and Garden Warblers is such that both are probably equally easy to catch during the breeding season. Hence ringing totals of birds caught during this time are probably capable of indicating the relative abundance of the two species with some accuracy. Ginn (1969) suggested this species-pair as one of a very few where annual ringing and nest record card totals could serve this purpose. Unfortunately, published ringing totals do not distinguish between migrant birds (including the few wintering Blackcaps) and the British breeding population. The former are trapped mainly at coastal bird observatories, often in considerable numbers, and include an unknown but probably substantial proportion of continental migrants, particularly Scandinavian birds arriving on the British east coast when en route for Iberia in the autumn. The published ringing totals do list birds ringed as pulli separately, but the numbers involved are insignificant. In general, therefore, any attempt to infer population changes among British Blackcaps and Garden Warblers from changes in annual ringing totals is complicated by the fact that not all the birds caught are of British origin.

The migration periods of both species over Britain are of similar length (Davis 1967), so that opportunities for trapping them at observatories are roughly equivalent. However, the Blackcap migrations are

earlier in spring and later in autumn than the Garden Warbler movements and this may mean that Garden Warblers are more likely to encounter fine weather and are less likely to be grounded in "falls" of migrants than Blackcaps. Weather conditions may accordingly produce year to year differences in the relative numbers of Blackcaps and Garden Warblers caught and, furthermore, progressive changes in weather patterns can potentially produce trends in relative abundance that may not be due to real population changes.

Ringling totals have no meaningful baseline against which they may be compared. Even comparisons of the numbers of Blackcaps and Garden Warblers caught each year against the corresponding annual totals of all species ringed are complicated by the variable impact made on the latter by such activities as special studies of seabirds or waders or other occasional projects involving large-scale ringling. However, some "calibration" of the Blackcap and Garden Warbler totals was attempted by extending the analysis to examine the annual ringling totals of the Whitethroat. The west-European population of this species underwent a dramatic decline in 1968/69, as mentioned above. The Whitethroat is closely related to the Blackcap and the Garden Warbler and, like them, is caught in Britain both as a migrant and as a breeding species. An examination of the numbers of Whitethroats caught coupled with the knowledge, from other sources, of the magnitude of an actual population change, can suggest how great a change in ringling totals may be associated with a really large change in numerical abundance.

The annual totals of Blackcaps, Garden Warblers and Whitethroats ringed in Britain during the period 1950 to 1978 were examined. They are published in British Birds (for years up to 1969), as a supplement to Bird Study (for the years 1970 to 1975) and (from 1976 onwards) in Ringling and Migration (Appendix 7-4). Totals from years before 1950 were too small to warrant consideration.

The totals of Blackcaps and Garden Warblers ringed in some other western-European countries were also examined for purposes of comparison. The analysis was confined to the period 1950-1978 but in practice the data examined came from shorter periods within this since some countries are up to ten years behind with the publication of their ringing reports and also the totals caught in the 1950s were often insignificant. Although ringing totals were sought for all western-European countries only a few of these were found to have published long series of national ringing reports (Appendix 7-5). Those examined and described below were from Norway (1960-1973; in Papers of the Norwegian Game Research Institute), Sweden (1960-1970; in supplements to Var Fagelvarld and, from 1964 onwards, in Reports of the bird ringing office, Swedish Museum of Natural History), Finland (1956-1967; in Mems. Soc. pro Fauna et Flora Fennica), Holland (1961-1978; in Limosa) and France (1956-1970; in Bulletin du centre de recherches sur les migrations des mammiferes et des oiseaux). In general, most of these countries have experienced a considerable increase in ringing activity over the past thirty years but the sizes of the ringing effort vary considerably from place to place.

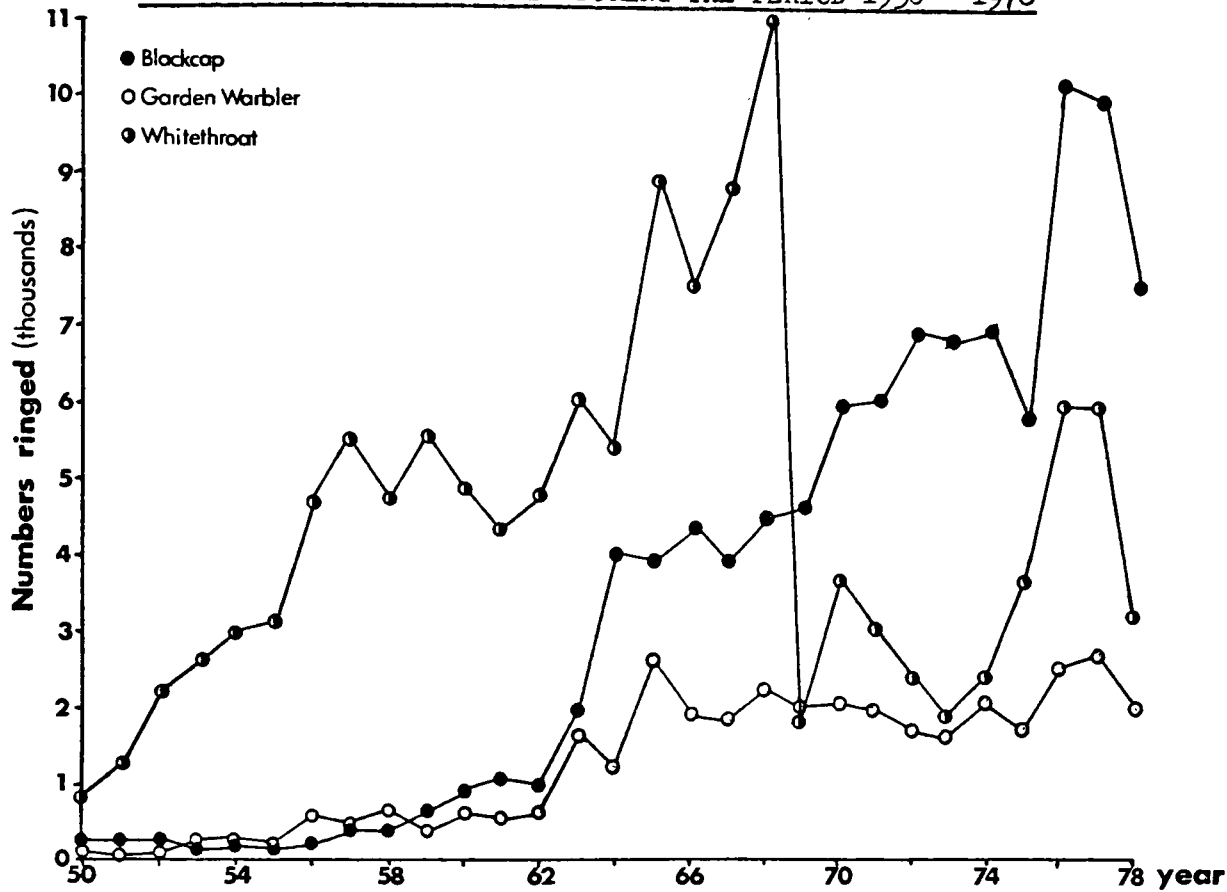
#### 7.5.1. Ringing totals in Britain.

The annual totals of Blackcaps and Garden Warblers ringed in Britain have shown an increase which clearly reflects the increase in ringing activity, but there are conspicuous differences between the capture totals of both species (Figure 7-4A). In the 1950s Garden Warbler captures exceeded Blackcap captures in some years but this may be of little significance since the total captures of each species were very low, only a few hundred birds. However, following big increases in the numbers of both ringed in the early 1960s, the annual Garden Warbler totals have remained fairly constant at about 2,000 birds. Blackcap captures, on the other hand, have increased dramatically to average over 7,000 birds per year during the 1970s and exceeding 10,000 birds in both 1976 and 1977. The increase of

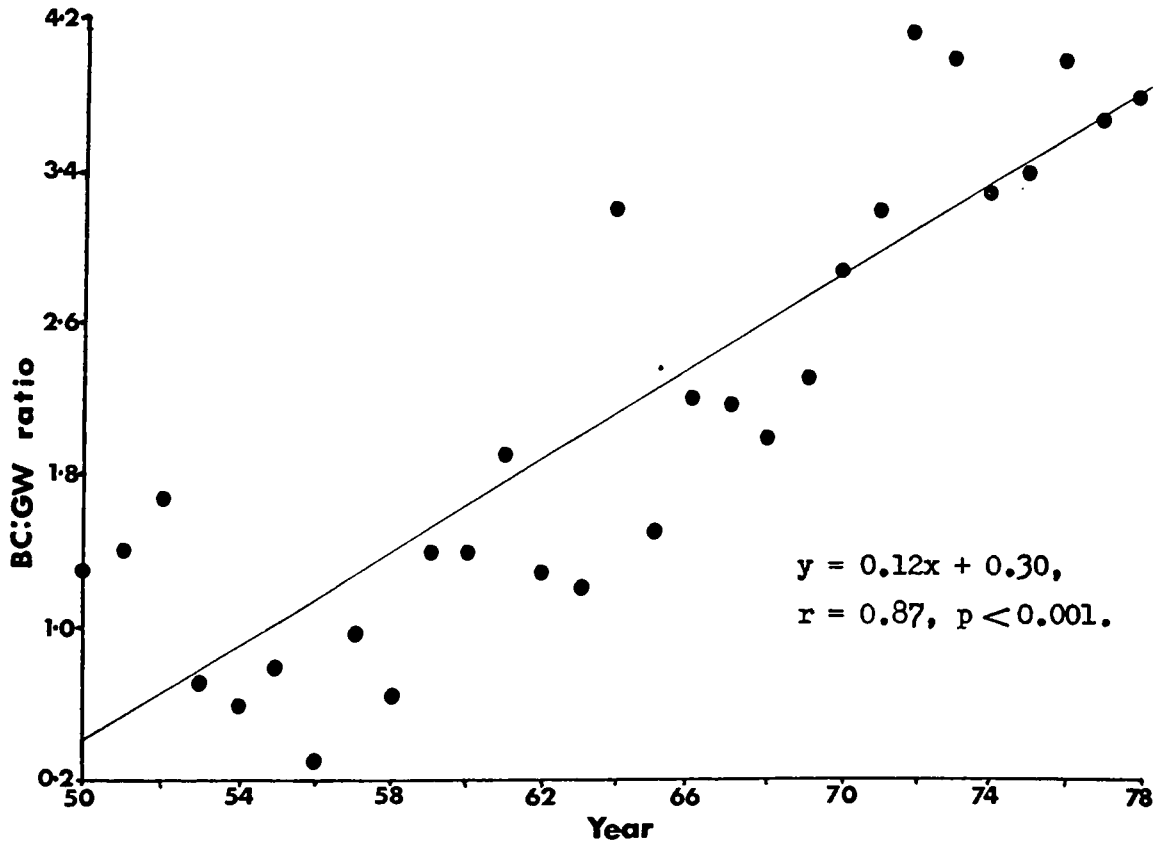


FIGURE 7-4.

A. THE NUMBERS OF BLACKCAPS, GARDEN WARBLERS AND WHITETHROATS  
RINGED ANNUALLY IN BRITAIN DURING THE PERIOD 1950 - 1978



B. THE RATIO OF BLACKCAP TO GARDEN WARBLER CAPTURES IN THE ANNUAL  
BRITISH RINGING TOTALS FOR EACH YEAR DURING THE PERIOD 1950 - 1978



Blackcaps relative to Garden Warblers can be seen most clearly by considering the ratio of Blackcap captures to Garden Warbler captures for each year during the period. The ratio shows a steep and significant increase over the period (Figure 7-4B).

The decline in the Whitethroat population during 1968/69, revealed by the Common Birds Census, is also clearly evident in Figure 7-4A. This confirms that ringing totals can indicate real changes in population-size provided that these are substantial and hence suggests that the increase in the numbers of Blackcaps ringed may indicate an increasing Blackcap population.

The relative stability in the annual numbers of Garden Warblers caught, viewed in conjunction with the increased trapping effort, strongly suggests that a decrease in Garden Warbler populations has occurred in the catchment-areas of the British ringing scheme.

In the case of Blackcaps it is possible that larger annual capture totals may have been brought about simply by changes in the birds' behaviour bringing more to the capture areas than before, without population sizes having increased. Langslow (1978) has analysed the conspicuous increases in the numbers of Blackcaps observed daily at the British bird observatories, which have paralleled the increases in numbers ringed, with this possibility in mind. He points out that easterly winds over northern and central Europe are now commoner, both in autumn and in spring, and this would bring more continental migrants to the British east coast observatories. He notes however that the south coast observatories have also recorded increased numbers of Blackcaps recently in spring; most of these would be likely to be British breeding birds, suggesting a real increase in the British population. Langslow considers, however, that the increases at the bird observatories have been too large to be explained by a real increase in population alone. He notes too that the increases in observer activity (and trapping intensity) have not been great enough to account for the large

numbers of Blackcaps seen and captured at observatories in recent years.

If the increases in numbers of British-ringed Blackcaps have been brought about at least partly by changes in wind directions then these have clearly not affected Garden Warblers in the same way. This could be due to the fact that the migration periods of the two species are different; for example; most of the increases in numbers of Blackcaps observed in Britain have occurred in October (Langslow 1978), when most Garden Warblers have already migrated south.

#### 7.5.2. Ringing totals in other European countries.

Langslow (1978) points out that there have not been recent increases in Blackcap numbers at certain continental observatories. He cites the Radolfzell scheme in West Germany, Falsterbo in Sweden and observatories from the Polish Baltic coast. However, he does not consider national ringing totals, which are more likely to serve as reliable indicators of population changes than those from smaller areas (Hjort & Lindholm 1978).

##### A. Fennoscandia (Norway, Sweden and Finland)

These three countries, situated east north east of Britain, form a geographical unit and may be considered together. They are the source of many of the continental migrants which occur in Britain.

The numbers of both trapped in Norway are very small and the year to year fluctuations which they exhibit probably do not represent real population changes. During the period 1960-1973 they averaged 81 Blackcaps and 124 Garden Warblers per annum. Most of Norway lies over 300 metres above sea level and, in comparison to Sweden and Finland, the country probably has a low breeding warbler population as a result. In Britain both species generally nest at altitudes below 250 metres (Mason 1976).

The total number of all bird species caught in Sweden during the period 1960-1970 fluctuated and did not show the steady increase seen

in the British ringing effort. The annual totals of Blackcaps and Garden Warblers ringed also varied (Figure 7-5A) but Blackcaps made up a fairly constant proportion of the catch of the two species (Figure 7-5C). There was therefore no trend suggesting a change in the abundance of either species in Sweden. However, no published ringing reports were available for years after 1970, when the largest increases in the numbers of Blackcaps caught in Britain occurred.

In Finland, the capture totals of both species increased steadily during the period examined, presumably as a consequence of a general expansion of the national ringing effort (Figure 7-5B). However, after a sharp and significant increase from the 1950s, the numbers of Blackcaps ringed remained quite stable relative to Garden Warbler captures during the 1960s. As for Sweden, ringing totals for later years do not appear to have been published yet. There is some independent evidence to support the apparent increase in Blackcap numbers during the late 1950s suggested by the ringing totals. Census evidence has revealed that the Blackcap has increased markedly in southwest Finland since the 1930s (Von Haartman 1969). This increase, which has also been noted in Norway and Sweden, has been thought to be at least partly due to the cessation of cattle grazing in the forests, enabling a regeneration of the undergrowth there (Von Haartman 1973).

The numerical preponderance of Garden Warblers over Blackcaps in the Fennoscandian ringing totals is in contrast with the situation in Britain and countries in central Europe, where more Blackcaps than Garden Warblers are caught. The difference is probably due to the fact that the Garden Warbler's range extends substantially further north than that of the Blackcap (Chapter 1), so that, overall, Garden Warblers are relatively more numerous in the northern countries than further south.

#### B. Holland

The numbers of Blackcaps and Garden Warblers caught in Holland increased steadily during the period 1961-1978, accompanying a general

FIGURE 7-5.

A. THE NUMBERS OF BLACKCAPS (●) AND GARDEN WARBLERS (○)  
RINGED ANNUALLY IN SWEDEN DURING THE PERIOD 1960 -  
1970

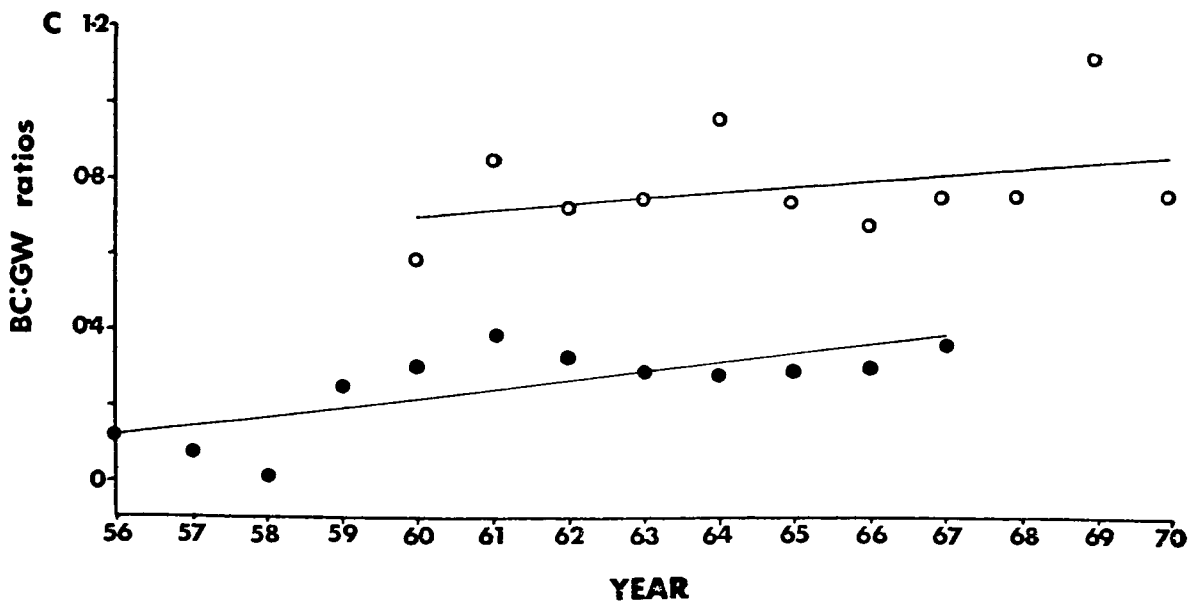
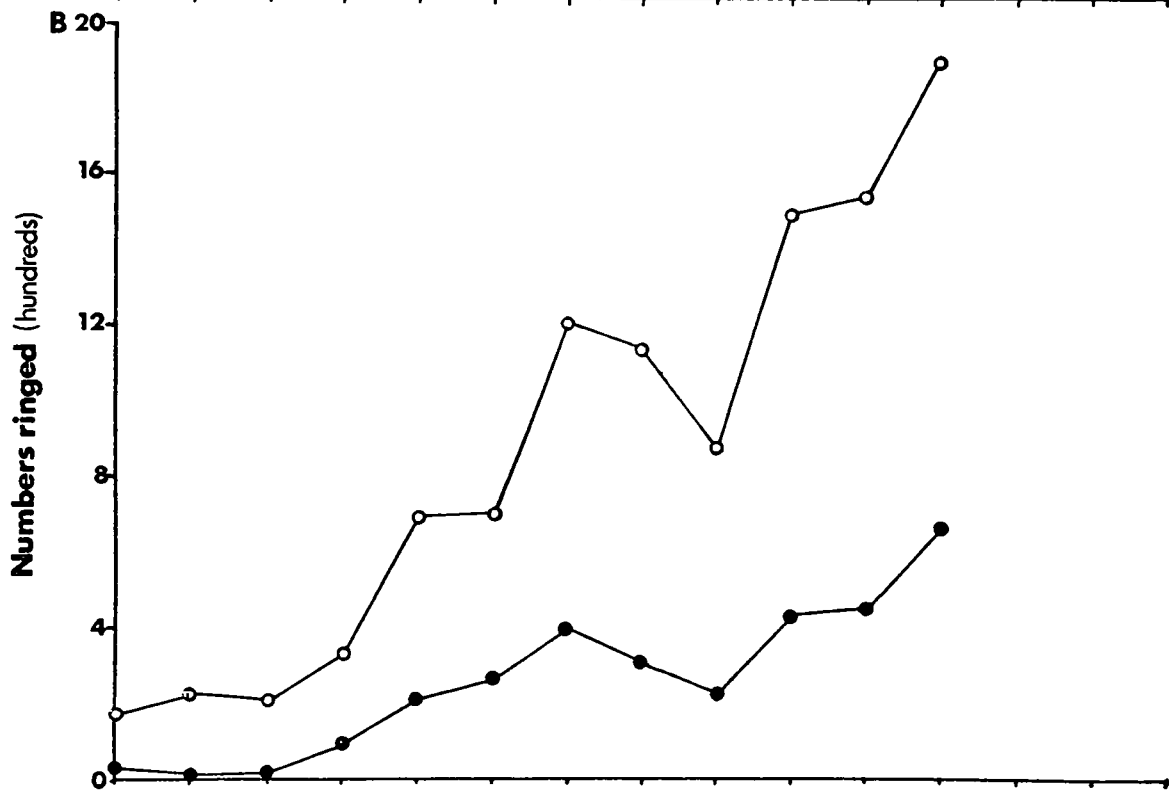
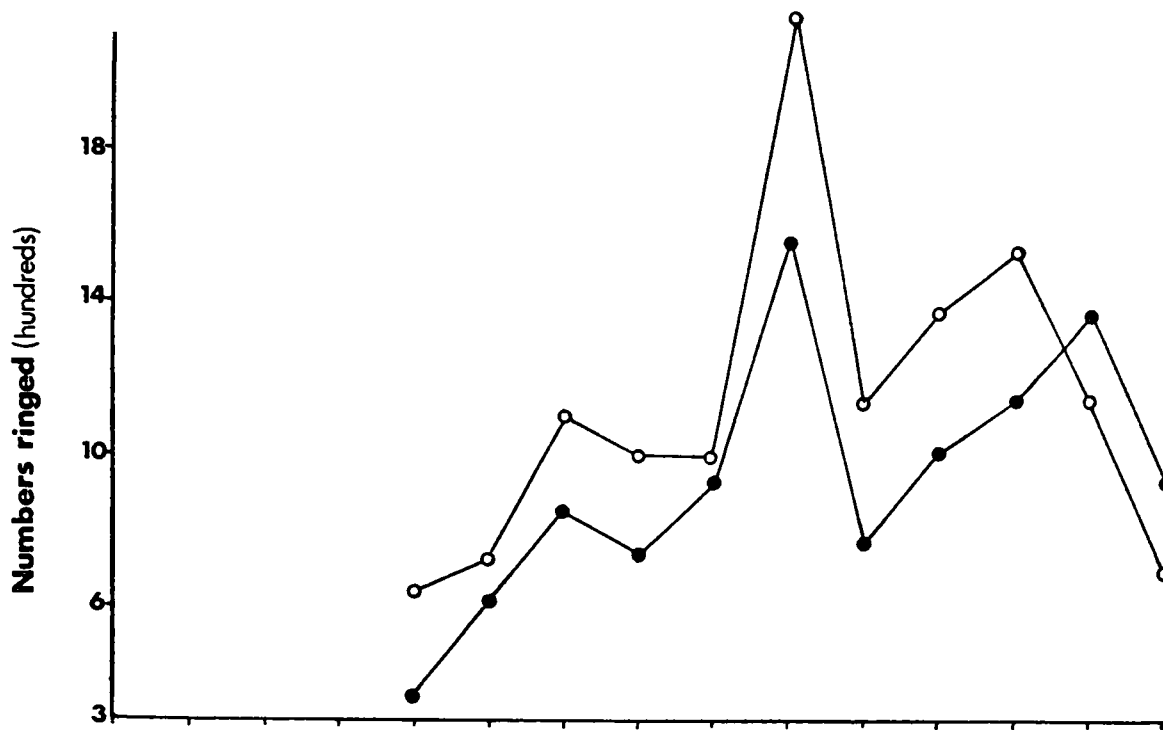
B. THE NUMBERS OF BLACKCAPS (●) AND GARDEN WARBLERS (○)  
RINGED ANNUALLY IN FINLAND DURING THE PERIOD 1956 -  
1967

C. THE RATIO OF BLACKCAP (BC) TO GARDEN WARBLER (GW)  
CAPTURES EACH YEAR IN THE ANNUAL SWEDISH AND FINNISH  
RINGING TOTALS EXAMINED

The fitted regression lines are shown.

SWEDEN (○);  $y = 0.02x + 0.68$ ,  $r = 0.36$ ,  $p > 0.05$ .

FINLAND (●);  $y = 0.02x + 0.10$ ,  $r = 0.71$ ,  $p < 0.01$ .



expansion of the Dutch ringing effort (Figure 7-6A). However, Blackcaps became conspicuously more numerous in relation to Garden Warblers over this period. At the start of the period they only represented some 30% of the combined capture totals of the two species but the proportion had risen to over 65% by the late 1970s. The increase of the Blackcap/Garden Warbler ratio over this period is highly significant (Figure 7-6B).

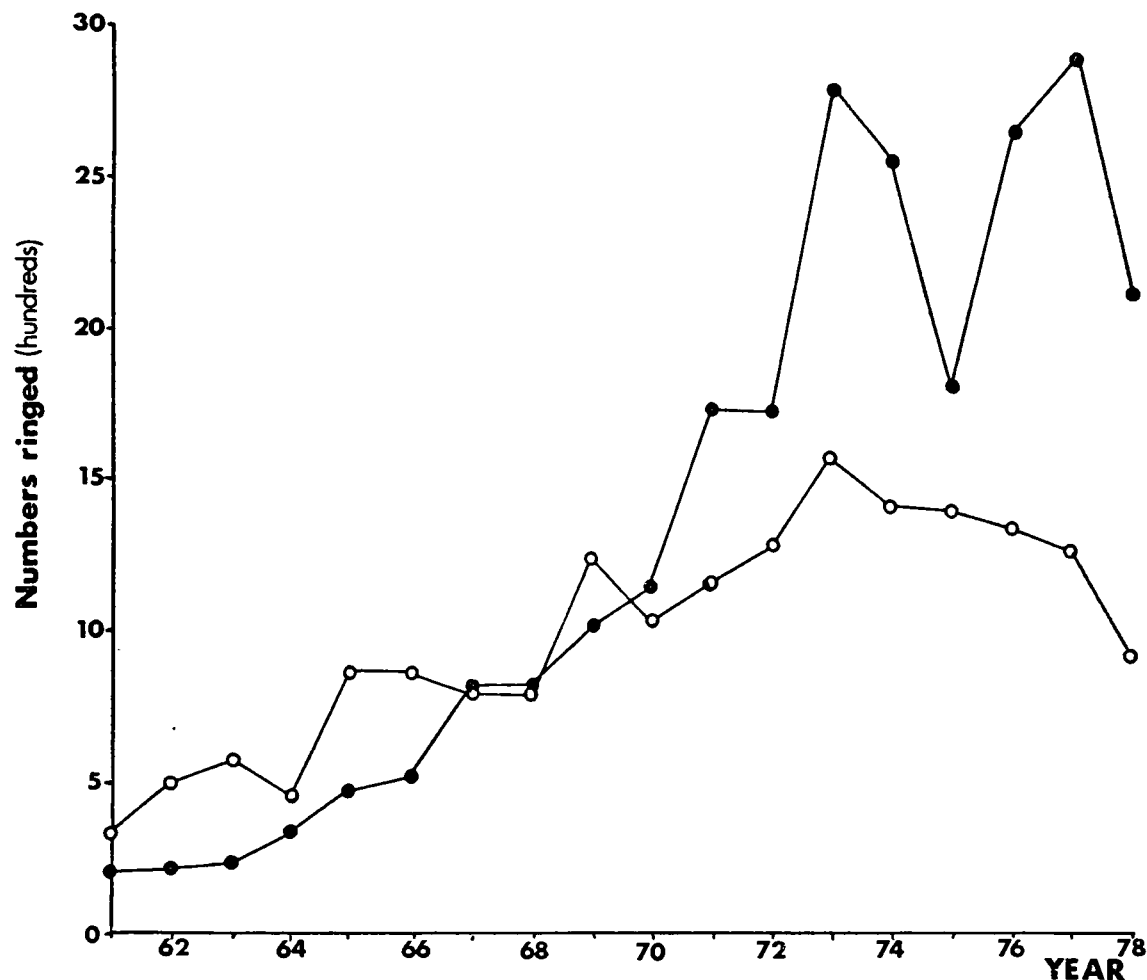
### C. France

Ringing activity expanded in France during the 1950s and 1960s and this was reflected in the numbers of Blackcaps and Garden Warblers caught (Figure 7-7A). The proportion of Blackcaps in the combined Blackcap and Garden Warbler capture totals showed only a gradual shift towards an increasing preponderance of Blackcaps; the slope of the regression of the Blackcap/Garden Warbler ratio over time is only weakly significant in comparison to those of the British and Dutch data examined (Figure 7-7B). However, the published data available did not extend into the 1970s, when the largest increases in the ratio were noted in Britain and Holland. It is worth noting therefore that the ringing station in the Camargue did provide evidence (in ringing reports published in Terre et Vie) of an increase in the ratio in southern France then. From 1930 to 1969 the ringing station captured 11,726 Blackcaps and 4,994 Garden Warblers, a ratio of 2.4 : 1. From 1970 to 1973 a further 3,037 Blackcaps were caught but only 842 more Garden Warblers, a ratio of 3.6 : 1. The change in proportions in favour of Blackcaps is highly significant ( $\chi^2 = 102.9$ ,  $p < 0.001$ , 1 d.f.).

The question arises whether the annual capture totals of Blackcaps and Garden Warblers within any of the countries considered are correlated. The matter cannot be answered simply by comparing Blackcap numbers with Garden Warbler numbers since for most countries both annual totals are each highly significantly correlated with time as a result of the progressive expansion of the national ringing efforts. Hence they will also appear to be correlated with each other. The problem was considered by determining the Kendall partial rank correlation coefficient

FIGURE 7-6.

A. THE NUMBERS OF BLACKCAPS (●) AND GARDEN WARBLERS (○) RINGED ANNUALLY  
IN HOLLAND DURING THE PERIOD 1961 - 1978



B. THE RATIO OF BLACKCAP (BC) TO GARDEN WARBLER (GW) CAPTURES EACH YEAR  
IN THE ANNUAL DUTCH RINGING TOTALS EXAMINED

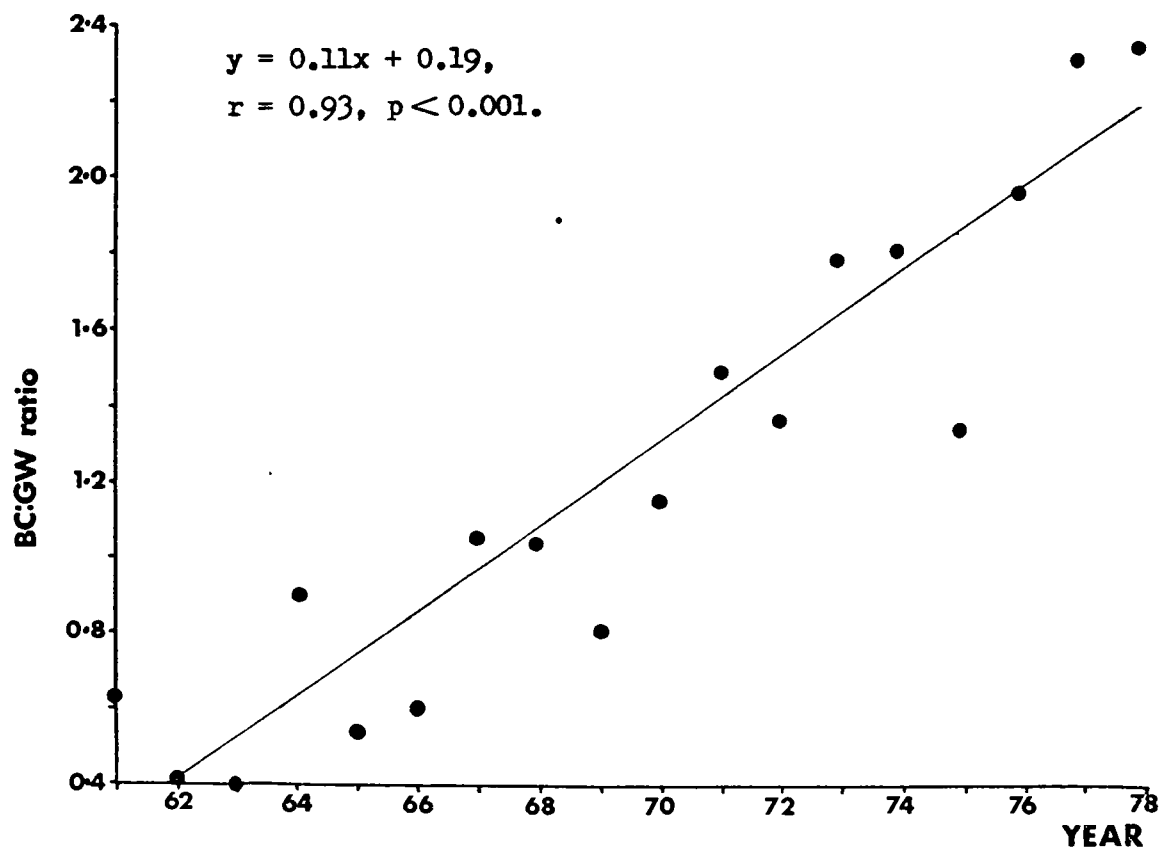
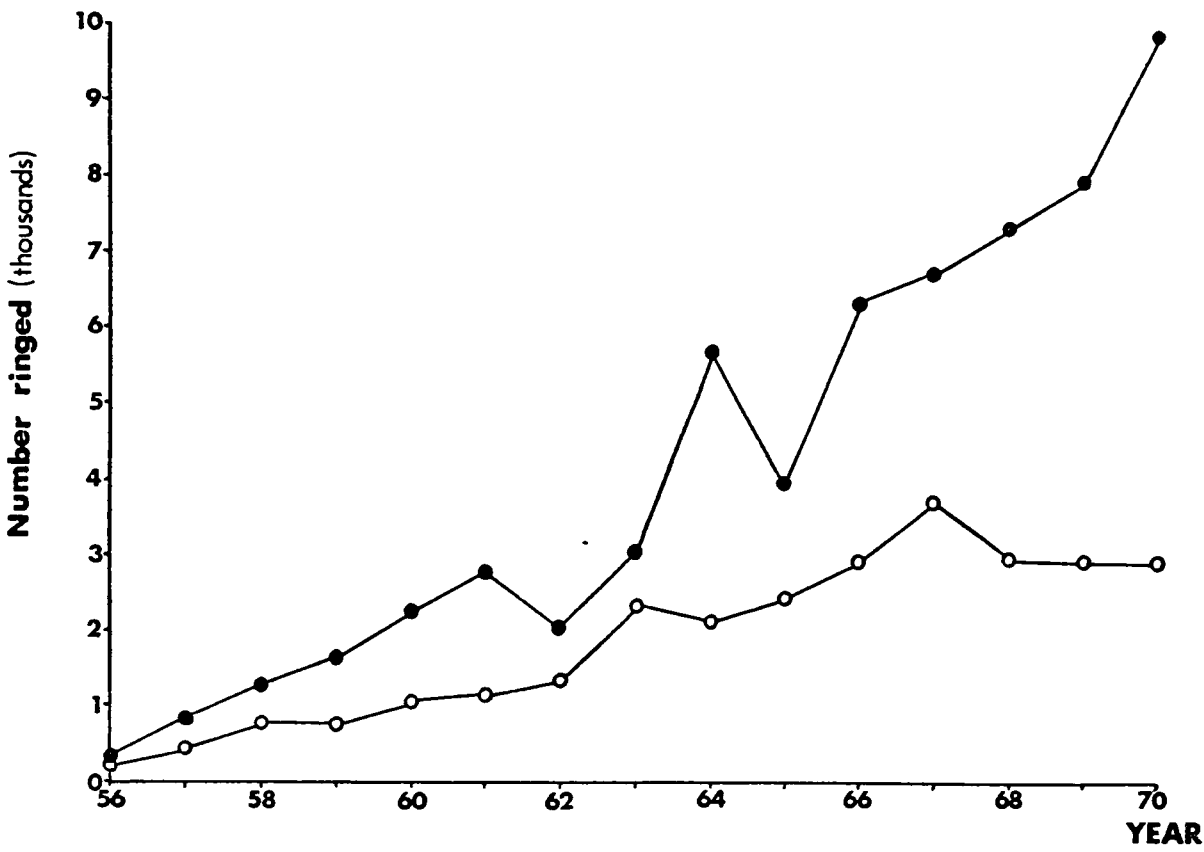




FIGURE 7-7.

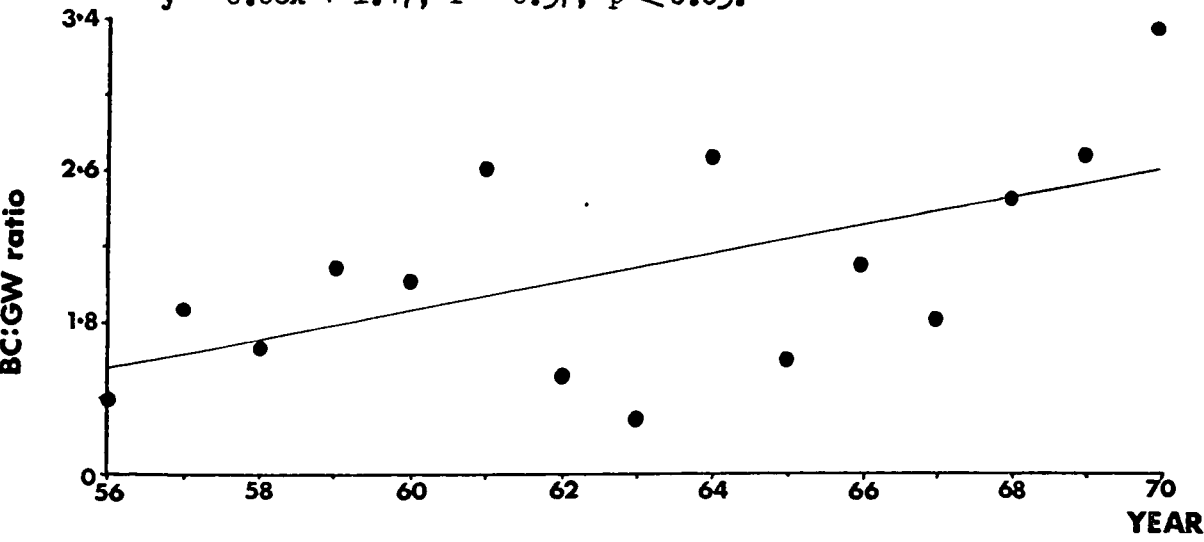
A. THE NUMBERS OF BLACKCAPS (●) AND GARDEN WARBLERS (○) RINGED ANNUALLY IN FRANCE DURING THE PERIOD 1956 - 1970



B. THE RATIO OF BLACKCAP (BC) TO GARDEN WARBLER (GW) CAPTURES EACH YEAR IN THE ANNUAL FRENCH RINGING TOTALS EXAMINED

The fitted regression line is shown.

$y = 0.08x + 1.47, r = 0.57, p < 0.05.$



for the Blackcap and Garden Warbler totals (Table 7-7). When the effect of time is partialled-out, the correlation between Blackcap and Garden Warbler numbers is very low for the ringing totals from Britain, France and Holland. However, the totals of the two species caught in Fennoscandia are positively correlated, significantly in the cases of the Swedish and Finnish data. It seems therefore that in Fennoscandia at least a good year for Blackcaps is also a good year for Garden Warblers and vice-versa, either because successful and unsuccessful breeding seasons for the two species tend to coincide or simply because years when catching opportunities for one species are good are also years when many of the other species are caught. In general, there is certainly no suggestion of a negative interrelationship between the numbers of the two species caught in any of the countries from which data was examined.

The general conclusion arising from the ringing totals presented is that Britain, France and Holland have experienced a very similar and large recent increase in the numbers of Blackcaps ringed relative to Garden Warbler captures. The actual numbers of Garden Warblers caught in the three countries have shown a tendency to stabilise despite an increase in the national ringing efforts, suggesting an actual decline in the Garden Warbler populations. On the other hand, the fact that Blackcap captures relative to Garden Warbler captures have risen over so wide a geographical area makes it less likely that the observations can be fully explained as due to behavioural changes or to deviations of migration routes by prolonged easterly winds. Instead the conclusion is that Blackcap numbers have shown a real increase within the catchment-areas of the British, French and Dutch ringing schemes. This increase does not appear to have occurred in Fennoscandia, with the exception of an early increase in Blackcaps visible during the 1950s. Since data from the 1970s, when the largest increases in Blackcap captures occurred in Britain, France and Holland, was not available from Sweden or Finland it is possible that a similar increase may have occurred there during that decade.

TABLE 7-7. VALUES OF THE KENDALL PARTIAL RANK CORRELATION COEFFICIENT  
( $r_{xy.z}$ ) FOR THE CORRELATION BETWEEN THE NUMBERS OF BLACKCAPS  
AND GARDEN WARBLERS RINGED EACH YEAR IN BRITAIN AND SOME  
NEARBY COUNTRIES, WITH THE EFFECT OF TIME PARTIALLED-OUT

| <u>COUNTRY</u> | <u>PERIOD OF RINGING TOTALS</u> |  | $r_{xy.z}$ |             |         |
|----------------|---------------------------------|--|------------|-------------|---------|
|                | <u>EXAMINED</u>                 |  |            |             |         |
| BRITAIN        | 1950 - 1978                     |  | 0.156      | $p > 0.05,$ | 26 d.f. |
| HOLLAND        | 1961 - 1978                     |  | 0.176      | $p > 0.05,$ | 15 d.f. |
| FRANCE         | 1956 - 1970                     |  | -0.058     | $p > 0.05,$ | 11 d.f. |
| NORWAY         | 1965 - 1973                     |  | 0.592      | $p < 0.05,$ | 6 d.f.  |
| SWEDEN         | 1960 - 1970                     |  | 0.790      | $p < 0.01,$ | 8 d.f.  |
| FINLAND        | 1956 - 1967                     |  | 0.737      | $p < 0.01,$ | 9 d.f.  |

NOTE. Significance levels are those of the Pearson product moment correlation coefficient, with  $N - 3$  d.f., for the reason explained in the text.

## 7.6. DISCUSSION

As has been pointed out, a variety of problems and biases attend the data presented in this chapter, making it difficult to draw any really rigorous conclusions from it. Nevertheless, the different data-sources examined have yielded mutually-compatible results, so that some tentative generalisations may be attempted regarding recent trends in the British Blackcap and Garden Warbler populations.

Blackcaps are now more numerous than Garden Warblers in Britain, both as breeders and as migrants. Garden Warblers are relatively more abundant in the north of the country but Blackcaps have become increasingly widespread there recently and now outnumber Garden Warblers in several northern English counties where the latter was formerly said to be the commoner of the two. Evidence of this northward spread of Blackcaps comes both from subjective assessments in regional guides and from the nest record card scheme.

There are good indications that Blackcaps have increased in numbers recently in the country as a whole, whereas the Garden Warbler population seems to be decreasing simultaneously. C.B.C. results show that these trends are strongly visible on farmland census plots but have been much less evident in woodland, which is presumably the optimum habitat for the two species. The N.R.C. scheme provides supporting evidence of an increase in Blackcaps relative to Garden Warblers, with indications of an accompanying spread of Blackcaps out of woodland into scrub habitats. British ringing totals, as well as those for France and Holland, also demonstrate an increase in Blackcaps relative to Garden Warblers, which appears to be due to a real increase in Blackcaps and possibly also to a decline in Garden Warbler populations.

The above patterns represent trends visible over a number of years but none of the data sources provides any good evidence to suggest that in any one year Blackcap numbers and Garden Warbler numbers are

negatively interrelated. Such an interrelationship, in which high Blackcap numbers are postulated to be incompatible with high Garden Warbler numbers, and vice-versa, would probably not be detectable in the ringing totals, N.R.C. scheme results or the overall C.B.C. results, unless they occurred simultaneously over large areas of the country. However, individual C.B.C. plot censuses might have been expected to show such a trend, if it exists, although it is concluded that the small sample of such C.B.C. data examined is insufficient to rule out that such an interaction occurs. Since the results of the removal experiment (Chapter 4) showed clearly that Garden Warbler numbers are affected by experimental manipulation of Blackcap numbers, a long-term study to investigate the possibility of numerical interactions between the two species would be of interest.

It may be that at present British Blackcap and Garden Warbler populations are not limited by overall habitat availability or food supplies in their breeding grounds but instead that events in their winter quarters or the problems encountered on migration may have a definitive effect on their abundance. If so, the explanation of their numerical fluctuations can not be found in Britain at all and interspecific territoriality in the breeding season may simply lead to a local redistribution of territory positions. However, if Blackcaps continue to increase, there must come a point when territorial behaviour begins to limit the densities of the two species.

There is no obvious explanation why Blackcaps have recently increased in Britain, and apparently also in nearby Europe. A possibility is that because many Blackcaps winter in Europe they have escaped the recent deterioration of the Sahel zone which has adversely affected the numbers of Whitethroats especially, but also of Garden Warblers and certain other Palearctic migrants. Blackcaps may even have benefitted from a possible reduction in interspecific competition for food during the breeding season due to the decline of such trans-Saharan migrants. Langslow

(1978) suggests that Blackcaps may increasingly be wintering in Europe and that a change in migration routes associated with this brings more to Britain on passage than before. This may have occurred but it will be difficult or impossible to prove since there is no solid information regarding what proportion of west-European Blackcaps penetrate into sub-Saharan Africa now or formerly. If the trend exists and is continuing then a progressive scarcity of Blackcaps in West Africa will confirm it. Indeed, if the numbers of Blackcaps in Britain continue to increase the question of whether or not they are numerically related to Garden Warbler numbers will become progressively easier to resolve.

## CHAPTER EIGHT

## CONCLUSION

CHAPTER EIGHTCONCLUSION8.1. THE FUNCTION OF INTERSPECIFIC TERRITORIALITY IN BLACKCAPS AND GARDEN WARBLERS

There is disagreement about whether or not interspecific territoriality is adaptive. Orians & Willson (1964) have argued that it is, because it prevents competition for food (especially) between species which have not achieved sufficient ecological divergence to permit their coexistence, either because they have not been sympatric for long enough for such a divergence to occur or because environmental constraints limit the evolution of the necessary differences in their ecology. On the other hand, Murray (1971) considers that interspecific territoriality is misdirected intraspecific territoriality and that it is not adaptive for at least one of the species concerned. The interspecific territoriality of Blackcaps and Garden Warblers is now assessed in relation to these theories.

Orians & Willson (1964) point out that interspecific territoriality may be expected between species which occupy structurally-simple environments, where opportunities for ecological divergence are consequently limited, between species specialised for feeding within the same stratum in more complex environments, and between species affected by the prior presence in their environment of other species exploiting the same resources. The first precondition does not apply to Blackcaps and Garden Warblers since they occupy structurally-complex habitats. The second is probably also not applicable since both species are clearly physically able to forage at all levels within their environment. The third is a possibility, and Orians & Willson mention the interspecific territoriality between Blackcaps and Garden Warblers reported by Raines (1945) and suggest that in their case the behaviour results from the "restricting influence of dominant titmice in the canopy", preventing the two species from specialising in



foraging at different vegetation levels. (It must be noted, however, that whereas tits and other canopy feeders may well be numerically dominant to the two warblers in the canopy, there is no evidence that they are dominant in direct interactions. On the contrary, Blackcaps defending nectar-sources (pers.obs.) and food on bird-tables (Leach 1981) attack tits and many other bird species successfully.)

The interpretation of the interspecific territoriality between Blackcaps and Garden Warblers as being a means of avoidance of competition for food during the breeding season is supported by the observations that both species apparently obtain all their food from within their territory boundaries and that nest-sites are not likely to be in short supply for either species. Neither seems at all prone to forming mixed pairs with the other; in a survey of known cases of bird hybridisation, Gray (1958) gives only two cases of Blackcap-Garden Warbler pairs. The possibility that interspecific territoriality has evolved as a way of spacing-out nests to reduce predation upon them (a possible function of territoriality in general suggested by Tinbergen 1957) is extremely unlikely in the present case. Their territories are large and neither species nests colonially. Hence, to be effective in this way, both Blackcaps and Garden Warblers should also direct their aggression against Dunnocks, Wrens, other warblers, thrushes, and all other species which nest low down in dense undergrowth, since probably no nest-predators specialise on Blackcap and Garden Warbler nests only. However, both species ignore most of the others which use similar nest-sites.

The possible reasons why Blackcaps and Garden Warblers are so similar in their morphology and ecology require consideration. The two are, of course, likely to be similar because of their close common ancestry, but the problem is to explain why they have not diverged ecologically subsequently. Perhaps they originally occupied closely-similar niches, but in different habitats, and have only recently come together in the same habitats. This could have happened as a result of human activity. Forestry and agriculture have destroyed most of the primeval breeding habitats of the two species.

Perhaps, originally, the Blackcap was a species of tall forest and the Garden Warbler a forest-edge species, or an inhabitant of open woodlands. Now, "open" and "closed" habitats occur as small patches mixed up with each other, bringing the species associated with them into close proximity. The overlap in the habitat now used by the two species may thus be seen as a result of the wholesale disappearance of the original habitats to which they are adapted.

An alternative explanation for the lack of strict habitat preferences evident among western-Palearctic sylviids is offered by Cody (1978). He points out that Sylvia habitats especially are intrinsically unreliable, the lower vegetation being successional. They change in time and, especially because of human activities, in space, so that warblers returning from migration may encounter considerable variation in the quantity of habitat available for settlement from year to year. Cody interprets the lack of strict habitat-preferences as being an adaptation to the changeability of the vegetation which they use. He also suggests (and this may have particular relevance to Blackcaps and Garden Warblers) that because mortality on the wintering grounds and on passage probably varies from year to year, the competitive regime which warblers find where they return to breed also varies, so that some habitats which may be crowded with competitors of other species in one year may be less crowded in another year. Warblers can take advantage of variations in the density of competing species by having broad habitat preferences, so that they can switch from one habitat to another as the situation permits.

Orians & Willson (1964) emphasise a lack of sufficient ecological segregation as being a principal factor promoting interspecific territoriality between species. If there are situations where interspecific territoriality leads to mutually-exclusive territories being defended in a uniform habitat, it is probable that such a lack will be perpetuated, since the behaviour results in species being sheltered from the competition which

would normally be expected to lead to ecological divergence. In the present case, Blackcaps and Garden Warblers may remain very similar in ecology because there are no selective pressures promoting differences between them, since they are only in direct competition for space. Murray (1971) suggests the converse of this; that interspecific territoriality actually leads to ecological divergence by forcing a subordinate species into a suboptimal habitat, to which it gradually becomes better-adapted, with the evolution of changes in foraging behaviour and morphology. Blackcaps and Garden Warblers are still in the process of ecological divergence, if Murray is correct.

Cody (1969, 1973) has put forward a more extreme interpretation of the structural similarity commonly characteristic of interspecifically-territorial species. He suggests that selection favours convergence in appearance or voice between such species, since this promotes the interspecific aggression which leads to the establishment of mutually-exclusive territories in a common habitat. He regards interspecific territoriality as adaptive and as a mechanism by which species avoid competing with each other for food. Cody's theory of character convergence, and his evidence for it, have been severely criticised by Brown (1976) and Murray (1976). Murray points out that none of the nine cases of interspecific territoriality presented in detail by Cody (1969) unambiguously links interspecific territoriality and convergence. In fact, interspecific territoriality was actually unreported in seven of the nine cases. A major problem with identifying cases of character convergence is that interspecific territoriality is most frequently between closely-related species, so that similarities due to a common ancestry are hard to separate from those postulated to be due to convergence.

The possible existence of character convergence between Blackcaps and Garden Warblers may now be examined. Brown (1976) gives four criteria which a valid example of it should show. Firstly, similarities in sympatry should be greater than would normally be expected for related species evolving in a similar environment (as he admits, this criterion is subjective and can

only be applied in conjunction with the others). Secondly, there should be convergence of the features from allopatry to sympatry in at least one of the species involved. Similarity in physical appearance would be one way in which interspecific aggression could be promoted, but this probably does not apply to Blackcaps and Garden Warblers, which look quite different from each other both in sympatry and in allopatry. A more probable difference is that their songs are more similar where their ranges overlap than elsewhere, and this remains to be tested. Thirdly, there should be the ecological complements of convergence, namely similarity of feeding characteristics and at least some interspecific spacing. This requirement is certainly fulfilled by Blackcaps and Garden Warblers. Finally, in the case of song, playback experiments should show an interspecific reaction consistent with the maintenance of spatial separation. Experiments do show that sympatric Blackcaps and Garden Warblers react strongly to playback of each other's songs. It would now be interesting to see whether such reactions are weaker, or absent, where the two species are allopatric and, if so, whether this can be linked to a decreased similarity between the two songs in allopatry.

The conclusion, then, is that Blackcaps and Garden Warblers may be a valid case of character convergence in song, but further investigations are required. It must be stressed, though, that the similarity of their songs is open to alternative interpretations, common ancestry apart. The tempo and principal frequency of songs of European Sylvia warblers are significantly negatively correlated with body weight and have probably only changed indirectly during evolution, together with weight, and not through direct adaptive processes (Bergmann 1976). There is also a significant correlation between the density of the tree layer in the breeding habitat and the percentage of short, wide-range elements in the songs of the genus (Bergmann 1978), and this is interpreted as an adaptation of song characteristics in response to the acoustical properties of the environment. Given these findings, song similarity between Blackcaps and Garden Warblers can be interpreted as

partly a function of the two species being almost identical in weight and that they share the same habitats, so that both songs are adapted to the same environments.

Murray's (1971) model explains interspecific territoriality as misdirected intraspecific territoriality; i.e. it occurs because species A does not recognise species B as species B, or misidentifies it for species A. The possibility that Blackcaps and Garden Warblers are unable to distinguish each other is hard to disprove, even if intuitively it seems unlikely to be true. The two species look different, and males seem able to recognise conspecifics whilst ignoring other small brown birds. The songs of the two species do sometimes sound similar and both Cody and Murray would suggest (for different reasons) that, as a result, Blackcaps and Garden Warblers do not distinguish between them and hence respond aggressively to each other's songs, both in nature and during song playback experiments. It would be remarkable if it could be shown conclusively that Blackcaps and Garden Warblers can not tell each other's songs apart, particularly since (as pointed out by Catchpole 1978) a variety of species have been shown to be capable of fine discrimination even of conspecific songs, being able to distinguish those of neighbours from those of total strangers (Weeden & Falls 1959, Brooks & Falls 1975, Pickstock & Krebs 1980). Moreover, Blackcap and Garden Warbler songs contain enough information to permit human listeners to distinguish them easily (with practice) and so it seems likely that they could be distinguished by the birds themselves.

Catchpole (1978) tested Reed, Sedge and Marsh Warblers with each other's songs, both in Britain and in Germany. He found significant interspecific responses only between sympatric species pairs and in each case only the first species of each pair to arrive on the breeding grounds showed an interspecific response. Interspecific responses involving the same species disappeared in allopatry. Catchpole suggests that different species have learned to recognise and to respond to the songs of invading competitors,

which they have regularly heard and encountered in competitive situations. This could possibly apply to Blackcaps and Garden Warblers, although their situation differs from that of the Acrocephalus warblers in that both species (and not just the first-arrived Blackcap) respond to each other's songs in sympatry. The learned-response hypothesis would be supported if it could be shown that the two species do not respond to each other's songs in allopatry. If they do still show an interspecific response, even where they normally never meet, then the character convergence hypothesis would be supported.

A reason why Murray (1971) considered theories that interspecific territoriality is adaptive for both species as unsatisfactory is that in most cases one species is clearly dominant over the other in interspecific interactions, so that the subordinate is probably unable to settle in optimal habitat because of competition for space with the dominant species. He does not consider that interspecific territoriality can space-out two species in a habitat of uniform quality. Rather, any habitat which is optimal to both species is claimed by the dominant. He did consider, however, that interspecific territoriality can be adaptive, but only for the dominant of the two species, if there are cases where one species forces another species out of its otherwise optimal habitat. Where two species compete for food or nest-sites, individuals of species A which exclude members of species B from their territories could be more successful in raising young than individuals of species A which did not do so. Murray knew of no such cases, but the Blackcap and Garden Warbler case has some of the characteristics of the above. Blackcaps and Garden Warblers apparently compete for food and they are interspecifically interactive. Blackcaps are dominant to Garden Warblers in interactions and they keep out the latter from habitats in which they could breed. It is not known for certain, however, whether the habitat from which Garden Warblers are excluded is of optimal or only marginal quality for them, nor whether Garden Warblers keep out Blackcaps from the areas which they themselves colonise.

It seems quite possible that interspecific territoriality is adaptive for Blackcaps since by it they can apparently exclude a close competitor for food from their territories. At first sight, however, it would appear that Garden Warblers are at a disadvantage since they are less aggressive than Blackcaps and arrive later than them in the breeding habitats. Perhaps, though, Garden Warblers are adapted to cope with the apparently-unfavourable competitive regime which they regularly encounter. There is no apparent physical reason why they should be subordinate to Blackcaps but possibly, because they arrive late, they need to avoid protracted disputes over territory and to settle down to breeding as soon as they can. It is unlikely that they could displace Blackcaps completely once the latter have paired and started nesting, so it probably pays them to settle for undisputed habitat patches. Once established they do defend territories against Blackcaps but, if these persist in intruding, the Garden Warblers simply avoid them, whilst not allowing themselves to be displaced completely. The usual result is that the Blackcap intruders move elsewhere.

The reason for the late-arrival of Garden Warblers is unknown. There may be ecological reasons why they cannot cross the Sahara sooner. It is possible too that Garden Warblers may arrive late to take advantage of reductions in the territory sizes of established Blackcaps, by settling in areas occupied by that species earlier in the year.

Human observers soon find that silent Blackcaps or Garden Warblers are very hard to keep track of in the dense vegetation where they live. In both species, the song output declines substantially once the birds have paired, and some individuals then become hard to locate, although they respond at once to song playback or to singing intruders of either species. It should be quite possible for silent intruders to forage unobserved within the territory boundaries of neighbours for long periods, without being detected by the territory holders. Such "sneaky" birds were not observed during this study, but they would be very hard to detect in the densest

parts of the habitat, where the strategy could be most feasible. Radio-transmitters light enough to be carried by Great Tits now exist (P.K.McGregor, pers.comm.). Radio-telemetry may eventually be usable on warblers too and it would not be surprising if it showed that territory boundaries are less well-defined than they seem to be to human observers.

The suggestion that interspecific territoriality serves to avoid interspecific competition for food between close-competitors would not be invalidated if it is shown eventually that neighbours often trespass on each other's territories. If the habitat is of uniform quality then interspecific territoriality would be successful if it limited the total number of birds which settled there. However, if the habitat is not uniform, then perhaps a subordinate bird (e.g. a Garden Warbler) could benefit by establishing a territory in poorer habitat next to optimal habitat occupied by a dominant bird (e.g. a Blackcap), and by occasionally foraging surreptitiously within the latter's territory. Observation tends to emphasise interactions between the birds which eventually settle in an area but the real importance of territorial behaviour, both interspecific and intraspecific, may be in preventing many other birds from settling at all. The removal experiment showed that extra Garden Warblers and Blackcaps exist, but these probably normally avoid areas where they hear conspecifics singing, so that direct interactions are less frequent than the number of potential settlers available would suggest.

## 8.2. INTERSPECIFIC TERRITORIALITY AND THE SIZES OF BLACKCAP AND GARDEN WARBLER POPULATIONS

The question of the possible relationship between territorial behaviour and bird population sizes has been reviewed by Watson & Moss (1970) and Klomp (1972). A controversy regarding the consequences of territorial behaviour is whether it limits the population density within a particular area or whether it merely serves to space-out resident birds.



In the situation envisaged by the "density-limiting" model of territoriality (Brown 1969), the dominant competitors exclude the less fit ones from optimal habitat, so that the latter are unable to breed at all or must settle in sub-optimal habitats, where they achieve a relatively poor breeding success. The "density-assessment" model of territoriality (Fretwell & Lucas 1969) sees all competitors as free to settle wherever they like. In this case, territoriality does not exclude any birds from any area but birds settle instead where they can achieve the highest reproductive success. This means that the average reproductive success is the same in all habitats used, although breeding-densities may vary between habitats according to resource availability. The latter model considers territory sizes in any one habitat as a function of the number of birds which settle there.

Where removal experiments show the existence of "surplus" birds which have failed to get territories in a particular area, the conclusion can be that territorial behaviour is limiting the local population density in that year, by setting a lower limit to territory sizes (Davies 1978). The removal of Blackcaps has shown that their territorial behaviour limits the local density of both breeding Blackcaps and Garden Warblers, since some birds of both species were being excluded from the removal zone by the resident Blackcaps. However, the analysis of breeding success of the two species in scrub and in woodland showed it to be about equal in the two habitats for both of them. This implies that woodland is not an optimal habitat, for which competition for space might be expected to be strong, since both species can achieve just as high a reproductive success in the scrub.

Three possibilities may explain the findings of the present study; that territorial behaviour excludes some birds from woodland but that, nevertheless, both species can achieve similar breeding success in either woodland or scrub.

a) The measure of success used is not good enough and, in fact, real reproductive success is better in woodland than in scrub.

b) The two particular habitats compared, scrub and woodland, look different to human observers but, as far as the birds are concerned, they are just subsets of the same habitat. Hence reproductive success is the same in both of them. Other (suboptimal) habitats exist, but were not included in the analysis. Perhaps, alternatively, the classifications "scrub" and "woodland" are too broad. Each includes optimal and suboptimal portions but when the two are combined together, as in this analysis, average reproductive success in each habitat as a whole does not differ between scrub and woodland.

c) The data supports an ideal-free model of habitat selection but the model of Fretwell & Lucas (1969) can not be applied exactly since individuals are not free to settle where they want to. A new model is needed which incorporates an element of competition for space. Perhaps what occurs is that in some years the total amount of all habitats available is insufficient to accommodate all the birds which have survived since the previous season. At first, birds colonise all habitats in the way suggested by the ideal-free model. However, eventually the densities in all habitats are such that territory sizes can no longer be compressed any further. At this point, territorial behaviour excludes surplus birds from both woodland and scrub (in this case) equally, and these extra birds are probably unable to breed at all.

It must be added that there is no evidence that Blackcaps and Garden Warblers prospect different habitats before they settle to breed in any one type. On the contrary, there is some evidence of fidelity to the same habitat (or site) in successive years, so that perhaps in nature there actually exist sub-populations of scrub Blackcaps and woodland Garden Warblers (etc.), which usually breed only in those habitats. Catchpole (1974) has shown that there is a strong element of tradition in habitat selection by Reed Warblers, birds tending to return in later years to the habitats in which they bred successfully.

The general conclusion of the present study is that the territorial behaviour of Blackcaps limits the local breeding densities of

both Blackcaps and Garden Warblers in woodland, in any one year. There is no evidence at present, however, that in the long term the numbers of Garden Warblers are regulated by the numbers of Blackcaps in Britain as a whole. Perhaps, as in Great Tits (Krebs 1970), territorial behaviour has only a weak density-dependent effect on the population sizes of either species; although it limits the breeding densities of both species each year it does not limit densities to the same extent every year. Nevertheless, if Blackcaps continue to increase in Britain, it is expected that, eventually, they should have a negative impact on the Garden Warbler population. As earlier suggested, a long-term census study of the two species would be of interest, particularly if it also involved colour-marking of adults and young, territory mapping and the sampling of food densities within each territory. It could be that Garden Warblers which have already bred in a particular area in one year are not easily kept out of the area the next year, should their former territory be settled by Blackcaps. However, they may have to accept smaller territories than usual in years of high Blackcap densities.

APPENDICES

APPENDIX A. SCIENTIFIC NAMES OF THE BIRD SPECIES NAMED IN THE TEXT

|                                |                                  |
|--------------------------------|----------------------------------|
| Blackcap                       | <i>Sylvia atricapilla</i>        |
| Chaffinch                      | <i>Fringilla coelebs</i>         |
| Chiffchaff                     | <i>Phylloscopus collybita</i>    |
| Duncock                        | <i>Prunella modularis</i>        |
| Firecrest                      | <i>Regulus ignicapillus</i>      |
| Flycatcher, Pied               | <i>Ficedula hypoleuca</i>        |
| , Spotted                      | <i>Muscicapa striata</i>         |
| Goldcrest                      | <i>Regulus regulus</i>           |
| Grouse, Red                    | <i>Lagopus lagopus</i>           |
| Oriole, Golden                 | <i>Oriolus oriolus</i>           |
| Sparrow, Song                  | <i>Melospiza melodia</i>         |
| Starling                       | <i>Sturnus vulgaris</i>          |
| Tit, Blue                      | <i>Parus caeruleus</i>           |
| Great                          | <i>P.major</i>                   |
| Marsh                          | <i>P.palustris</i>               |
| Vireo, Philadelphia            | <i>Vireo philadelphicus</i>      |
| Red-eyed                       | <i>V.olivaceus</i>               |
| (Warblers, <u>Sylvia</u> )     |                                  |
| Warbler, Arabian               | <i>Sylvia leucomelaena</i>       |
| Barred                         | <i>S.nisoria</i>                 |
| Cyprus                         | <i>S.melanothorax</i>            |
| Dartford                       | <i>S.undata</i>                  |
| Desert                         | <i>S.nana</i>                    |
| Garden                         | <i>S.borin</i>                   |
| Marmora's                      | <i>S.sarda</i>                   |
| Menetries'                     | <i>S.mystacea</i>                |
| Orphean                        | <i>S.hortensis</i>               |
| Ruppells                       | <i>S.ruppelli</i>                |
| Sardinian                      | <i>S.melanocephala</i>           |
| Spectacled                     | <i>S.conspicillata</i>           |
| Subalpine                      | <i>S.cantillans</i>              |
| Tristram's                     | <i>S.deserticola</i>             |
| (Warblers, not <u>Sylvia</u> ) |                                  |
| Warbler, Blue-winged           | <i>Vermivora pinus</i>           |
| Grasshopper                    | <i>Locustella naevia</i>         |
| Great Reed                     | <i>Acrocephalus arundinaceus</i> |
| Marsh                          | <i>A.palustris</i>               |
| Reed                           | <i>A.scirpaceus</i>              |
| Sedge                          | <i>A.schoenobaenus</i>           |
| Willow                         | <i>Phylloscopus trochilus</i>    |
| Wood                           | <i>P.sibilatrix</i>              |
| Whitethroat                    | <i>Sylvia communis</i>           |
| Whitethroat, Lesser            | <i>S.curruca</i>                 |
| Wren                           | <i>Troglodytes troglodytes</i>   |
| Wren, Bewick's                 | <i>Thryomanes bewickii</i>       |

APPENDIX B. SCIENTIFIC NAMES OF THE PLANT SPECIES NAMED IN THE TEXT

|                 |                              |
|-----------------|------------------------------|
| Ash             | <i>Fraxinus excelsior</i>    |
| Beech           | <i>Fagus sylvatica</i>       |
| Birch           | <i>Betula pendula</i>        |
| Blackthorn      | <i>Prunus spinosa</i>        |
| Bramble         | <i>Rubus fruticosus</i>      |
| Chestnut, Sweet | <i>Castanea sativa</i>       |
| Dog's Mercury   | <i>Mercurialis perennis</i>  |
| Elder           | <i>Sambucus nigra</i>        |
| Elm             | <i>Ulmus procera</i>         |
| Fir, Douglas    | <i>Pseudotsuga taxifolia</i> |
| Hawthorn        | <i>Crataegus monogyna</i>    |
| Hazel           | <i>Corylus avellana</i>      |
| Holly           | <i>Ilex aquifolium</i>       |
| Hornbeam        | <i>Carpinus betulus</i>      |
| Ivy             | <i>Hedera helix</i>          |
| Larch           | <i>Larix decidua</i>         |
| Maple (Field)   | <i>Acer campestre</i>        |
| Nettle          | <i>Urtica dioica</i>         |
| Oak             | <i>Quercus robur</i>         |
| Sycamore        | <i>Acer pseudoplatanus</i>   |
| Wayfaring Tree  | <i>Viburnum lantana</i>      |
| Willow, Goat    | <i>Salix capraea</i>         |

APPENDIX 2-1. THE COMMON BIRDS CENSUS RESULTS ANALYSED

| <u>CENSOR</u>             | <u>CODE</u> | <u>LOCATION</u> | <u>YEARS' DATA EXAMINED</u> |
|---------------------------|-------------|-----------------|-----------------------------|
| AUSTIN, M.J.              | 033         | STAFFS          | 1966 - 1976                 |
| BERTENSHAW, J.A.          | 085         | ESSEX           | 1964 - 1968                 |
| CANFORD MAGNA SCHOOL      | 136         | DORSET          | 1964 - 1968                 |
| DAVENPORT, M.             | 183         | KENT            | 1965 - 1968                 |
| DENNIS, M.K.              | 190         | ESSEX           | 1975 - 1976                 |
| DIMSDALE, R.F.            | 184         | HERTS           | 1965 - 1966                 |
| FINCHER, F.               | 282         | WORCS           | 1964 - 1965                 |
| HOLLINGS, M.              | 383         | SUSSEX          | 1964 - 1967                 |
| HOPKINS, W & HARRISON, P. | 385         | SOMERSET        | 1965 - 1971                 |
| PEART, R.                 | 649         | KENT            | 1970 - 1971                 |
| PENISTON, M.J.            | 641         | GLOS            | 1966 - 1971                 |
| PREECE, M.V.              | 642         | BRECKNOCK       | 1966 - 1970                 |
| STEWART-HESS, H.          | 737         | DEVON           | 1965 - 1971                 |
| SUMMERS-SMITH, D.         | 736         | N.YORKS         | 1964 - 1971                 |
| SWAN, J.H.                | 739         | BEDS            | 1965 - 1966                 |
| WALKER, B.W.              | 851         | CUMBRIA         | 1965 - 1975                 |
| WOODELL, S.               | 865         | BUCKS           | 1968 - 1975                 |

Additional censuses examined but used only in the analysis described in Chapter 7 (Table 7-2, q.v.).

|                |     |       |             |
|----------------|-----|-------|-------------|
| BOLTON, D.     | 906 | MON   | 1968 - 1972 |
| CADDICK, H.M.  | 141 | GLOS  | 1966 - 1971 |
| WILLIAMSON, K. | 853 | BUCKS | 1966 - 1973 |

APPENDIX 2-2. THE BREEDING BIOLOGY OF BLACKCAPS AND GARDEN WARBLERS COMPARED BETWEEN NORTH AND SOUTH BRITAIN

Data based on the nest record cards examined during the present study.

|                                                                       | <u>BLACKCAP</u>                |                                | <u>GARDEN WARBLER</u>          |                               |
|-----------------------------------------------------------------------|--------------------------------|--------------------------------|--------------------------------|-------------------------------|
|                                                                       | SOUTHERN                       | NORTHERN                       | SOUTHERN                       | NORTHERN                      |
|                                                                       | NESTS                          | NESTS                          | NESTS                          | NESTS                         |
| MEAN DATE OF FIRST EGG (S.D.)                                         | MAY 19 (15 days)<br>n = 643    | MAY 20 (14 days)<br>n = 133    | MAY 27 (14 days)<br>n = 385    | MAY 29 (14 days)<br>n = 70    |
| MEAN CLUTCH SIZE ( $\pm 1$ S.E.)                                      | 4.62 ( $\pm 0.03$ )<br>n = 660 | 4.63 ( $\pm 0.06$ )<br>n = 138 | 4.41 ( $\pm 0.04$ )<br>n = 254 | 4.41 ( $\pm 0.09$ )<br>n = 61 |
| PRODUCTIVITY - mean number of young leaving all nests ( $\pm 1$ S.E.) | 2.38 ( $\pm 0.08$ )<br>n = 694 | 2.47 ( $\pm 0.19$ )<br>n = 143 | 2.46 ( $\pm 0.11$ )<br>n = 326 | 2.51 ( $\pm 0.28$ )<br>n = 59 |

The three variables were compared within-species between northern and southern nests by d-test. No differences are significant.

NOTE The centres of northern and southern Britain, as defined in Chapter 7, are about 600 kilometres apart.



# APPENDIX 6-1

## THE RESPONSE PARAMETERS OF SUBJECTS WHICH RESPONDED TO BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG PLAYBACK COMPARED BETWEEN EXPERIMENTS CONDUCTED IN 1978 AND IN 1980

Mean responses ( $\pm 1$  S.E.).

### A. RESPONSES OF BLACKCAP SUBJECTS

|              | Responses to BC song |                      | Responses to GW song |                      |
|--------------|----------------------|----------------------|----------------------|----------------------|
|              | playback             |                      | playback             |                      |
|              | in 1978<br>(n = 9)   | in 1980<br>(n = 15)  | in 1978<br>(n = 8)   | in 1980<br>(n = 17)  |
| LATENCY (s)  | 94.8 ( $\pm 17.6$ )  | 85.9 ( $\pm 15.8$ )  | 157.9 ( $\pm 35.8$ ) | 101.1 ( $\pm 15.0$ ) |
| DISTANCE (m) | 4.1 ( $\pm 1.3$ )    | 2.7 ( $\pm 0.9$ )    | 5.9 ( $\pm 1.2$ )    | 3.9 ( $\pm 1.0$ )    |
| TIME (s)     | 123.8 ( $\pm 26.1$ ) | 152.7 ( $\pm 23.4$ ) | 91.5 ( $\pm 29.9$ )  | 118.8 ( $\pm 17.8$ ) |

### B. RESPONSES OF GARDEN WARBLER SUBJECTS

|              | Responses to GW song |                      | Responses to BC song |                      |
|--------------|----------------------|----------------------|----------------------|----------------------|
|              | playback             |                      | playback             |                      |
|              | in 1978<br>(n = 12)  | in 1980<br>(n = 11)  | in 1978<br>(n = 10)  | in 1980<br>(n = 7)   |
| LATENCY (s)  | 123.0 ( $\pm 25.3$ ) | 68.4 ( $\pm 17.3$ )  | 148.7 ( $\pm 31.9$ ) | 83.0 ( $\pm 32.7$ )  |
| DISTANCE (m) | 10.3 ( $\pm 2.3$ )   | 4.8 ( $\pm 2.1$ )    | 6.3 ( $\pm 1.0$ )    | 9.6 ( $\pm 1.9$ )    |
| TIME (s)     | 45.0 ( $\pm 24.7$ )  | 152.8 ( $\pm 26.0$ ) | 77.6 ( $\pm 19.3$ )  | 112.4 ( $\pm 41.4$ ) |

Responses to each song were compared between the two years for both Blackcap and Garden Warbler subjects, by Mann-Whitney U test (2-tailed). Garden Warblers approached the speaker significantly more closely in response to Garden Warbler song in 1980 than in 1978 ( $p < 0.05$ ). No other differences are significant.

## APPENDIX 6-2.

### THE EFFECT OF SEQUENCE OF PRESENTATION ON THE INTENSITY OF RESPONSES TO THE EXPERIMENTAL TAPES DURING SONG PLAYBACK EXPERIMENTS

The experiment which tested whether Blackcaps discriminate between two different types of Garden Warbler song (6.6.1.D) showed that all subjects reacted to Garden Warbler song the first time it was presented but some failed to do so on the second presentation, even though the second tape was different from the first one they had heard. This suggested that sequence of presentation affects the magnitude of responses given to different experimental tapes.

The suggestion is supported by the data in Table 6-i, where a comparison is made between the first and second responses obtained from each subject, regardless of whether Blackcap or Garden Warbler song was presented first. Blackcaps approached significantly closer, and remained near the speaker for a significantly longer time (more than twice as long) on their first encounter with song playback than on the second. For Garden Warbler subjects, the differences between Latency and Distance scores are not significant but that between Time scores is significant and striking; on the first presentation of playback birds stayed near the speaker nearly three times as long on average as they did the second time they responded.

The data used in Table 6-i was from 1978 and 1980 subjects which responded to both songs. Five further Blackcaps and four Garden Warblers were tested with both songs but failed to respond to one of them (both in the case of one Blackcap). The Garden-Warbler non-responders had all previously responded to the first tape presented to them. For Blackcaps there is no obvious effect of presentation sequence on whether or not a bird responded, but the sample is very small (Table 6-ii). In 1979, Blackcaps were tested solely with two different Garden Warbler songs. Responses to the first presentation averaged stronger than to the second, although the differences are not significant (Table 6-iii).

TABLE 6-i. A COMPARISON BETWEEN THE FIRST AND SECOND RESPONSES OBTAINED FROM BLACKCAP AND GARDEN WARBLER SUBJECTS WHICH RESPONDED TO BOTH BLACKCAP AND GARDEN WARBLER SONG PLAYBACK

Mean responses ( $\pm 1$  S.E.).

A. RESPONSES OF BLACKCAP SUBJECTS (n = 15)

|              | Responses to the<br>FIRST tape presented | Responses to the<br>SECOND tape presented | COMPARISONS |
|--------------|------------------------------------------|-------------------------------------------|-------------|
| LATENCY (s)  | 81.3 ( $\pm 14.3$ )                      | 111.4 ( $\pm 21.2$ )                      | n.s.        |
| DISTANCE (m) | 2.4 ( $\pm 0.8$ )                        | 6.0 ( $\pm 1.1$ )                         | p < 0.02    |
| TIME (s)     | 165.8 ( $\pm 15.8$ )                     | 76.9 ( $\pm 20.2$ )                       | p < 0.01    |

B. RESPONSES OF GARDEN WARBLER SUBJECTS (n = 15)

|              | Responses to the<br>FIRST tape presented | Responses to the<br>SECOND tape presented | COMPARISONS |
|--------------|------------------------------------------|-------------------------------------------|-------------|
| LATENCY (s)  | 95.3 ( $\pm 23.4$ )                      | 131.7 ( $\pm 25.1$ )                      | n.s.        |
| DISTANCE (m) | 7.9 ( $\pm 1.5$ )                        | 10.4 ( $\pm 2.0$ )                        | n.s.        |
| TIME (s)     | 133.2 ( $\pm 26.0$ )                     | 46.9 ( $\pm 18.1$ )                       | p < 0.02    |

- NOTES.
1. Statistical comparisons are by the Wilcoxon test (2-tailed).
  2. The table distinguishes solely between whether Blackcap song preceded Garden Warbler song playback, or vice-versa. Responses to other experimental tapes are ignored.
  3. About half the subjects encountered Blackcap song before Garden Warbler song, and vice-versa.
  4. The data shown is a re-grouping of that in Table 6-4.

TABLE 6-ii. THE NUMBERS OF BLACKCAP AND GARDEN WARBLER SUBJECTS WHICH DID NOT RESPOND TO PLAYBACK OF EITHER BLACKCAP (BC) SONG OR GARDEN WARBLER (GW) SONG, SHOWN ACCORDING TO WHETHER THEY FAILED TO RESPOND TO THE FIRST OR SECOND TAPE WHICH THEY MET

| NO RESPONSE<br>GIVEN TO; | <u>BLACKCAP SUBJECTS</u> |                    | <u>GARDEN WARBLER SUBJECTS</u> |                    |
|--------------------------|--------------------------|--------------------|--------------------------------|--------------------|
|                          | SONG MET<br>FIRST        | SONG MET<br>SECOND | SONG MET<br>FIRST              | SONG MET<br>SECOND |
| BC SONG                  | 1                        | 2                  | 0                              | 4                  |
| GW SONG                  | 1                        | 0                  | 0                              | 0                  |

- NOTES.
1. A Blackcap which responded to neither tape is excluded.
  2. Encounters with the other experimental tapes used are ignored in the table.

TABLE 6-iii. THE RESPONSES TO TWO DIFFERENT GARDEN WARBLER SONGS BY BLACKCAPS TESTED IN 1979 SHOWN ACCORDING TO THE ORDER IN WHICH THE SONGS WERE PRESENTED

|              | Responses to the<br>FIRST song presented<br>(n = 12) | Responses to the<br>SECOND song presented<br>(n = 7) |
|--------------|------------------------------------------------------|------------------------------------------------------|
| LATENCY (s)  | 62.3 ( $\pm$ 17.5)                                   | 107.7 ( $\pm$ 37.4)                                  |
| DISTANCE (m) | 9.9 ( $\pm$ 3.5)                                     | 10.8 ( $\pm$ 4.3)                                    |
| TIME (s)     | 123.4 ( $\pm$ 29.3)                                  | 118.7 ( $\pm$ 52.2)                                  |

Mean responses ( $\pm$  1.S.E.).

- NOTES.
1. The three variables do not differ significantly between the two sets of data (Mann-Whitney U test, 2-tailed).
  2. Responses to long and short songs are combined; comparisons are simply between the first and second songs to which the birds responded. Five birds did not respond during their second encounter with song playback.

The design of the song playback experiments included the presentation of tapes to different subjects in random order. Any given tape was encountered first (or second or third) by a similar proportion of subjects (except for the experiments with Whitethroat and Garden Warbler song presented to Blackcaps) and hence comparisons of the responses to different tapes are probably independent of any effect of presentation-sequence on response intensities. Nevertheless it is of interest to know whether tape presentation sequences affect how strongly birds respond since such information can show how sensitive subjects are to the artificial features of song playbacks.

Table 6-iv compares responses to Blackcap and to Garden Warbler song playback separately between those individuals which encountered the songs before any other experimental tape whatsoever and those which were presented with the same songs only after they had already been tested with other tapes (including perhaps the Great Tit song or either of the two whitethroat songs). The comparisons are thus between two independent sets of information. Almost without exception, responses averaged stronger on first presentations than on subsequent ones. In most cases the differences are not significant but Garden Warblers responding to Garden Warbler song stayed near the speaker significantly longer on average when the song was presented first than when it was presented later.

Table 6-v determines whether birds which have previously responded to song playback respond to Blackcap and to Garden Warbler song less strongly than those which have not responded to any song, even though they may have been presented with them. Blackcaps which have previously responded to another experimental tape respond less strongly on average to Blackcap song than those which have not, but the differences are not significant. However, when Blackcaps are responding to Garden Warbler song, subjects whose exposure to the song was not preceded by an earlier response respond more strongly than others, and the differences in Distance and Time

TABLE 6-iv. A COMPARISON OF THE RESPONSES OF SUBJECTS TO BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG PLAYBACK, ACCORDING TO THE ORDER OF PRESENTATION OF THE EXPERIMENTAL TAPES

Mean responses ( $\pm 1$  S.E.).

A. RESPONSES OF BLACKCAP SUBJECTS

|              | Responses to BC song<br>playback |                                      | Responses to GW song<br>playback |                                      |
|--------------|----------------------------------|--------------------------------------|----------------------------------|--------------------------------------|
|              | 1. SONG MET<br>FIRST<br>(n = 9)  | 2. SONG NOT MET<br>FIRST<br>(n = 15) | 3. SONG MET<br>FIRST<br>(n = 8)  | 4. SONG NOT MET<br>FIRST<br>(n = 17) |
| LATENCY (s)  | 84.9 ( $\pm 18.9$ )              | 91.9 ( $\pm 15.3$ )                  | 127.4 ( $\pm 28.1$ )             | 115.5 ( $\pm 19.7$ )                 |
| DISTANCE (m) | 1.7 ( $\pm 0.3$ )                | 4.1 ( $\pm 1.1$ )                    | 3.0 ( $\pm 1.3$ )                | 5.1 ( $\pm 1.0$ )                    |
| TIME (s)     | 156.3 ( $\pm 21.1$ )             | 133.1 ( $\pm 25.2$ )                 | 123.9 ( $\pm 20.6$ )             | 102.0 ( $\pm 18.0$ )                 |

All statistical comparisons within songs (columns 1 v 2, 3 v 4) show no significant differences. Between-song comparisons of first presentations (columns 1 v 3) also show no significant differences.

B. RESPONSES OF GARDEN WARBLER SUBJECTS

|              | Responses to GW song<br>playback |                                      | Responses to BC song<br>playback |                                     |
|--------------|----------------------------------|--------------------------------------|----------------------------------|-------------------------------------|
|              | 1. SONG MET<br>FIRST<br>(n = 6)  | 2. SONG NOT MET<br>FIRST<br>(n = 16) | 3. SONG MET<br>FIRST<br>(n = 9)  | 4. SONG NOT MET<br>FIRST<br>(n = 9) |
| LATENCY (s)  | 105.5 ( $\pm 31.4$ )             | 96.4 ( $\pm 20.7$ )                  | 121.6 ( $\pm 30.4$ )             | 113.8 ( $\pm 35.7$ )                |
| DISTANCE (m) | 2.8 ( $\pm 0.9$ )                | 9.8 ( $\pm 2.2$ )                    | 7.8 ( $\pm 1.4$ )                | 6.8 ( $\pm 1.5$ )                   |
| TIME (s)     | 162.0 ( $\pm 40.8$ )             | 62.9 ( $\pm 21.7$ )                  | 102.2 ( $\pm 22.7$ )             | 98.4 ( $\pm 36.3$ )                 |

Time scores differ significantly between columns 1 & 2 ( $p < 0.05$ ). All other statistical comparisons within songs (columns 1 v 2, 3 v 4) show no significant differences. Between-song comparisons of first presentations (columns 1 v 3) show birds approached the speaker significantly closer when responding to Garden Warbler song than to Blackcap song ( $p < 0.05$ ); other differences are not significant.

NOTES. 1. Statistical comparisons are by the Mann-Whitney U test, 2-tailed.

2. Songs met first were those encountered by subjects before any other experimental tape whatsoever.

3. Late-season responses, and those of Blackcaps in 1979 (when they were only tested with Garden Warbler song), are not included above.

TABLE 6-v. A COMPARISON OF THE RESPONSES OF SUBJECTS TO BLACKCAP (BC) AND GARDEN WARBLER (GW) SONG PLAYBACK, ACCORDING TO WHETHER OR NOT THEY HAVE PREVIOUSLY RESPONDED TO ANY PLAYBACK TAPE

Mean responses ( $\pm 1$  S.E.).

A. RESPONSES OF BLACKCAP SUBJECTS

|              | Responses to BC song<br>playback preceded by<br>a previous response ? |                      | Responses to GW song<br>playback preceded by<br>a previous response ? |                      |
|--------------|-----------------------------------------------------------------------|----------------------|-----------------------------------------------------------------------|----------------------|
|              | 1. YES                                                                | 2. NO                | 3. YES                                                                | 4. NO                |
|              | (n = 14)                                                              | (n = 10)             | (n = 14)                                                              | (n = 11)             |
| LATENCY (s)  | 92.0 ( $\pm 13.7$ )                                                   | 85.4 ( $\pm 21.3$ )  | 112.6 ( $\pm 20.1$ )                                                  | 127.7 ( $\pm 26.3$ ) |
| DISTANCE (m) | 3.0 ( $\pm 0.7$ )                                                     | 3.5 ( $\pm 1.6$ )    | 2.5 ( $\pm 0.8$ )                                                     | 7.1 ( $\pm 1.0$ )    |
| TIME (s)     | 145.2 ( $\pm 19.7$ )                                                  | 137.1 ( $\pm 32.9$ ) | 141.5 ( $\pm 18.6$ )                                                  | 77.3 ( $\pm 21.8$ )  |

There are significant differences between columns 3 & 4 in Distance scores ( $p < 0.001$ ) and Time scores ( $p < 0.025$ ). All other statistical comparisons within songs (columns 1 v 2, 3 v 4), and between-song comparisons of first presentations (columns 1 v 3) show no significant differences.

B. RESPONSES OF GARDEN WARBLER SUBJECTS

|              | Responses to GW song<br>playback preceded by<br>a previous response ? |                      | Responses to BC song<br>playback preceded by<br>a previous response ? |                      |
|--------------|-----------------------------------------------------------------------|----------------------|-----------------------------------------------------------------------|----------------------|
|              | 1. YES                                                                | 2. NO                | 3. YES                                                                | 4. NO                |
|              | (n = 12)                                                              | (n = 10)             | (n = 11)                                                              | (n = 7)              |
| LATENCY (s)  | 88.8 ( $\pm 21.6$ )                                                   | 111.0 ( $\pm 27.5$ ) | 107.9 ( $\pm 26.3$ )                                                  | 133.3 ( $\pm 43.7$ ) |
| DISTANCE (m) | 4.2 ( $\pm 1.5$ )                                                     | 12.4 ( $\pm 2.7$ )   | 7.5 ( $\pm 1.3$ )                                                     | 7.1 ( $\pm 1.8$ )    |
| TIME (s)     | 139.9 ( $\pm 30.9$ )                                                  | 29.9 ( $\pm 12.5$ )  | 128.7 ( $\pm 25.6$ )                                                  | 55.7 ( $\pm 29.9$ )  |

Time scores differ significantly between columns 1 & 2 ( $p < 0.01$ ) and between columns 3 & 4 ( $p < 0.05$ ). All other statistical comparisons within songs (columns 1 v 2, 3 v 4), and between-song comparisons of first responses (columns 1 v 3), show no significant differences.

NOTES. 1. Statistical comparisons are by the Mann-Whitney U test, 2-tailed.

2. Subjects are divided according to whether or not their encounters with BC or GW song had been preceded by a response to any tape. Thus (for example), responses of birds which were tested with Whitethroat song before Blackcap song and responded to the former are included in one data set and responses of birds which were tested in the same sequence but did not respond to the Whitethroat song are included in the other data set.

3. Late-season responses, and those of Blackcaps in 1979 (when they were only tested with Garden Warbler song), are not included above.

scores are highly significant (Table 6-v A). Garden Warblers which have previously responded to another tape respond less strongly on average to both Blackcap and Garden Warbler song playback than "naive" subjects, and the difference in Time scores is striking and significant in both cases (Table 6-v B).

Tables 6-iv and 6-v may also be used to examine the conclusion, based on Table 6-4, that Blackcaps and Garden Warblers respond as strongly to playback of each other's songs as to that of conspecific songs. Between-column comparisons (1 v 3) in both tables show that the conclusion is justified in the case of Blackcap subjects. The Latency and Time scores of Garden Warbler subjects similarly do not differ significantly between birds responding to either Garden Warbler or Blackcap song; the Distance scores show a stronger response to Garden Warbler song than to Blackcap song but only when absolute first responses are compared (Table 6-iv B).

### CONCLUSION

There are grounds for believing that the sequence in which tapes are presented to subjects affects the intensity of the responses which they give. The effect is most conspicuous with Garden Warbler subjects. In both species, mean Latency scores are not significantly affected by order of presentation, suggesting that most subjects respond to Blackcap or Garden Warbler song as soon as they hear the tapes. Distance and Time scores are significantly affected by presentation-sequences in some of the comparisons made, and others show a similar trend, stronger responses being given by subjects with no previous history of response to song playback. This suggests that once a bird begins to respond, the intensity of his response is affected by his past experience.

Two possible reasons suggest themselves as likely explanations of why subsequent exposures to song playback elicit weaker responses than earlier ones. Habituation to the songs themselves can be discounted since



no song was presented to any subject more than once. Perhaps the observations can be regarded instead as habituation to the song playback situation. The experiments are intended to simulate intrusions by other males into the territories of the subjects. However, the artificial intruders differ from real ones especially in that in song playback experiments no intruder can be found by a responder and also that the tape is not responsive to the vocalisations of the territory holder, as a real intruder may be, but instead sings on inexorably, oblivious of the close proximity of an aggressive, perhaps singing bird. A subject encountering an intruder with these unusual characteristics (invisibility and persistence while singing in the face of likely aggression) may well recall its earlier unprofitable search for a similar interloper the next time song playback is presented to it and so may respond less strongly on future occasions. In addition, since all presentations to each bird were made from the same position within its territory, subjects may associate the location with an unprofitable search for a rival and so may give up more easily the next time than would happen if all presentations were made from different positions. (This latter possibility could easily be tested-for by comparing responses of birds to successive presentations of song playback broadcast from a fixed site within the territory or from several separate sites.) The fact that it is the persistence of responders (Time scores) that is most clearly affected by previous experience of song playback supports the above suggestions.

APPENDIX 7-1. THE VALUES OF THE COMMON BIRDS CENSUS ANNUAL INDICES  
FOR BLACKCAP AND GARDEN WARBLER POPULATIONS IN  
WOODLAND AND ON FARMLAND

| <u>YEAR</u> | <u>BLACKCAP INDEX</u> |          | <u>GARDEN WARBLER INDEX</u> |          |
|-------------|-----------------------|----------|-----------------------------|----------|
|             | WOODLAND              | FARMLAND | WOODLAND                    | FARMLAND |
| 1962        | -                     | 24       | -                           | 49       |
| 1963        | -                     | 44       | -                           | 63       |
| 1964        | 91                    | 80       | -                           | 105      |
| 1965        | 84                    | 68       | 123                         | 86       |
| 1966        | 100                   | 100      | 100                         | 100      |
| 1967        | 92                    | 86       | 101                         | 84       |
| 1968        | 99                    | 114      | 97                          | 117      |
| 1969        | 104                   | 105      | 92                          | 77       |
| 1970        | 101                   | 127      | 86                          | 94       |
| 1971        | 95                    | 115      | 82                          | 88       |
| 1972        | 115                   | 157      | 100                         | 61       |
| 1973        | 118                   | 173      | 94                          | 56       |
| 1974        | 100                   | 144      | 97                          | 43       |
| 1975        | 93                    | 142      | 63                          | 47       |
| 1976        | 100                   | 123      | 74                          | 30       |
| 1977        | 111                   | 161      | 66                          | 42       |
| 1978        | 83                    | 134      | 92                          | 47       |
| 1979        | 92                    | 138      | 80                          | 39       |
| 1980        | 116                   | 185      | 98                          | 43       |

APPENDIX 7-2. THE ANNUAL DENSITIES (birds/km<sup>2</sup>) OF BLACKCAPS AND GARDEN  
WARBLERS ON WOODLAND AND FARMLAND COMMON BIRDS CENSUS PLOTS

The densities given are based on the total number of territories of each species found within the combined area of all the census plots.

| <u>YEAR</u> | <u>BLACKCAP DENSITY</u> |          | <u>GARDEN WARBLER DENSITY</u> |          |
|-------------|-------------------------|----------|-------------------------------|----------|
|             | WOODLAND                | FARMLAND | WOODLAND                      | FARMLAND |
| 1962        | -                       | 0.3      | -                             | 0.4      |
| 1963        | -                       | 0.6      | -                             | 0.5      |
| 1964        | 13.1                    | 1.7      | -                             | 0.9      |
| 1965        | 11.7                    | 1.4      | 7.1                           | 0.8      |
| 1966        | 13.6                    | 1.7      | 5.6                           | 0.9      |
| 1967        | 15.7                    | 1.5      | 6.8                           | 0.7      |
| 1968        | 14.4                    | 1.9      | 7.4                           | 1.1      |
| 1969        | 15.2                    | 1.7      | 6.3                           | 0.8      |
| 1970        | 17.0                    | 2.5      | 6.9                           | 1.0      |
| 1971        | 15.4                    | 1.9      | 7.1                           | 0.7      |
| 1972        | 16.8                    | 2.8      | 6.9                           | 0.6      |
| 1973        | 12.7                    | 2.9      | 4.3                           | 0.6      |
| 1974        | 11.4                    | 2.3      | 3.9                           | 0.5      |
| 1975        | 9.6                     | 2.6      | 2.6                           | 0.6      |
| 1976        | 10.8                    | 2.2      | 3.7                           | 0.4      |
| 1977        | 13.0                    | 2.7      | 3.6                           | 0.6      |
| 1978        | 12.6                    | 2.2      | 4.2                           | 0.7      |
| 1979        | 14.4                    | 2.3      | 4.4                           | 0.5      |
| 1980        | 19.5                    | 3.2      | 6.3                           | 0.6      |

APPENDIX 7-3. THE NUMBERS OF NEST RECORD CARDS SUBMITTED ANNUALLY FOR  
BLACKCAP AND GARDEN WARBLER NESTS DURING THE PERIOD  
1949 - 1978

| <u>YEAR</u> | <u>BLACKCAP CARDS</u> | <u>GARDEN WARBLER CARDS</u> |
|-------------|-----------------------|-----------------------------|
| 1949        | 8                     | 7                           |
| 1950        | 25                    | 9                           |
| 1951        | 38                    | 14                          |
| 1952        | 31                    | 15                          |
| 1953        | 18                    | 18                          |
| 1954        | 19                    | 21                          |
| 1955        | 32                    | 13                          |
| 1956        | 12                    | 22                          |
| 1957        | 18                    | 15                          |
| 1958        | 27                    | 16                          |
| 1959        | 11                    | 14                          |
| 1960        | 27                    | 18                          |
| 1961        | 23                    | 17                          |
| 1962        | 39                    | 38                          |
| 1963        | 21                    | 27                          |
| 1964        | 52                    | 22                          |
| 1965        | 55                    | 44                          |
| 1966        | 101                   | 52                          |
| 1967        | 65                    | 37                          |
| 1968        | 98                    | 45                          |
| 1969        | 77                    | 33                          |
| 1970        | 63                    | 30                          |
| 1971        | 36                    | 35                          |
| 1972        | 71                    | 33                          |
| 1973        | 57                    | 19                          |
| 1974        | 59                    | 32                          |
| 1975        | 38                    | 31                          |
| 1976        | 46                    | 18                          |
| 1977        | 78                    | 32                          |
| 1978        | 57                    | 25                          |

APPENDIX 7-4. THE NUMBERS OF BLACKCAPS, GARDEN WARBLERS AND WHITETHROATS  
RINGED ANNUALLY IN BRITAIN DURING THE PERIOD 1950 - 1978

| <u>YEAR</u> | <u>BLACKCAPS</u> | <u>GARDEN WARBLERS</u> | <u>WHITETHROATS</u> |
|-------------|------------------|------------------------|---------------------|
| 1950        | 164              | 130                    | 780                 |
| 1951        | 169              | 120                    | 1240                |
| 1952        | 196              | 113                    | 2137                |
| 1953        | 112              | 151                    | 2654                |
| 1954        | 152              | 250                    | 2912                |
| 1955        | 140              | 169                    | 3119                |
| 1956        | 177              | 562                    | 4660                |
| 1957        | 318              | 335                    | 5453                |
| 1958        | 386              | 574                    | 4766                |
| 1959        | 575              | 415                    | 5614                |
| 1960        | 874              | 623                    | 4848                |
| 1961        | 1022             | 527                    | 4377                |
| 1962        | 908              | 685                    | 4750                |
| 1963        | 1935             | 1633                   | 6040                |
| 1964        | 4070             | 1261                   | 5497                |
| 1965        | 3988             | 2680                   | 8890                |
| 1966        | 4367             | 1957                   | 7614                |
| 1967        | 3970             | 1848                   | 8848                |
| 1968        | 4532             | 2279                   | 11005               |
| 1969        | 4603             | 2015                   | 1897                |
| 1970        | 5999             | 2067                   | 3764                |
| 1971        | 6153             | 1941                   | 3126                |
| 1972        | 7053             | 1700                   | 2424                |
| 1973        | 6846             | 1696                   | 1954                |
| 1974        | 7032             | 2147                   | 2433                |
| 1975        | 5888             | 1726                   | 3788                |
| 1976        | 10271            | 2560                   | 6040                |
| 1977        | 10087            | 2717                   | 6055                |
| 1978        | 7604             | 2007                   | 3207                |

APPENDIX 7-5. THE NUMBERS OF BLACKCAPS (BC) AND GARDEN WARBLERS (GW)  
RINGED ANNUALLY IN HOLLAND, FRANCE AND FENNOSCANDIA DURING  
CERTAIN YEARS WITHIN THE PERIOD 1950 - 1978

| <u>YEAR</u> | <u>HOLLAND</u> |      | <u>FRANCE</u> |      | <u>FINLAND</u> |      | <u>SWEDEN</u> |      | <u>NORWAY</u> |     |
|-------------|----------------|------|---------------|------|----------------|------|---------------|------|---------------|-----|
|             | BC             | GW   | BC            | GW   | BC             | GW   | BC            | GW   | BC            | GW  |
| 1956        | -              | -    | 301           | 222  | 22             | 188  | -             | -    | -             | -   |
| 1957        | -              | -    | 829           | 439  | 19             | 232  | -             | -    | -             | -   |
| 1958        | -              | -    | 1260          | 754  | 3              | 208  | -             | -    | -             | -   |
| 1959        | -              | -    | 1630          | 775  | 84             | 338  | -             | -    | -             | -   |
| 1960        | -              | -    | 2227          | 1074 | 207            | 696  | 369           | 640  | -             | -   |
| 1961        | 201            | 318  | 2813          | 1103 | 267            | 719  | 612           | 727  | -             | -   |
| 1962        | 209            | 511  | 2083          | 1387 | 404            | 1221 | 847           | 1204 | -             | -   |
| 1963        | 229            | 580  | 3013          | 2394 | 318            | 1145 | 747           | 1007 | -             | -   |
| 1964        | 402            | 448  | 5735          | 2147 | 238            | 889  | 936           | 1001 | -             | -   |
| 1965        | 473            | 872  | 3941          | 2492 | 431            | 1511 | 1574          | 2176 | 31            | 32  |
| 1966        | 520            | 874  | 6322          | 2950 | 454            | 1548 | 767           | 1142 | 123           | 51  |
| 1967        | 824            | 793  | 6792          | 3778 | 667            | 1913 | 1015          | 1389 | 154           | 386 |
| 1968        | 821            | 794  | 7336          | 2997 | -              | -    | 1148          | 1550 | 67            | 88  |
| 1969        | 1029           | 1253 | 7910          | 2945 | -              | -    | 1380          | 1248 | 31            | 55  |
| 1970        | 1138           | 1021 | 9893          | 2934 | -              | -    | 689           | 935  | 29            | 31  |
| 1971        | 1749           | 1180 | -             | -    | -              | -    | -             | -    | 82            | 73  |
| 1972        | 1742           | 1287 | -             | -    | -              | -    | -             | -    | 154           | 142 |
| 1973        | 2803           | 1587 | -             | -    | -              | -    | -             | -    | 63            | 260 |
| 1974        | 2579           | 1437 | -             | -    | -              | -    | -             | -    | -             | -   |
| 1975        | 1836           | 1392 | -             | -    | -              | -    | -             | -    | -             | -   |
| 1976        | 2637           | 1358 | -             | -    | -              | -    | -             | -    | -             | -   |
| 1977        | 2906           | 1271 | -             | -    | -              | -    | -             | -    | -             | -   |
| 1978        | 2130           | 920  | -             | -    | -              | -    | -             | -    | -             | -   |

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