

Abstract of D.Phil. Thesis.

A COMPARATIVE BEHAVIOUR STUDY OF
THE PARIDAE.

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MS. D.Phil. d, 874

App. 3:51

ABSTRACT

I. Introduction

The family Paridae contains five important genera - Parus, Aegithalos, Psaltiriparus, Auriparus and Remiz. Each of these genera includes a group of very similar species, but the different genera appear to be widely separated from each other.

The objects of the present study were:-

(i) To ascertain the annual cycle of behaviour of the Great Tit (Parus major), and to attempt an analysis of some aspects of it.

(ii) To compare the behaviour of the Great Tit with that of other tits, particularly with other species of Parus. To this end parallel observations were made on the other members of the family present in the study area, and the relevant literature was reviewed. Comparative study is of value in facilitating the interpretation of behaviour patterns, and in indicating relationships between species and genera.

The study was carried out in Wytham Wood, Berkshire.

II. Methods

A field study was made on a wild population of tits. Birds were trapped and ringed so that individuals were recognisable in the field.

III. Flocking

Outside the breeding season Great Tits live in flocks which show a moderate degree of integration and which move irregularly over a limited area at rates of up to 200 yds. per hour. The flocks show two types of movement :- (i) Drifting movements occurring during feeding. (ii) Integrated movements, during which the birds stop feeding and move for some distance. In the latter the flocks are integrated by: (a) The 'Twink' call, which brings other individuals into a ready-to-fly mood. (b) The situation "other-bird-flying-away" which releases flying. The tendency to integration of the flock is balanced by certain disruptive tendencies, the most important of which are due to aggressive behaviour.

IV. Winter Fighting

Fighting over food is common in winter flocks. The most important behaviour patterns are:- (i) The supplanting attack, in which one bird flies at another and dispossesses it of its food. (ii) The wings-raised, and (iii) the head-forward postures, used to threaten nearby individuals. (iv) Avoiding behaviour; tits with food avoid others which approach too closely. (v) Flying away with food particles too large to be eaten immediately. The study of such behaviour can be amplified by allowing the tits to feed in front of a mirror: they then behave towards their image as they would towards a rival. The image may provoke attack, or flight, or intermediate responses. Supplanting attacks are

most common in mid-winter, and occur sufficiently often for such behaviour to be of definite ecological importance.

V. Movements

Adult Great Tits are completely sedentary, and remain on or near their previous year's territory the whole year round.

Juvenile Great Tits disperse soon after becoming independent of their parents: they may wander up to several miles from their birth-place. Many juveniles have settled in a restricted range by the Autumn, though some continue to wander until the nesting season. The winter range is approximately 10-20 acres.

VI. Pair Formation

The Great Tit flocks begin to break up in January, but the process is gradual, and in cold weather some flocks may be seen as late as April. Some birds are paired during the winter, but most pair formation takes place when the flocks break up. The mechanism is not yet fully understood, but it appears that the male makes supplanting attacks on other members of the flock, and that his further behaviour depends on that of the attacked individual. Once pair formation has occurred, there is a marked difference in the behaviour of the sexes, the males being much more 'alert' and less retiring than the females. Certain courtship displays appear at this time of year.

VII. Territory

Soon after the pairs separate out from the flock, the male

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Great Tits start to use certain sites in preference to others for singing. Fighting against other males is more intense in the neighbourhood of these sites (preferred stations) than elsewhere. In this way an area round the preferred stations (the preferred area) comes to be defended from other Great Tits. The boundaries of this area become defined through skirmishes with other pairs. The preferred area is at first unstable and its boundaries vague: it changes only gradually into a territory in the classical sense. Territorial behaviour is thus much less rigid in the titmice than in most species which have previously been studied. The average size of Great Tit territories in the study area was 2.0 acres. Territories seem to differ considerably in size for the same species in different areas, and also for different Parus species in the same area. The biological value of territorial behaviour is difficult to assess.

VIII. Song

Each Parus species has a characteristic song, though in each species there is considerable variation. The song period is roughly similar in all the Parus species studied: song starts in December, becomes common and well marked in early spring, and dies away at about the time when the young leave the nest. Song may also be heard from juvenile birds in late summer, and during the autumn period of sexual behaviour. The singing of a male attracts females and warns off other males. The stimulus situations in

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which it occurs are similar to those in other passerine species.

IX. Reproductive Fighting

Reproductive fighting occurs in relation to the defence of a female, a territory and a rest-site. The most important behaviour patterns are: (i) The supplanting attack. (ii) The head-up posture. (iii) Upright flight, and (iv) Displacement pecking. Although the behaviour is complex, it can be understood on the assumption that each of the combatants is activated by two drives - a fighting drive and an escape drive. The fighting drive is expressed primarily in the supplanting attack, and the escape drive in flying away. In a skirmish the two drives are in approximate equilibrium. The strengths, and relative strengths, of these two drives determine which of the several possible responses will be given to each stimulus situation. In the Great Tit the head-up posture is very elaborate, and is accentuated by a black ventral stripe. In the Blue Tit the posture is less elaborate, and there is no corresponding structure. Although the displays used in intraspecific reproductive fighting are very similar in the different parus species, they do not appear in the intraspecific disputes over nest-sites.

X. Copulation and Courtship Feeding

In all parus species it is usually the male who initiates copulation, though the female sometimes does so. The precopulatory display consists of a rapid shivering of the wings, a crouching

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posture, and a high pitched 'zeedling' note. This is given by both sexes.

Courtship feeding often follows copulation. It becomes very common during the egg-laying period, the female begging almost continuously all day. The male continues to feed the female during incubation. The begging display of the female is similar to the precopulatory display, and to the begging of the young. Wing shivering seems to be a ritualized intention movement of flight.

XI. Nest Site

All Parus species build in holes. The different species have slightly different requirements for nest-sites, though there is a very large overlap. During the pre-nesting season the male inspects suitable sites, and his display causes the female to shiver her wings and inspect the hole.

XII. Nest Building

Building is usually carried out by the female alone. The males possess the necessary nervous structure, but the motivational factors are usually too low for them to exhibit complete building behaviour. The female at first builds in several different sites, but soon becomes conditioned to one of them.

XIII. Incubation

In all Parus species incubation is carried out by the female

alone. Periods on the nest of about 30 minutes alternate with periods off of about 8 minutes. There is a slight tendency for the periods off to be longer in the afternoon than in the morning.

XIV. Care of the Young

The young are brooded by the female for the first few days after hatching. During this time they are fed principally by the male. Later both sexes share in bringing food, and also in nest sanitation, though the male normally does more than the female. The young leave the nest in rapid succession, and are fed by the adults for another 2-4 weeks. The begging display of the young is similar to that of the female in courtship feeding. In some years a few pairs lay a second clutch at about the time when the first brood leaves the nest. All birds show some recrudescence of sexual behaviour at this time.

XV. Aggressive and Sexual Behaviour in Late Summer and Autumn

Juveniles of all Parus species show indications of sexual behaviour soon after they become independent. This appears principally in song and reproductive fighting. The latter is often associated with food fighting. In P. palustris this sexual behaviour is more marked than in the other species.

There is also a recrudescence of sexual behaviour in early autumn, manifested by paired behaviour, song and reproductive fighting.

XVI. The Relations between the Forms of Aggressive Behaviour

Food fighting and reproductive fighting are released by different stimulus situations, depend on different internal states (drives) and utilize different motor patterns. They are thus distinct. Nevertheless there are indications of certain relations between them. These are: (i) The activation of one type of fighting behaviour seems to lower the threshold for the appearance of other types: (ii) An animal with a high reproductive fighting drive appears also to have a high food fighting drive, and vice versa.

XVII. Behaviour towards Predators

The response towards a predator depends on the activation of three drives: (i) The drive which had been previously governing the activities of the animal. (ii) Escape. (iii) Attack. Grey Squirrels are normally ignored, or a weak escape response is given: once, however, a Great Tit was seen to give an elaborate display to a Grey Squirrel. In winter, man causes a simple escape response, which is subject to slight variation according to the strength of the drive. The full response occurs in two stages: in the first the bird flies up into a branch, giving the alarm call, and then its further behaviour is determined by the stimulus situation. In spring an attack component is also activated, and complex behaviour (scolding) results: the exact nature of this depends on the strengths of the three drives. When disturbed on the nest, a display is used which gives a human observer the

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impression that a snake is in the hole. Tits also have a complicated distraction display which is released by the cry of the young.

Tits show two responses to avian predators. If the predator is in flight, they take cover in thick bushes and utter a special alarm note. If the predator is perched, they come towards it and scold it in a manner similar to that used against human intruders in spring.

XVIII. Roosting

Tits of the genus Parus, with certain exceptions, roost in holes in winter and in foliage in summer. When the birds are in pairs, Great and Blue Tits have a "Good-night" ceremony which is performed at roosting time: the male also waits outside the female's roosting site after she has gone to roost and before she emerges at dawn.

Data on the winter roosting and awakening times were obtained for P. major and P. caeruleus, and also for Dryobates major and Sitta europaea, all of which roost in holes. The average length of the day's activity for each of these species increased with decreasing body size: all had shorter days than at least the majority of the species living in the same area which did not roost in holes. In all cases the roosting times were later (relative to sunset) in mid-winter than in Autumn or spring: in Dryobates major and P. major this is even more marked

in high latitudes than in England. The dawn emergency times (relative to sunrise) of P. major and P. caeruleus remained constant from late November to March in the area of the present study: P. major in the sub-arctic, and Dryobates major in both sub-arctic and mid-temperate latitudes, emerge earlier relative to sunrise in mid-winter than in spring. All species emerged at dawn at a lower light intensity than that at which they went to roost.

During egg-laying and incubation, males emerge earlier and females later than during winter.

In general, there is an optimum length of the active day which varies with the latitude and season. Each bird has an internal diurnal rhythm of activity which causes it to be active for a period near to the optimum. This internal rhythm is also modified by certain environmental stimuli which are not considered here.

III. Periodic variations in the frequency of instinctive Activities

As well as the obvious rhythm of roosting and awakening, many other activities show a marked diurnal periodicity. Those associated with flocking behaviour, and many of those associated with the reproductive drive, show a peak of activity early in the day, a minimum in the afternoon, and sometimes a second peak in the evening. Other activities show different types of diurnal

fluctuation.

Within the main diurnal rhythm, shorter fluctuations in activity can be distinguished. Each activity appears at irregular intervals, which are determined by the fluctuations of the internal drive, by interactions between drives, and by the changing stimulus situation.

XX. The Genus Parus

In the preceding sections comparisons have been made between various aspects of the behaviour of the different parus species. This comparison has shown that there are few essential differences between the behaviour of the different species: most of the differences which do exist are of degree only.

D.Phil. Thesis.

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SECTION I. INTRODUCTION.

- A. General.
- B. Nomenclature.
- C. The Study Area.
- D. Annual Cycle.
- E. Presentation of the Results.
- F. Acknowledgements.

SECTION I. INTRODUCTION.

A. General.

The family Paridae contains five important genera. These are Parus, Aegithalos, Psaltriparus, Auriparus and Remiz. There are also a few others whose position is doubtful, and about which little information is available. Each of these genera includes a very uniform group of species, but, except for certain similarities between Aegithalos and Psaltriparus, there are few indications of links between the different genera. As yet, however, our knowledge of the behaviour of the genera other than Parus is very scanty.

The objects of the present study were two-fold:-

(i) To obtain as complete as possible a picture of the annual cycle of the Great Tit (Parus major), and to attempt an analysis of some aspects of its behaviour.

(ii) To compare the behaviour of the Great Tit with that of the other Parus species, and also with that of the other genera in the family. To this end a limited number of observations were made on the other Parus species present in the study-area, and also on Aegithalos caudatus, and the available relevant literature was examined. A comparative study may (a) facilitate the interpretation of behaviour patterns, and (b) indicate relationships between species and genera. Some examples of the value of the comparative study of behaviour for systematics have been given by Tinbergen (1942). Our knowledge of the Paridae is still too meagre for much progress to be made in this direction, but the first

steps must consist of a description of the behaviour patterns of the different species. References to species other than members of the Paridae have not been included except where specially relevant.

The study is based primarily on observations made in Marley Wood, Wytham, Berkshire, between September, 1948, and May, 1950. The work was carried out while the writer was a member of the Edward Grey Institute, Department of Zoological Field Studies, Oxford, and was planned to fit in with other studies of the Great Tit being carried out there. Many aspects - particularly ecological ones - of the annual cycle of the Great Tit have therefore been omitted.

B. Nomenclature.

Those members of the Paridae which were present in the study area are referred to in the text by their English names. These are:-

Parus major newtoni - Great Tit.

Parus ater britannicus - Coal Tit.

Parus caeruleus obscurus - Blue Tit.

Parus atricapillus kleinschmidtii - Willow Tit.

Parus palustris dresseri - Marsh Tit

Aegithalos caudatus rosaceus - Long-tailed Tit.

All other species, and the American race of Parus atricapillus (the Black-capped Chickadee, P. a. atricapillus) are referred to by their Latin names.

C. The Study Area.

Marley Wood consists of an area of about 55 acres of mixed wood - largely hazel and elder coppice with scattered mature oak, beech and ash trees, and some open spaces. Most of the dead trees have been removed. Nesting boxes were present at a density of about two per acre.

The winters of both 1948/9 and 1949/50 were mild, but differed in that the beechmast, which may form an important part of the food of tits in winter, was plentiful in 1948/9 but absent in 1949/50.

D. Annual Cycle.

A brief summary of the annual cycle of the Great Tit is given below. The exact dates at which the different phases of the cycle appear are, of course, influenced by meteorological conditions.

January. Great Tits in flocks. Much pair formation probably takes place in this month. Some birds show paired behaviour and reproductive fighting in the early mornings. Song becoming frequent.

February and March. Usually in pairs, but return to flocking behaviour in the afternoons, especially if the weather is cold. Reproductive fighting. Territories become fairly clearly defined in late March.

April and May. Nest-building, egg-laying, incubation and feeding the young in the nest.

June. Young out of the nest. In some years a few pairs start second broods in late May or June.

July and August. Juveniles in loose flocks. Much fighting among the juveniles.

September and October. Flocks more stable and integrated. Some recrudescence of sexual behaviour.

November. In flocks.

December. In flocks. A little song. Reproductive fighting occasional. A few birds form pairs, though there is little other paired behaviour at this time.

E. Presentation of the Results.

Two points concerning the presentation of the results need to be emphasized. First, an attempt has been made to include all the important references to the behaviour of the genus Parus. Although this attempt was by no means completely successful, it was necessary, for considerations of space, to omit references to species other than those of the genus Parus except where directly relevant.

Secondly, it has been necessary to use verbal representations of many of the calls of the birds. These are, at best, only moderately satisfactory; but they do provide a method of referring to the different notes and calls. A section exclusively devoted to calls has not been included, because it is felt that the somewhat anthropomorphic treatment of calls which ^{this} ~~such treatment~~ usually entails is highly misleading (see e.g. p. 241-250). Instead, the different calls are referred to in the sections dealing with the behaviour patterns with which they are associated.

F. Acknowledgements.

I am indebted to Dr. D. Lack, under whose supervision the work was carried out, and who gave particularly helpful advice in the presentation of the results. I am also indebted to all the members of the staff of the Edward Grey Institute, most of whom were also working on the genus Parus, for some invaluable discussion as well as practical help: although it is not possible to mention them all by name, I hope that they will recognise my gratitude. I must, however, particularly mention J. A. Gibb, who erected all the boxes in the study area, provided the automatic recorder, and with whom I was able to keep in very close touch; and P. H. T. Hartley, who gave much valuable advice. I am grateful to H. Kenrick for advice on colour ringing.

Finally I would like to state my particular gratitude to Dr. N. Tinbergen for much helpful discussion, a great deal of which concerned his unpublished work on the Herring Gull and Three Spined Stickleback.

SECTION 2. TECHNIQUES.

- A. Trapping.
- B. Ringing.
- C. Age and Sex of Trapped Birds.
- D. The Automatic Recorder.

SECTION 2. TECHNIQUES.

A. Trapping.

Trapping was carried out from November to March each winter. A variety of traps were used, but the most successful consisted of $\frac{1}{4}$ inch wire netting over an 18-inch cube wire frame. The birds entered through a semi-circular funnel (8" long, and of radius $2\frac{1}{2}$ " decreasing to $1\frac{1}{2}$ ") placed at ground level. A small door at one side served for removing the birds, and could be left open when the trap was not in use. The traps were baited with sheep's fat. Much of the success of the trapping depended on adequate pre-baiting: the traps were left open and baited, with more fat hanging up nearby, at all times when trapping was not in progress.

B. Ringing.

All birds trapped were marked with a numbered Aluminium British Museum ring on one leg, and with two or three coloured rings on the other. The coloured rings enabled individuals to be distinguished at distances of up to about thirty yards. Some of the birds had been marked previously by J. A. Gibb, so that some of their previous history was known.

C. Age and Sex of Trapped Birds.

It is not always possible to distinguish the age and sex of Parus spp. in the field. The sex of an adult Great Tit can always be recognised by its plumage: in the Blue and Coal Tits the sexes can often, but not always be distinguished in the field. The sexes of the Marsh and Willow Tits appear identical in the field.

Juvenile Great, Blue and Coal Tits can be separated from adults by their plumage up to the time of the autumn moult. Juvenile Marsh and Willow Tits are less easily distinguished, but their plumage is less worn than that of the adults.

After the autumn moult it is impossible to distinguish in the field between birds in their first and second years. There is, however, a difference in the average wing lengths of the first year and second year birds, and Kluijver (1939) has shown that it is possible to use this difference to assess the age of individuals of the Continental race of the Great Tit (P. m. major). Accordingly the wing lengths of all the trapped Great Tits were measured.

Table 1. Distribution of wing lengths of trapped Great Tits.

Length in mms.	68	69	70	71	72	73	74	75	76	77	78	79
1st year males.					2	10	11	4				
2nd year males or more.							2	7	8	1		1
Unknown males.					2	11	14	11				
1st year females		1	2		5	1						
2nd year females or more.			1	2	3	6	4	1				
Unknown females.	1	3	6	3	5	1						

The measurement of the wings of live birds presents considerable difficulties, and it was found that there was little agreement between the results obtained by different workers. These differences, however, were due to the slightly different techniques used: by using a standardised technique it was possible to obtain measurements which, when checked by subsequent remeasurements, were accurate to the nearest millimetre. All the measurements given in Table 1 were made with the bird held in the right hand, the radius and ulna held out from the body by the thumb and fore-finger, and the primaries lying parallel to the body. From the measurements of individual birds whose age was known the ranges of the wing length of 1st and second year birds can be determined. It will be seen that males with wings of under 74 mms. can be assumed to be first year birds; and those with wings over 75 mms. can be assumed to be second year or older. Males with intermediate measurements, and females, can not be aged by this method.

D. The Automatic Recorder.

The rhythm of various nesting activities were studied by means of an automatic recorder. A trigger was placed in the entrance to the nest box in such a way that the bird made one contact every time that it entered, and another each time it left. Each contact operated a pencil writing on a revolving drum. The apparatus was designed and constructed by J. A. Gibb.

SECTION III FLOCKING.

A. General.

B. Flocking of Parus major.

1. Occurrence of flocking.
2. Size of flocks.
3. Other species associated with Great Tit flocks.
4. Movement of flocks.
5. Calling.
6. Degree of integration of the flocks.
7. Mechanism of flock integration.

C. Other genera.

SECTION III FLOCKING.

A. General.

The term "Flock" is a vague one, and has been used to cover groups of birds ranging from the closely united flights of waders to mere feeding aggregations. In the present discussion it is applied to birds whose behaviour is so modified by the presence of other birds of the same or related species, that they become concentrated in some areas to a greater degree than if they were distributed at random. The term "Flock" thus includes both closely integrated groups of birds, and more or less formless concentrations in which the individuals show only slight social behaviour. An aggregation of birds formed merely by the presence of food does not constitute a flock.

Great Tits are found in flocks from late summer to early spring. The flocks are not very closely integrated, and move fairly slowly. Great Tits thus provide suitable material for the study of the mechanism of flock integration. It will be seen that the flocks are held together by a series of behaviour patterns apparently similar in fundamentals to those found in other instinctive activities. In view of this, we must presume that flocking gives some biological advantages. Probably the most important of these is an increased immunity from predators: on the approach of a predator the first bird to see it gives an alarm call which warns the others.

All other members of the genus Parus for which information is available also show some degree of flocking behaviour, though it is much

less marked in some species than in others. Thus P. inornatus (Henshaw, 1875; Adams, 1898, in Brent, 1946; Dixon, 1949) and P. lugubris (Dresser, 1881) show little flocking behaviour. In the absence of detailed studies further comparison with other species is not profitable; for it will be shown later that in the Great Tit the degree of integration may vary even within a single day.

In the following section the appearance and behaviour of Great Tit flocks in the field is described. This is followed by a discussion of the mechanism of integration of the flocks, so far as this is understood.

B. Flocking of Parus major.

1. Occurrence of flocking.

Within a week or two of leaving the nest the young Great Tits began to wander away from their parents; and even while the young were still being fed by adults, some of the "broods" came to consist of the offspring of different parents, (see p.222). Within a further ten days young Great Tits were associating with the young of other tit species. In this way flocks, similar to those seen throughout the winter, appeared for the first time about a month after the young left the nest. (See section V for a brief account of the movements of individuals through the year).

These summer flocks, however, differed in many ways from the winter flocks. In particular they were usually little integrated, and there was much less calling than later in the year. During the afternoons, calling was practically non-existent. The adult birds remained on or near their

territories, associating with the flocks when these passed by, but not following them far from their nesting place. Later this attachment to territories became less marked, but the adults remained near them as long as the weather remained mild. The composition of the flocks changed frequently, as the juveniles were still wandering.

Although some wandering went on throughout the winter, many birds had become settled by early autumn. From this time on the flocks became much more stable, and it was usually possible to predict in which part of the wood they would be found. The behaviour of these winter flocks is described in the sections below.

2. Size of flocks.

The tit flocks in Wytham contained anything from two to over fifty Great Tits. Normally there were about a dozen. As the flocks also contained individuals of other species, the larger ones contained a total of well over a hundred birds of all species. Such large flocks were seen in pure beech wood during the autumn of 1948, when the crop of beech mast was particularly heavy: flocks observed in the same period in an area of mixed wood, less than a mile away, rarely contained more than fifteen Great Tits. Indeed, the distribution of food must play a large part in determining the size of the flocks: whenever⁴ food was locally abundant the tits were concentrated in the area of abundance. During the autumn of 1949, when the beechmast failed, large flocks were rare.

The size of the flocks varies also with the time of day, being largest in the morning. As the day progresses the large flocks break up

into smaller, less integrated, ones.

Odum (1941) found that flocks of P. a. atricapillus contained from four or five to ten or fifteen individuals, which agrees approximately with the data given by other writers, (e.g. ~~Butler, 1931~~; Wallace, 1941). The flocks round feeding stations tended to be larger than those elsewhere: Odum, however, comments on the great variability in the size of the flocks.

3. Other species associated with Great Tit flocks.

Great Tits often made up only a small proportion of the total number of birds in the flock. The degree to which the Great Tits associated with the other tits seemed to be influenced by whether or not their food was the same. Thus, when beechmast was very plentiful and the majority of Great Tits were feeding on the ground, some Blue, Coal and Marsh Tits fed amongst them, and the whole party moved together. Meanwhile, the tits feeding in the trees moved more than those on the ground, and left the main flock more easily. The long-tailed Tits (Aegithalos^u candatus), which seldom fed on the ground and moved rather more rapidly and smoothly than the Parus species, often seemed to pass through the main body of the flock and then to return to it, so that they completed circles over and round it. Even when all species were feeding on the same food, and were apparently well mixed, there was a marked tendency for individuals of the same species to keep together during flock movements. Thus, when the birds crossed a gap in succession, they would do so in groups of the same species - so that one might see successively: three Great Tits, five Blue, ~~four~~ Great, two Marsh, six Blue, and so on.

As well as ~~other~~ members of the Paridae, various other species were to be found amongst the tit flocks. Of these the most important were Nuthatches (Sitta europaea), Tree Creepers (C^othia familiaris) and Goldcrests (Regulus regulus). These species were to be found at all times in the tit flocks, moving about the wood with them. It is interesting that all these species have flight notes very similar to those of the tits. Chaffinches (Fringilla coelebs) also were often closely associated with the tit flocks, and joined with them in flock movements. In the spring of 1949 the tit flocks broke up rather earlier than the Chaffinch flocks, and pairs of Great Tits were often seen with the Chaffinch flocks. Chiff chaffs (Phylloscopus collybita), Willow Warblers (Phylloscopus trochilus) Black caps (Sylvia atricapilla) and Spotted Flycatchers (Musc^{ia}pa striata) also occurred in tit flocks in late summer and early autumn. They usually, but not always, followed the tits when the latter moved, but were not so closely attached to the flocks as were the Nuthatches and Tree Creepers. Odum (1941) gives a similar list of the species which associate with P. a. atricapillus in U.S.A.

4. Movement of flocks.

Great Tits rarely feed for long in the same place: the flocks move about the wood, but keep in the same general area and often return again and again to the same spot. Two types of flock movement can be distinguished.

(1) Drifting movements. These take place in the course of feeding: birds move about in search of food, but their social behaviour keeps them together and converts the almost random movements of individuals into a slow

drifting movement of the flock as a whole. A flock may continue to drift in a more or less constant direction for some time, but progress is slow and such movement usually accounts for only a small proportion of the total distance covered by the flock. Although drifting movements are seen most easily when the birds are feeding in the trees, they also occur on the ground. Thus when a closely integrated flock of about half a dozen Great Tits is feeding under a particular tree, they usually drift slowly round its base in a group.

(ii) Integrated movements. In these there is an almost complete cessation of feeding activity, and the birds move from one area to another some distance away. The function of these movements is not evident, as the birds often leave behind them an abundant supply of food, to which they return half an hour later. Apparently when food is distributed more or less equally over the wood, these movements take place in any direction; but when food is concentrated in limited areas, i.e. under a few beech trees, each movement appears from the start to be directed to one of the other sources of food.

A typical integrated movement takes place as follows. The birds are feeding on the ground when one of them flies up into a low bush and starts calling "Twink, twink". As he calls he hops higher and higher in the bush. His calling has no apparent effect on some of the birds, but others stop feeding and also hop up into the bushes, twinking. After a short while, say $\frac{1}{4}$ minute, one bird flies off, and one or two others follow him. These leading individuals fly from bush to bush, calling between flights. The remaining birds gradually stop feeding and hop up, calling, one by one,

until all have moved off. It must be emphasized that although these are called "Integrated Movements" the flock is far less integrated than, say, a flock of Dunlin (Calidris alpina) twisting over the shore. Several minutes may elapse between the departure of the first Great Tit and that of the last. There are no fixed leaders and successive movements may be initiated by different individuals. Usually they start gradually, and it is hardly possible to say by which bird the movement is initiated.

Up to 200 yards may be covered in the course of a single integrated movement, though it is unusual for Great Tits to fly as far as this in one hop. Rather they fly from bush to bush, avoiding open spaces. When an area of open ground has to be crossed, the birds hesitate on the border and cross it in succession.

The speed at which flocks move varies greatly. During the late summer and early autumn of 1949 no flock was recorded as moving more than 50 yards in an hour, though flocks in September 1948 were certainly moving more rapidly than this. During the winter the flocks sometimes moved with quite considerable speeds. Great Tit flocks were often recorded as moving 200 yards in an hour, and in other habitats this is probably often exceeded.

The speed at which the flocks move varies also with the time of day, movement being greatest in the morning and much reduced in the afternoon. The results of some measurements made between October, 1948 and January, 1949, are shown in Table 2. There was no noticeable

Table 2. Speed of movement of Great Tit flocks.

Hour beginning G.M.T.	08	09	10	11	12	13	14
No. of records	7	13	16	14	7	6	9
Range yds. per hour	80-220	50-180	40-230	50-240	30-140	60-120	0-90
Average yds. per hour	160	131	108	97	105	85	61

seasonal change during this period. Obviously, owing to the great variability in the results, the figures in the table are only indicative of a general trend: for this reason it is not worth while to allow for the change in day length during the period concerned. Figures for the first and last hours of the day, when such changes would be particularly noticeable, have not been included. Behaviour at these times was also complicated by other factors: in the very early morning the birds often seemed to move about without forming clearly defined flocks, and in the evening they often became so dispersed that it was impossible to measure the speed of flock movement. Clearly behaviour at these times is also influenced by whether roosting sites are scattered, or concentrated into certain areas.

Flocks do not defend the areas in which they are habitually to be found, nor do these 'flock areas' have clearly defined boundaries. Often the area of one flock overlaps slightly, but not extensively, with that of another. When a large flock breaks up into smaller ones during the day, each of the smaller ones moves over the whole of the original flock area.

Flock areas are not rigid, but may remain constant for weeks or even months at a time, even when the individuals composing the flock change. They contain the roosting sites of the members of the flock. In Table 3 are given the approximate sizes of some flock areas, with estimates of the number of Great Tits in the flocks; other species of tits were, of course, also present.

Table 3 . Size of flock areas.

Period, 1948/9.	Nov. 1-11.	Nov-Dec.	Dec-Jan.
No. of Great Tits in flock.	c.40	c.12	c.18
Flock area, acres.	c.22	c.12	c.13

Odum (⁹1941) found that flocks of P. a. atricapillus moved on an average c.475 yds. per hour. Periods of fairly rapid movement, with little feeding, alternated with periods of little or no movement when the birds were actively feeding: these evidently correspond to the integrated and drifting movements described for the Great Tit. From Odum's description it is clear that the behaviour of chickadee flocks is closely similar to that of Great Tit flocks. The size of flock areas averaged 36.1 acres, though Butts (1941) gives 40-70 acres.

5. Calling.

During the slow drifting movements through the trees the thin 'tsit' or 'tseet' flight notes are used. These calls, which are also used in the course of integrated movements, do not provide such a fruitful field for investigation as the 'twinks', and will not be considered further.

Integrated movements are accompanied by two calls - the 'twink' which may be uttered in phrases of up to 5 notes, and the 'chich ich ich', similar to the scolding note but less harsh. Often the two calls are combined into a single phrase - 'twink twink chich ich ich'. Either may be used at the beginning or end of a movement, or when the birds settle on intermediate perches during its course. In closely integrated long-range movements the 'twink' alone is used: the 'chich ich ich' call is heard ^{more} most often at the end of movements than at the beginning. Calls similar to these are also used in other situations - such as the mobbing of predators. Both calls are extremely variable: all gradations between 'twink' and 'tseet' flight notes on the one hand, or song on the other, may be heard.

The 'twink' call of the Great Tit is audible over considerable distances. It is clearly defined, and distinguishable from all the other calls to be heard in the wood (except sometimes the 'Spink spink' call of the Chaffinch, but even this can nearly always be distinguished with practice). For these reasons the twink call has been used for special study.

The frequency with which the call is heard varies greatly throughout the day. In order to analyse this variation, the following technique was used. Four points in the wood were selected, forming the corners of a quadrilateral with sides of about 200 yards. On certain days each of the four points was visited for one five minute period in each half hour. The number of twinks heard was counted, and the results obtained for the eight periods in each hour were then averaged. Since counts were made only on reasonably still days, when twink calls were audible up to at least 200 yards, and since several flocks were within audible range of the quadrilateral, any variations due to

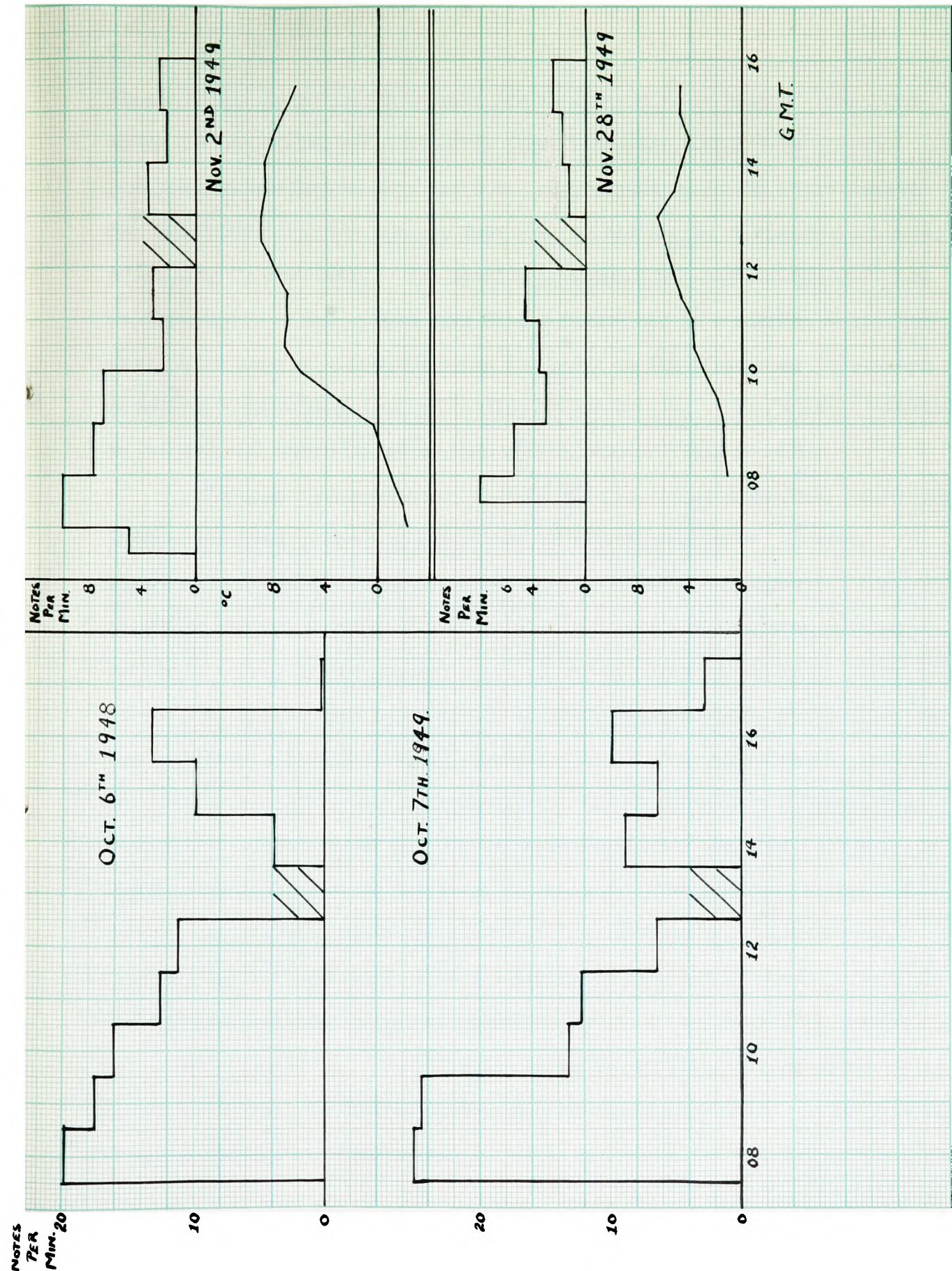


Figure 1 . Winter Flocks - Diurnal Variation in Frequency of "Twinks". (Shaded areas indicate that no observations were made).

flocks coming in or out of earshot can be assumed to be small. The twink calls are associated primarily with flock movements, which take place at irregular intervals, so that there was much variation in the eight records for each hour; but the average does give an indication of the general level of calling in that hour. The results of several all-day watches are shown in Figure 1. They show that twinkling was at a maximum soon after dawn, dying away to a comparatively low level in the afternoon. There was sometimes a subsidiary peak of calling in the evening. The diurnal variation of calling was thus similar to that of the rate of flock movement.

Although the population of Great Tits in the wood was much higher in late summer than in winter, the amount of calling was less. Indeed, twinkling practically ceased in the afternoons of July and August. For this reason it was not considered worth while to devote whole days to counting twinks in summer by the method described above. Therefore, a few counts made at the four points were supplemented by recording the number of twinks heard in two or three fixed five minute periods per half hour in whatever part of the wood I happened to be. The number of twinks per minute obtained on all occasions in each hour of the day for each month were averaged, and give an approximate indication of the level of calling. The results are shown in Table 4. In each month the calling followed the same sort of diurnal rhythm; and the amount of calling increased from month to month. Most of the increase had taken place by September - i.e. by the time that the moult was more or less over. The differences in the amount of twinkling are really more marked than the figures show, since the total population was decreasing when the calling was increasing.

Table 4. Amount of twinkling, in twink per minute, in late summer and autumn, 1949. Great Tit population - end of breeding season 300+; October, c.32; November, c.43; (J. A. Gibb, personal communication).

<u>Hour beginning</u> <u>G.M.T.</u>	<u>August</u>	<u>September</u>	<u>October</u>	<u>November</u>
04	1.8			
05	6.1	8.7		
06	1.3	7.6	6.4	9.4
07	1.8	6.6	8.0	6.6
08	3.0	3.6	4.6	3.9
09	2.4	2.9	3.4	2.4
10	2.4	2.3	1.9	2.8
11	0	0.9	0.2	1.8
12	0	0.7	-	2.2
13	0.1	0.7	0.7	1.8
14	0.1	2.1	1.7	2.2
15	0.3	0.8	1.0	
16	0.5	1.0	0.8	
17	0.9	0.8		
18	0.2			

Calling is much reduced on dull days, and with a sudden shower it almost ceases. From Figure 1 it appears that on November 2nd, 1949, when the temperature increased rapidly, the amount of twinkling showed a coincident rapid fall; on November 28th, when the temperature increased slowly, the decrease in twink frequency was also gradual. From this relation, and from the generally low level of twinkling in late summer, it seems probable that temperature has a direct effect on twink frequency. Observations made in an attempt to confirm this suggested that temperature did indeed effect the frequency of twinkling, but that there was also an underlying internal rhythm: it was not possible to obtain proof under the conditions of field observation.

It has been said that twinks were given in phrases of up to five notes. It was not possible to relate phrases of different length to particular situations. In general, the more birds that were calling, the greater the average number of notes per phrase. It thus seems probable that the number of notes in a phrase is dependent on the strength of the drive. Phrases of more than five twinks were heard when a bird suddenly came across a Sparrow Hawk dummy.

Table 4 shows that in August there was a considerable outburst of twinking at dawn, which soon died away. This outburst occurred in dispersed flocks (see next section) and was not associated with integrated flock movements: sometimes the individuals which were calling moved about within the flock, but sometimes they merely sat up in bushes calling steadily for a minute or two. The same is true of flocks just before pair formation in the spring, and also to a lesser degree, of dispersed flocks in September and October. Thus although integrated movements are always associated with twinks, the reverse is by no means true. Also, flight often occurs without associated twinks, especially in the afternoon. Flocking behaviour will be understood fully only when the precise natures of the 'twink' and 'chich ich ich ich' calls are known: this is clearly the direction which future research must take. The calls are discussed further on p.249, where some more observations on the use of the calls in other situations are given.

6. Degree of integration of the flocks.

It has already been said that the degree of integration of Great Tit flocks varies greatly. On some days the only evidence that the birds are

in flocks is that they are more dense in some parts of the wood than in others, while on other days the flocks are closely knit and the birds move about the wood together. In general the flocks are larger and more closely integrated in the morning than later in the day. As the day progresses each flock becomes scattered by direct breaks, when it separates into two or more smaller parts, and by a gradual diminution in the integration of the smaller units. A direct break may take place in a number of ways. One part of the flock may not follow when the rest moves off; or, when a movement starts, some birds may go in one direction and some in the other. Sometimes one wing of a flock moving on a fairly broad front comes to an abundant food supply and stays to feed^d whilst the rest moves on. Naturally large flocks split up more readily than small ones: sometimes it is possible to see a large flock split up into several parts which later re-unite several times in the course of a few hours.

The gradual diminution in the integration of the flocks becomes evident in a number of ways. Birds tend to drift apart when feeding: sometimes an individual stops feeding and flies away from the others without calling, and without being followed. Birds which become separated from the flock in the morning showed a type of appetitive behaviour, (~~see p. —~~) which ^{is} was much less marked, or absent, in the afternoon. In the afternoon flocks, birds feeding close together tend to remain so, whereas birds which wander a little way away from the others tend to lose contact altogether. The flocks thus come to consist of nuclei of a few birds with other individuals scattered round about.

In 1949/50 an attempt was made to assess the degree of integration of the flocks. Each flock observed was placed in one of the following

categories:-

0. Independent. Birds distributed more or less at random through the wood, or aggregated only by the presence of locally abundant food supplies. In practice the tits always showed some degree of flocking behaviour, and this category was never used.

1. Dispersed. Birds concentrated in some areas and absent from others in a way that could not be explained wholly by food distribution. Only drifting movements occurred. Outbursts of twinks were rare: they did not occur synchronously in all the birds in the flock, and did not lead to integrated movements.

2. Weakly Integrated. Birds in flocks which made occasional integrated movements. When one bird started twinking there was a greater tendency for others to follow suit than in dispersed flocks.

3. Integrated. The birds fed close together, and integrated movements occurred fairly frequently. A bird which became separated from the flock usually showed appetitive behaviour (v. infra.).

It might be thought that the above definitions rest on two different properties: (a) how close together the birds are, and (b) how frequently they move. However, as will be seen later, integrated movements play a large part in keeping the flock together, and the two properties are inter-dependent.

The results of this investigation are shown in Table 5. The records for each month have been divided according to the four quarters of the day. In order to facilitate comparison a figure indicating the average degree of integration of the flocks has been calculated by awarding each dispersed flock 1 mark, each weakly integrated flock 2 marks, and each integrated flock 3 marks, and taking the average for each period. Thus if all flocks had

been dispersed the average integration would have been one; if all flocks had been integrated it would have been three.

Table . Degree of integration of Great Tit flocks.
For explanation see text.

<u>Period.</u>	<u>No. of flocks assessed.</u>	<u>Quarters of the day.</u>			
		1	2	3	4
July	18	1.8	1.4	-	-
August	62	1.4	1.4	1.0	1.0
September	71	1.3	1.1	1.1	1.0
October	46	1.2	1.1	1.0	1.0
November	75	2.3	1.6	1.2	1.3
December	92	2.1	2.1	1.7	1.4
January	87	2.4	1.9	1.9	1.5

The Table shows that in all months the flocks tended to be less integrated in the afternoon than in the morning, and that the late summer flocks showed little integration at any time. (Lebeurier et Rapine, 1941, also noted that Great Tit flocks are most integrated in mid-winter).

Unfortunately the method for assessing the integration of the flocks in 1949/50 was based on observations made in 1948/49. It turned out that the flocks in 1949/50 were far less closely integrated than those in the previous year. Although no figures in support of this are available, there is no doubt of its truth: in the earlier year well integrated flocks were often seen in September, whereas in 1949/50 they did not become at all common until November. The reason for this is quite obscure. Perhaps the very warm dry summer or the failure of the beechmast crop in 1949/50 was responsible.

The break-up of the flocks is described on page 73 .

7. Mechanism of flock integration.

In the preceding sections we have seen that there are two types of flock movement - drifting and integrated - and that the rate of movement, the calling, and the degree of integration of the flocks all show roughly the same type of diurnal and seasonal variations. We shall now consider in more detail how the flocks are held together.

(a) Drifting Movements. It seems probable that the 'tsit' or 'tseet' flight calls are important in holding together the flocks while they are feeding. It is clear that some visual stimulus must also be involved, but its characters are unknown. Birds arriving near a flock, which they could hear but not see, turn their heads and appear to be 'looking for' the other birds.

It will be noted that both of these signals can function only over short ranges: in the afternoon, when integrated movements become rare, individuals wandering away from the immediate neighbourhood of the main body may lose contact and become detached altogether. It is for this reason that the afternoon flocks often come to consist of a small integrated nucleus with other individuals scattered round it.

Birds do not keep a constant distance apart when they are feeding in flocks. For instance, the members of a flock of Great Tits feeding on beechmast under a beech tree may be on the average only 2 feet apart, whereas the same birds feeding amongst hazel twigs would probably be at least 8 feet apart. We must thus presume that the distance at which the birds feed from each other is to some extent related to their method

of feeding, as well as depending on the various integrative and disruptive factors which are considered elsewhere in this chapter.

(b) Integrated Movements. The 'Twink' and 'chich ich ich' calls are undoubtedly the most important signals in the integration of long distance flock movements. These are usually associated with a readiness-to-fly or a having-just-flown on the part of the caller. At the beginning of an integrated movement they produce the following effects on other birds:-

- (i) Cessation of feeding
- (ii) Hopping up in the bushes
- (iii) Twinking
- (iv) Possibly flight.

In some cases flight occurs apparently without any further stimulus but, more usually, an additional stimulus is given by a neighbouring bird taking wing. In a normal integrated movement several individuals are up in the bushes, twinkling and apparently ready to fly, before one actually does so: then the others follow one by one at intervals of a few seconds. Here again the actual characters of the visual stimulus are unknown, but the white tail feathers may be important. The stimulus situation will be referred to as 'other-bird-flying-away'.

Twinks may also have a directive significance. This is certainly the case when an individual flies towards a flock which it can hear but not see; but it must be remembered that in an integrated movement the first few individuals are flying away from the twinks of the majority.

Neither the twink nor the 'other-bird-flying-away' produce an immediate response in the members of the flock. The twink produces a readiness-to-fly which may be inhibited by other drives. For instance a bird opening a nut usually finishes it before following the flock. In such cases some form of memory of the way the flock has gone seems to be involved. Even the

response to the other-bird-flying-away may be delayed for several seconds or longer.

Integrated movements play an important part in keeping the flock together, since individuals which have wandered a little way away from the flock respond to the twinks and join in the movement. Also the birds nearly always settle down at the end of the movement much closer together than they were at the beginning.

(c) Absence of the flock companion. An individual which becomes separated from the flock shows a type of behaviour which is presumably to be regarded as a form of appetitive behaviour. Typically it hops from twig to twig, and flies from bush to bush, looks around, and calls 'twink' and 'chich ich ich' persistently. The 'chich ich ich' is louder and harsher than the call usually used in flock movements. Such behaviour is less frequent in the afternoons than in the mornings.

(d) External factors. As well as the behaviour patterns which have been sketched above, certain environmental factors may also have a marked effect on the integration of the flocks. The most obvious of these is food. Locally abundant food supplies cause the birds to come together to certain areas to feed: once aggregated, their flocking behaviour tends to keep them together.

Although no precise data on the point were obtained, it seemed that the degree of integration was greatly influenced by the air temperature, cold weather being associated with more closely integrated flocks.

(e) Disruptive factors. In the preceding paragraphs the factors which tend to keep the individuals in a flock together have been sketched.

We must, however, also consider the factors which tend to disrupt the flock. These are:

- (i) Factors tending to produce random dispersal. The food seeking movements of individuals in a drifting flock would tend (in a uniform habitat) to produce a random dispersal if they were not guided by the flocking behaviour. Occasions when birds tend to fly off in opposite directions at the start of an integrated movement also tend to disperse the flock in the same way. Such factors may be considered to be acting continually in opposition to the flocking behaviour patterns.
- (ii) Factors tending to produce over-dispersal (i.e. the birds more dispersed than in random dispersal). As will be seen in the next chapter, aggressive behaviour concerned with food, and the behaviour patterns which protect individuals from being robbed of food by others, have the effect of keeping an area round each bird (Individual distance) empty of other birds. The birds composing the flock are thus over-dispersed within the limits of the flock. Such behaviour probably provides a limit to the integration of the flock. (On the other hand the fact that birds fly off with nuts to open them outside the flock probably acts as a disruptive factor at all levels of integration.). In spring, territorial behaviour produces over-dispersal over the wood as a whole, and flocking ceases.

C. Other Genera.

All the other genera of the Paridae form flocks outside the breeding season.

Miller (1921) has given a description of the flocking of Psaltiriparus minimus, and includes details of the behaviour of the birds over a period of $2\frac{1}{2}$ hours. The flocks consisted of about 70, 25 and 20 birds, but Miller comments on the way in which they varied in size and on their straggling nature. The general behaviour of the flocks seems to be closely similar to that of Great Tit flocks, (see also Addicott, 1938).

Aegithalos caudatus was present in the present study area in flocks of 6 to 15 birds, though flocks of over 50 individuals have been recorded. This species rarely feeds on the ground, but rather individuals fly from twig to twig, peering round at neighbouring twigs after each flight. As in the other species which have been discussed, flocks move either in a slow drifting fashion, or in long integrated movements. At all times, however, the flocks are more closely integrated and move faster than Great Tit flocks. The only flock which was followed for any length of time moved 375 yards between 0920 and 1055 on December 30th, 1948, but another flock was seen to travel 300 yards in the course of a single integrated movement. Drifting movements are associated with gentle 'tup tup' calls made during short hops from branch to branch. Sometimes another call, 'tsirrrup' or 'Trrrrrp' - difficult to render in words but sounding like many 'tup' calls in rapid succession - is used on these flights, especially when the flock is drifting fairly rapidly. This note is also used in

mobbing predators. Longer integrated movements are preceded by numerous 'tsrrrrup' calls and very high-pitched shrill 'tsees'. The birds stop feeding and hop up higher in the trees, before flying off one by one. The shrill high pitched notes always accompany these long movements. Paechnatz (1936) also says that flocks typically feed in one place for a while and then suddenly depart and fly from tree to tree for 100 - 500 metres.

Little seems to be known of the flocking behaviour of Remiz or Auriparus spp.

SECTION IV WINTER FIGHTING.

A. General.

B. Behaviour Involved in Fighting over Food.

1. *Parus major* and *caeruleus*

- (a) Supplanting attacks
- (b) Combat
- (c) Stealing
- (d) Head-up posture
- (e) Wings-raised posture
- (f) Head-forward posture
- (g) Flying off with food
- (h) Avoiding behaviour
- (i) Re-entering the flock
- (j) "Individual distance"

2. Other Parus species

C. Experiments with a Mirror.

D. The Biological Value of Fighting over Food.

E. Fighting over Roosting Sites.

SECTION IV WINTER FIGHTING

A. General.

In the last chapter the integration of winter flocks was considered. It was seen that the factors involved in this were balanced by other factors tending to disruption, of which 'Aggressive Behaviour' was one of the most important. 'Aggressive behaviour' is a comprehensive term used to include all forms of fighting. Collias (1944) states that the situations which lead to aggressive behaviour "in groups of children (Durbin and Bowlby, 1939) and in subhuman vertebrates seem to be fundamentally the same: the intrusion of strangers, possession of some object, and frustration". Aggressive behaviour arising because of the intrusion of strangers (together with that concerned in the establishment and maintenance of so-called social hierarchies) may be considered as an indirect form of aggressive behaviour concerned with the possession of an object. The object in these cases is potential, not actual. Aggressiveness caused by frustration (at least in the sense inferred by Collias) is of doubtful biological value. We may therefore conclude that aggressive behaviour is nearly always concerned with the possession of some object, actual or potential, (aggressive behaviour in the predator-prey relation is not considered here, although it could be said to differ only in degree from, say, food-robbing).

Aggressive behaviour concerned with the possession of an object may be subdivided according to the nature of that object. We may thus distinguish reproductive fighting, in which the object is something essential for reproduction, from fighting for food, or fighting for roosting sites,

and so on. The validity of such distinctions will be considered in a later chapter. The present chapter deals only with two types of fighting which occur in winter - namely fighting over food and over roosting holes. Reproductive fighting occurs to a limited extent in winter flocks, but is dealt with in a later chapter. The question of position in a social hierarchy is considered briefly: a high position may lead to advantages both in connection with food and, later, with reproduction.

Fighting does not necessarily imply physical contact between the individuals concerned. Where contact does occur, it is referred to as 'combat'. Combat is rare, and fighting usually consists of more or less stereotyped behaviour patterns. Thus in the present study the ~~form~~^{term} "fighting" has been used to include both "display-fighting", in which the participants do not strike each other, and "actual fighting" or "combat".

B. Behaviour Involved in Fighting over Food.

1. Parus major and caeruleus

In the following sections the behaviour patterns involved in the fighting of Great and Blue Tits over food is described. Both offensive and defensive behaviour is included.

(a) Supplanting attack.

In a supplanting attack for a food object, the aggressor flies at the possessor of the food, causing the latter to fly off, and feeds in his place. Usually the aggressor flies down from a position above the other

bird: if both are initially on the ground, the aggressor usually flies up an inch or two before attacking. It is difficult to analyse the movements exactly, but often the attacker appears to glide for the last foot or two of his attacking flight, and sometimes a hard 'tit tit tit tit' call is heard: this is particularly marked with Blue Tits.

Sometimes a bird flies down as though to attack, but holds off when about a foot away and lands elsewhere. The attacks take place most often on a bird which is opening a nut, or has just dug a pit amongst fallen leaves, or is feeding in other ways which involve its being in the same place for at least several seconds.

The feeding bird nearly always hops aside or flies away, abandoning the food; though occasionally he takes the food with him. In either case it is rare for it to show any very marked further reaction: sometimes it raises its crest, flicks its wings, or wipes its beak on a branch. Occasionally a supplanted bird immediately attacks another, without attempting to rob it of food. Similar behaviour was witnessed by Colquhoun (1942) in Blue Tits, and is presumably a displacement activity, though Collias (1944) believes that it may be regarded as due to 'frustration'. Although supplanting attacks are nearly always successful, they are sometimes resisted. The behaviour can not, therefore, be classed as 'supersedence' (Tompkins, 1933).

It is often difficult to be certain whether a supplanting attack is concerned with food or not. Occasionally a feeding bird makes such an attack on another which approaches it too closely: here the attack is clearly concerned with food, though its object is not food/robbery. Sometimes there is clearly no reference to food. Thus one tit may supplant

another which is not feeding (e.g. during integrated flock movements): sometimes an attack is followed by several more in succession, or by a chase, so that both birds fly far away from any possible food object. Such behaviour was seen particularly at three times of year - amongst the juvenile flocks in late summer, during the autumn recrudescence of sexual behaviour, and from mid-December until the time at which the flocks break up. It is clear that in these cases the supplanting attacks are relevant to reproductive fighting. They are discussed on page 234.

Colquhoun (1942) used the term "approach threat" to describe such attacks, but it is clear that more than threat is involved.

(b) Combat

Occasionally the victim of a supplanting attack may jump up and meet his aggressor in the air. The birds face each other, with their bodies upright, striking with their beaks and claws and fall quickly to the ground. Occasionally a head-forward threat (see below) develops into combat. Combats rarely last for more than a few seconds: they were infrequent before Christmas, but were seen quite often in January and February. Hamerstrom (1942) found that 'fights' occurred more frequently in large flocks and in severe weather in P. a. atricapillus.

(c) Stealing

In some cases the attacking bird does not attempt to supplant the possessor, but goes straight for the food. Blue Tits occasionally robbed Great Tits in this way, seizing the food and flying off almost before the Great Tit has moved.

(d) Head-up posture

The head-up aggressive posture, which normally appears in reproductive fighting, occurred occasionally in food disputes between Great Tits during the period before the break-up of the flocks. In flocks in late January and February it was quite common. Typically, one Great Tit supplanted another and adopted a head-up posture for a second or two before feeding on his spoil. On December 29th, 1949, two Great Tits feeding on opposite sides of a piece of fat, which was hanging at one of the feeding stations, used very vigorous head-up postures. Occasionally birds feeding in front of a mirror postured in this way. Such posturing was usually immediately effective, the other bird flying off; sometimes, however, the bird postured at seemed to take no notice of it at all. Sometimes a bird giving the wings-raised posture (see below) gave incipient head-up postures at the same time. This is discussed further on p. 234.

(e) Wings-raised posture

In this posture the wings are held half open and raised to the level of the back, or even higher. The tail is sometimes in the normal position, sometimes spread, and sometimes raised. The posture may be given with varying degrees of intensity - the wings may be only just opened and hardly raised at all, or they may be lifted above the back. Illustrations of Great and Blue Tits using the posture in a dispute over a milk bottle have been given in a previous paper (Fisher and Hinde, 1949). Sometimes the displaying bird turned round so that its back was directed towards its opponent.

The wings-raised posture is commonly given by a feeding bird which is approached too closely by another. The threatening bird usually continues

feeding at the same time as he postures. It is also used occasionally in reproductive fighting, especially in inter-specific disputes.

(f) Head-forward posture

In the head-forward posture the threatening bird ceases feeding and faces towards its opponent. It holds its head down and forward, its beak usually pointing towards its opponent. In the Blue Tit the feathers of the cheeks and crown are sometimes raised, though I have not observed this in the Great Tit. The beak is sometimes opened. Sometimes the wings are scarcely unfolded, but in reactions of high intensity the wings are held as in the wings-raised posture and the tail is spread. The posturing bird may remain still and threaten, or may advance on its opponent. Usually the threatened bird gives way almost immediately, and hops or flies off, though sometimes two birds will threaten each other simultaneously in this way.

Like the wings-raised posture, the head-forward posture is used as a threat when one bird is approached too closely by another. Possibly it should be regarded as a high-intensity form of the wings-raised posture. It differs from the latter, however, in that feeding or searching for food must cease while the posture is held. It is also used by birds which are not feeding.

Sometimes the feeding bird ceases feeding for a moment and turns its head momentarily to look at a nearby bird. The latter usually flies off. This may be a normal preliminary to the head-forward posture.

(g) Flying off with food

When a tit finds a piece of food so big that it cannot be swallowed immediately, it flies off and eats it elsewhere. Nuts and beechmast are always dealt with in this way. The value of this behaviour to the individual

may be that he can thereby open and eat his nut in a place where he is less exposed to being robbed by other birds. Sometimes many individuals from a flock carry their booty to the same bush; but even so they probably gain some immunity from attack, as the neighbouring birds are feeding, not searching for food. The carrying away of the food may also be of value in that the bird opens its nut in a position where it is less exposed to predators.

The birds readily become conditioned to carrying their food to a particular bush: at houses where the tits habitually open the milk bottles and carry away the stoppers, piles of stoppers are found behind their favourite bushes.

In periods of great food abundance tits sometimes carry off food, and then leave it without eating it and return for more. Blue, Coal and Marsh Tits were often seen doing this during the heavy beechmast crop of 1948. The Marsh Tits usually flew down to the ground with the nut and pushed it into the moss: the same individual would return repeatedly to the same area, but not to the same spot: so that in a few minutes several nuts would be deposited within an area of a few square yards. The Coal and Blue Tits usually pushed the nuts into cracks in bark or into the holes in the centre of elder boughs. Similar behaviour has been recorded previously in Great and Willow Tits, and also in P. bicolor, as well as in the species noted above (Fatio and Studer, 1889; Lewis, 1923; Astley, 1923; Hibbert-Ware 1929; Forbush, 1929; Morgely, 1942; Owen, 1945^a; Bent, 1946; Southern, 1946^b). ^{Richards, 1949.} In all cases for which adequate data were given, food was temporarily super-abundant, and each particle of food was carried to a slightly different place, being usually pushed into a crevice

in a stump or behind ivy. It seems unlikely that the bird remembers later where it put each particle of food, but it may remember the general area, so that this is probably real food-storing behaviour. Certainly it is not merely a case of a behaviour pattern being cut short because part of the adequate stimulus (hunger) for the final act (actual eating) is missing. The chain is cut short before the nut is opened, and in most cases the food is not merely dropped, but hidden. The behaviour forms so definite a pattern that it must have survival value. Food-storing behaviour seems to be rare in birds, but is known in Balanosphyra formicivora and Asyndesanes^{us} lewis (see Bent 1939).

(h) Avoiding behaviour

Tits which are either searching for food, or opening nuts outside the flock, often fly off if they are approached too closely by another bird. If they have food they may carry it off with them.

(i) Re-entering the flock

When a Great Tit flock is feeding on the ground, an individual which is returning to it first perches above the flock and inspects the ground before flying down to feed. It seems that this enables him to settle near, but not too near, other individuals, as well as to settle on a suitable feeding ground.

(j) "Individual Distance"

The behaviour patterns described above have the effect of keeping a small area round each bird free from other birds. This area has been called "Individual Distance" (e.g. Burckhardt, 1944; Conder, 1949).

Conder describes "Individual Distance" as "an area which has no visible boundaries, which moves with the bird, and into which no other bird can come". These authors describe "Individual Distance" in Larus ridibundus, Aythya fuligula, and other species, and note that each bird's area is kept free by avoiding and threat reactions. This is also the case with the Great and Blue Tits. It must be noted, however, not only that "Individual Distance" is an area, but that it is a compressible area. Another individual at a distance of, say, 2 feet, may evoke only a slight wings-raised posture, whereas at one foot he may evoke a head-forward posture of full intensity. Further, the distance at which another bird is tolerated may vary with the physiological state of the individuals, with their position relative to their own territory (see p. 47) and even with where the flock is feeding (i.e. on the ground or in the trees, see p. 29).

The biological advantage of the maintenance of "Individual Distance" in the Tits is probably the relative immunity which it gives from the food-robbing behaviour of other birds. This, however, is not necessarily always its function: in other species it may provide sufficient room to spread the wings in sudden flight, or prevent the spread of parasites, or serve other purposes.

2. Other Parus Species.

Behaviour patterns very similar to all those described in the last section have also been seen in the present study in Coal, Marsh and Willow Tits. One Coal Tit very often opened its beak when using the head-forward posture. Marsh and Willow Tits were not actually seen to raise the cheek feathers when using the head-forward posture. Birds of each species

used the postures against individuals of other Parus species, as well as against members of its own species.

C. Experiments with a Mirror.

During the winter of 1949/50 the aggressive behaviour of the tits was studied by allowing them to see their own reflections in a plane mirror placed at one of the feeding stations. The mirror was 3 feet long and one foot high: It was placed vertically with one of the long sides on the ground. A piece of fat was left on the ground immediately in front of the mirror. Tits which came to feed on the fat were able to see their reflections and reacted in one or more of the following ways:-

(i) Some birds flew down towards the fat but, on seeing their reflection, immediately flew off in haste. Some of these actually landed on the fat for a fraction of a second before flying off, whereas others did not even land, but turned about in mid-air. Some of the birds which behaved in this way did not return to the mirror, at least during the period of observations. Others, however, returned again and again: in these cases the time between visits decreased, and the time spent in front of the mirror increased with each visit, until the bird was feeding normally. Occasionally a bird would settle so that its image was hidden from it by the fat, and would continue feeding until it saw its reflection, when it flew off.

(ii) Some individuals came to the mirror and looked at their reflections for some seconds, and then fed without display. In such cases

the bird usually appeared to be uneasy - looking round, flicking its wings, and often standing with raised crest.

(iii) In other cases the bird noticed its reflection and did not display, but fed without signs of uneasiness.

(iv) Sometimes the wings-raised posture was used, the bird feeding and posturing simultaneously. The posture might be so slight as to be barely noticeable, or very intense, with the wings raised above the back. The display became more intense if the bird moved closer to the mirror. Posturing of intermediate intensity usually subsided in a minute or two. Very intense wings-raised posturing usually led to head-forward posturing.

(v) Birds which showed the head-forward posture did so in intervals of feeding. The posture was usually accompanied by raising of the wings, which persisted during feeding.

(vi) Some birds actually attacked their own image. The attack was usually preceded by the wings-raised and head-forward postures. Two forms of attack could be distinguished. In the first place, the bird remained on the ground, with wings raised and tail spread, and pecked at its image. In the second it fluttered up against the glass and pecked. In either case it usually soon worked along to the end of the mirror, when, of course, the image disappeared. It then hopped around, usually with flicking wings and raised crest, until it saw its image again. After attacking for a few seconds it returned to feeding.

It will be seen that different individuals showed responses varying from immediate flight to almost immediate attack. The observations made were not sufficient to show the reasons for these differences in behaviour

but it was clear that (i) any one individual usually (but not always) showed the same type of response on successive visits and (ii) that certain second year birds, whose territories were known to be several hundred yards away, fed with signs of great uneasiness, whereas birds which spent much of their time close to the feeding station often attacked their images. It thus seems probable that some of the differences are connected with the birds' familiarity with the area.

Colquhoun (1942) has shown that in Blue Tits 'a clear social hierarchy exists within the flock in winter; residents are dominant to nomads and the social order of the residents is related to territory'. The five Blue Tits which occupied the first places in the 'dominance hierarchy' possessed territories at successively greater distances from the feeding station. A similar result has been obtained for P. major by Brian (1949). In the present study, the birds which were seen often round the feeding stations usually supplanted strangers at the food. Odum (1942) and Hamerstrom (1942) found that there is a dominance order in winter flocks of P. a. atricapillus, though the order is not always fixed or linear. Both these authors found that strangers were subordinate to the other members of the flock, and exhibited 'uneasiness' on approaching the food. Odum remarks that the three highest males in the hierarchy were the ones that remained on or near the winter feeding range to establish territory. He thus implies that a high position in the dominance order precedes the establishment of territory. The observations made by Colquhoun (loc.cit.) started in December, and those by Brian (loc.cit.) in January. In these cases the establishment of territories, or at least of preferred areas, had already taken place and the authors infer that the dominance order was a result of the territorial

organisation. The question is discussed further on p.¹³⁶.

The existence of social hierarchies raises the question of whether any fighting occurs purely to settle position in the social hierarchy, and without reference to food or other objects actually present at the time. This may be the case: it is known that 'the first thing two hens will do on meeting is to settle their future dominance relations' (Collias, 1943). There is as yet little evidence to show that such fighting occurs in wild populations of tits. Indeed Odum's (1941b) description of the behaviour of birds released into a strange flock suggests that they were at first subordinate to all other birds, and that their ultimate position in the new flock may have been settled in encounters over food. Even if such fighting does occur, it must be regarded as aggressive behaviour directed (perhaps indirectly) towards the possession of some object (food, territory, etc.) in the same way as other types of fighting.

The behaviour of the tits towards their reflection can be taken as behaviour towards a strange bird. The behaviour of each bird towards a stranger thus probably depends largely on the place where the encounter takes place: no doubt it also depends on other factors such as sex, (females rarely showed anything more than a slight wings-raised posture), hormonal condition and degree of hunger. (See Collias 1943, 1944; Allee, MS).

D. The Biological Value of Fighting over Food.

We have seen that in winter the supplanting attack is nearly always offensive in function, and is used in stealing food from other birds.

It will be asked whether such behaviour is of survival value - whether sufficient food is obtained in this way to make the behaviour biologically valuable. In order to give a partial answer to this question, a note was made of every occasion when such an attack was seen during routine observations on winter flocks. The incidence of attacks in each month was expressed as the number observed per hour spent watching flocks in the field. This, of course, provides only a very rough means of comparing the frequency of such attacks in different months, but does give some indication. In addition, in a few cases, the actual number of attacks seen during a given period of observation on one flock was counted.

The records are shown in Table 6 by half monthly intervals from September 15th to February 14th, 1948/49 and for June 1949, and by monthly intervals from July to January 1949/50.

Table 6. No. of supplanting attacks seen per hour spent in routine observations on flocks, (all *Parus* species).

<u>Period.</u>	<u>Hours of observation</u>	<u>Total No. of attacks</u>	<u>Ratio inter/intra specific attacks.</u>	<u>Average No. of attacks per Hour.</u>
1948/49				
Sept (ii)	51	13	0.6	0.3
Oct (i)	7	2	(1.0)	0.3
Oct (ii)	25	15	(1.5)	0.6
Nov (i)	24	31	0.24	1.0
Nov (ii)	33	48	0.20	1.5
Dec (i)	36	84	0.20	2.3
Dec (ii)	16	65	0.38	4.3
Jan (i)	24	83	0.20	3.5
Jan (ii)	41	134	0.25	3.3
Feb (i)	47	82	0.24	1.7
1949/50				
June (i)	26	2	0.00	0.1
June (ii)	19	9	0.00	0.5
July	13	12	0.1	1.0
Aug.	25	19	0.05	0.8
Sept.	24	20	0.05	0.8
Oct.	16	8	0.3	0.5
Nov.	11	22	0.15	1.9
Dec.	20	45	0.12	2.2
Jan.	25	50	0.00	2.0

Unfortunately it was not always possible to be certain whether the supplanting attack was made with the object of food-robbery or not. Therefore all supplanting attacks were counted except those probably associated with reproductive fighting, i.e. (i) leading to a chase, (ii) in which the attacker supplanted the same bird more than once within the course of a few seconds, and (iii) in which the attacker did not feed and used the head-up posture or other posture appropriate to sexual fighting. Instances of stealing food were included as supplanting attacks.

In both years attacks became most common in December, the figure being 4.3 attacks per hour in 1948/49, and 2.2 in 1949/50. In 1948/49 the tits fed almost entirely on beechmast throughout the autumn and winter so that in this year, at any rate, the change in the frequency of the attacks through the season cannot be accounted for by a change in the size of the food particles. The fact that the peak occurred in midwinter in both years might be taken as good evidence that the attacks are of biological value. This, however, is not necessarily the case since a number of other factors contribute to this result. Thus:-

(i) Attacks occur more often in closely integrated flocks than in dispersed ones. The flocks became more integrated as the winter advanced.

(ii) Although definite instances of reproductive fighting were excluded, some of the supplanting attacks may have been associated with pair formation. Such behaviour became more marked from December onwards.

(iii) On warm days in January and later the birds fed in pairs and not in flocks, so that food robbery was rare. On the other hand, supplanting attacks were particularly common when the tits fed in flocks during cold spells at this season.

It seems unlikely, however, that a behaviour pattern of this type, which can be casually observed over four times an hour, is biologically valueless. In fact, when it was possible to watch one flock in one place for any considerable period, the number of attacks was much higher than this. In two periods of 36 and 40 minutes on Jan 6th and Feb 4th, 1949, respectively, in each of which flocks estimated at ten birds were kept in sight continuously, 13 and 17 attacks directly connected with food were counted. If all the birds in the flock were attacked equally often, this would mean that each was attacked about twice an hour. In practice some birds must have been attacked much more often than this. As far as could be seen, these birds were taking little other food than beechmast, and were taking on the average three minutes to find a beechnut. In another flock (estimated at 27 tits) which was watched on Dec 2nd, 1948, the birds were taking on the average only 13 seconds to find a beechnut, and only two attacks were seen in half an hour.

Table 7. Number of supplanting attacks observed between the tit species.

(a) 1948/49.

<u>Attacked species.</u>	<u>Attacking species</u>			
	<u>Great Tit.</u>	<u>Blue Tit.</u>	<u>Coal Tit.</u>	<u>Marsh Tit.</u>
Great Tit	<u>265</u>	28	1	2
Blue Tit	22	<u>136</u>	1	0
Coal Tit	12	2	<u>5</u>	5
Marsh Tit	21	17	0	<u>52</u>

(b) 1949/50.

<u>Attacked species.</u>	<u>Attacking species</u>			
	<u>Great Tit.</u>	<u>Blue Tit.</u>	<u>Coal Tit.</u>	<u>Marsh Tit.</u>
Great Tit	<u>68</u>	4	0	0
Blue Tit	5	<u>78</u>	0	0
Coal Tit	1	2	<u>8</u>	1
Marsh Tit	0	1	0	<u>22</u>

Table 7 shows the frequency with which attacks were observed between each of the Parus species in the wood. Attacks involving individuals of the same species (underlined figures) were much more common than those involving different species. In the interspecific attacks, Great and Blue Tits robbed Coal and Marsh Tits more often than vice versa. Blue Tits robbed Great Tits about as often as they were robbed by them. On a few occasions tits were supplanted by Great Spotted Woodpeckers (Dryobates major) and Nuthatches (Sitta Europaea); and Great and Blue Tits supplanted Chaffinches (Fringilla coelebs), Robins (Erithacus rubecula) and Hedge Sparrows (Prunella modularis).

The ratio of interspecific attacks to intraspecific attacks (Table 6) was consistently higher in 1948/49 than in 1949/50. In the first year there was a very good beechmast crop, which formed a high proportion of the food of all the tits throughout the winter. In 1949/50 the beechmast failed. Thus the higher proportion of interspecific attacks in 1948/49 may have been due simply to the fact that the different species were feeding on the same food whereas in 1949/50 they fed mainly in different places. In the year when the beechmast failed the tits were probably feeding on smaller particles than in the previous year: this may also have reduced the proportion of interspecific attacks.

E. Fighting over Roosting Sites

On a number of occasions during the winter a tit was seen to arrive at its roosting hole to find it already occupied. Sometimes the

newcomer was another tit; more usually it was a Great Spotted Woodpecker (Dryobates major). On such occasions the dispossessed bird usually made several attempts to enter the hole, and both the head-forward and wings-raised posture were used. On one occasion (February 21st, 1949) a Great Tit, finding its hole occupied, flew to a branch some distance away and gave a momentary head-up posture although no other tit was near. (See also p.266).

Tits may be seen inspecting holes (see p.42) all through the winter, though such behaviour becomes much more common in the weeks preceding the nesting season. When a tit in a winter flock inspects a hole, it often happens that another bird flies at it and supplants it at the hole. Sometimes the first bird resists, and a combat ensues. Such fighting may be relevant to the possession of roosting sites.

SECTION V MOVEMENT OF INDIVIDUALS.

A. General.

B. Parus major.

1. Post-breeding Season.
2. Autumn and Winter.
3. Winter Range.

C. Parus caeruleus.

D. Parus palustris.

E. Ringing returns.

F. Other Parus species.

G. The concept of 'Domicile'.

H. Homing.

SECTION V MOVEMENT OF INDIVIDUALS.

A. General.

All gradations from sedentary to regular migratory behaviour can be found in the genus Parus. Even one subspecies may differ markedly in its migratory behaviour in different parts of its range. Such variations clearly depend on local differences in the relative survival values of sedentary and migratory behaviour.

The British races of the Great and Blue Tits (Parus major newtoni and P. caeruleus obscurus) are almost completely sedentary, except for local movements. Individuals of the continental races also occur in the British Isles in winter, sometimes in fair numbers, (see e.g. the records for 1910 in British Birds, vols IV and VI) but little is known of their movements inland. On the continent the situation is often very complicated, since there are some areas where the winter population consists partly of local and partly of migratory birds (e.g. Belgium, van Beneden, 1933; Delmée, 1940); others in which the adults are sedentary and the juveniles migrate long distances (e.g. Finland, Grote, 1913; see also Mogall, 1939); and probably others where all birds are migratory.

A brief account of the movements of the tits in Wytham is given in the following sections. The reader is referred to Plattner and Sutter (1946, 1947) and to Kluijver (in litt.) for recent reviews of the literature on the movements of tits.

B. Parus major.

1. Post-breeding Season.

Within a week of leaving the nest, some of the broods in the wood were found to consist of the young of more than one pair. Thus the young started to wander from their parent's territories very soon after leaving the nest. No doubt this mixing of the broods occurs far more readily when the population is high, and the territories close together, than when the population is sparse.

Two broods of Great Tits were given colour rings: four weeks after leaving the nest they had become scattered all over the wood. No attempt was made to study the movements of the juveniles between July and November.

2. Autumn and Winter.

Most of the adults remained on or near their previous years' territories throughout the autumn and winter. (Other authors have stated that they disappear during the moult and reappear again in autumn (see summary in Plattner and Sutter, 1948-7) but this was certainly not the case with the colour-ringed adults watched in the present study). They formed part of the flock whose flock-area included their nest-site, and moved about with it, but spent more time in the neighbourhood of their last year's territory than in other parts of their range. During cold spells this attachment to a limited area became much less marked, and all birds wandered over far greater areas than they had done previously. One pair, which had never been seen more than 100 yards from its breeding territory throughout the whole summer, autumn and early winter of 1949, appeared at a feeding station 400 yards away during

a cold spell in January 1950; and continued to use it occasionally during the subsequent milder weather. Gibb (in litt.) found that all the tits left the wood during the severe winter of 1947/8. In a very few cases adults changed their range completely during the winter, moving to a different part of the wood. It is, of course, possible that some of the adults which disappeared had moved elsewhere.

It is not known how much the juveniles continued to wander about in the autumn, but by November it was clear that some of them had already taken up residence in a limited area. These birds remained in the same area for the rest of the winter. They moved about with a flock and showed no marked preference for any particular part of the flock area, but when the flocks broke up they immediately showed behaviour associated with the establishment of a 'preferred area' and a territory. No doubt these individuals, like the second year birds, would have moved about more had the weather been colder.

Not all the first year birds became sedentary as early as November however. Many which had appeared to be settled in November subsequently moved to quite a different part of the wood. All through the winter there were birds which turned up at the traps one day and disappeared the next. Some movements of this type occurred throughout the winter, but it seemed to be most marked in February and March. Indeed, Maynard (1936) considered Great (and Blue) Tits to be mainly non-resident at this time of year, new birds arriving at the traps about every five days. This movement immediately preceding the breeding season was probably largely due to the return of birds which had moved out of the woods into the hedges and into populated areas in the early part of winter. In the British Trust for Ornithology enquiry into the opening

of milk bottles by birds, many of the correspondents stated that their milk bottles were opened most frequently in the winter; and commented that there were always more tits about the houses at that time of year: these observers were untrained, but they were also independent and unbiassed.

Since the adults remain in the breeding area throughout the winter, and there are no indications that they actively drive their young away, (unless they are rearing a second brood (cf. Stein, 1927)), it is probable that the dispersal of the juveniles is due to an innate tendency to move, independent of the environmental situation. Indeed Kern (1940) found that juveniles accustomed to feed at a well-stocked feeding station moved off in September in spite of the food supply. On the other hand, their further movements during the autumn and winter probably depend largely on the availability of food. Certainly the Great Tit population becomes higher in the areas where food is very abundant than where it is scarce. Presumably a juvenile has a greater tendency to change its range when food is difficult to find than when it is easy.

Other authors also have concluded that the extent to which the birds move about is linked with the availability of food (e.g. Lebourier et Rapine, 1941). Promptor and Lukina (1937) consider that they have proved it experimentally. Steinfatt (1938) notes that P. palustris moves into pine woods in winter - presumably a direct effect of local food conditions. The problem is, however, by no means a simple one, as in winter the tits need roosting sites as well as an adequate food supply. In some cases they may feed at some distance from where they sleep (see Plattner and Sutter 1946, 1947).

If it is true that the winter movements of juveniles are largely dependent directly on the availability of food, the movements differ from true migration in two ways:- (i) The movements are not orientated. (ii) The move-

ment occurs as a direct result of the biological need, or, in other words, the proximate and ultimate factors are the same. In the latter respect they resemble hard weather movements, but these are orientated.

A habitat that is favourable for the Great Tit in winter is not necessarily favourable for breeding. A pre-nesting movement may be induced by some form of habitat selection, the birds moving about until they find a suitable area. The spring movement of tits is probably not orientated. In true migration both autumn and spring movements are orientated, and ~~in~~ the movement precedes^e the biological need.

3. Winter Range.

The feeding range of an individual in any part of the winter usually corresponds to the flock area of the flock to which it belongs (i.e. the feeding range of the flock, c. 10-20 acres: see p.20). Some individuals, however, spent some of their time in one flock and some in another, and this had a considerably larger range than this. On the other hand some second year birds, which tended to remain near their previous year's territory, had a range rather smaller than that of the flock. It was rare for a bird to be seen regularly at points more than 400 yards apart. A number of birds changed their range during the course of the winter, in some cases gradually and in others more or less abruptly.

C. *Parus caeruleus.*

All that has been said about the Great Tit applies also to this species. The adults remained throughout the winter in the neighbourhood

of their previous year's territory, though forming part of the flock whose flock-area included it. The winter range of the Blue Tits seemed to be rather larger than that of the Great Tits - a number of birds were known to wander regularly over about 25 acres. As in the Great Tits, there were indications of an increased amount of movement among the Blue Tits in Wytham in February and March.

Kenrick (1940) states that the birds caught at his traps near Birmingham could be divided into four categories:- A. Fully resident (three-eighths); B. Summer residents (one-eighth); C. Winter visitors (one quarter) and D. Winter passage migrants (one quarter, mostly seen in February and March). Categories A, C, and D would be expected if the general movement of Blue Tits is similar to that sketched above for Great Tits. Category B indicates that the adults move rather more than do the adult Great Tits, but more concise evidence is needed on this point. As in the Great Tit, the amount of wandering no doubt depends largely on the availability of food (see Lebeurier et Kapine, 1944).

D. *Parus palustris*.

No mixing of broods was seen in the Marsh Tits - presumably because the territories were so much larger than those of the Great and Blue Tits (see p. 96). In two broods the young were colour-ringed. They remained on their parents' territories until they were about a month old, and then suddenly scattered all over the wood.

The adult Marsh Tits showed an even greater tendency to remain on or near their territories through the winter than did the Great and Blue Tits.

Although they often joined flocks of juveniles, they did not usually follow them outside their own territories.

E. Ringing Returns.

The number of recoveries of tits ringed under the British Museum Bird Ringing Scheme is as yet insufficient to give a clear picture of their movements. Their analysis is complicated by two factors; (i) among the birds ringed as adults it is usually impossible to differentiate between 1st year and older birds, and (ii) many birds move over such short distances that their movements are not shown by the ringing returns. In Table 8 only those birds which were recovered dead, or which were re-caught by a person other than the original ringer, have been included. In this way the bias which would be caused by birds re-trapped by the original ringer is eliminated. The adults have been divided into two categories - those first ringed between March 20th and July 10th, which may be assumed to be at least one year old when ringed (category A) and those first ringed at other times of year (category B).

(a) Great Tits. Of the 13 birds ringed as adults during the nesting season, none showed any movement. Quite a number of the birds in category B showed some movement, but this category may have included some first year birds. There are few recoveries of nestlings, but quite a large proportion show some movement. The one adult which moved 95 miles was ringed at Birmingham on Dec. 29th, 1935, and recovered at Denver, Norfolk, on Jan. 14th, 1938: this may have been a specimen of the Continental P. m. major. Two

Table 8 . Numbers of Great and Blue Tits recovered at various distances from point of ringing, excluding those re-trapped by the original ringer.

<u>Species.</u>	<u>Distance recovered.</u> <u>Miles.</u>	<u>1m.</u>	<u>3m.</u>	<u>5m.</u>	<u>10m.</u>	<u>20m.</u>	<u>30m.</u>	<u>Over 30.</u>
Great Tit.	Nestling	15	5	2	2			
	Adult A	13						
	Adult B	96	4	3	5	4	1	1 at c.38 miles. 1 at c.95 miles.
Blue Tit.	Nestling	7	4	2			1	
	Adult A	13			1			1 at c.42 miles. 1 at c.47 miles.
	Adult B	179	8	2	4	2	1	1 at c.53 miles.

birds ringed in the autumn of one year were re-caught by the trapper several times during the winter and then moved 10 and 38 miles respectively in February/March.

(b) Blue Tits. Of the 16 birds recovered which were first ringed as adults in the breeding season, 3 had moved a considerable distance. This possibly indicates a difference from the Great Tit, though the movement shown by adults in category B is similar to that in the Great Tit. Few ringed nestlings have been recovered, but a high proportion show some movement. There are two records of birds ringed in the autumn, which were known to be sedentary during the winter, but which moved 8 and 17 miles respectively in February/March.

F. Other Parus Species.

No attempt will be made here to review the literature on the migratory behaviour of the species mentioned above in other areas, or of the other Parus species. The following generalisations can be made:

(i) In all cases the juveniles move farther than the adults.

Adults are in fact sedentary in all regions except those in which conditions are extremely severe. Kluijver (in litt.) has shown that adult females of P. m. major have a very slightly greater tendency to wander between successive breeding seasons than adult males. If this is generally true for other species and other areas, we can say that the relationship between the amount of movement shown by adult males, adult females and juveniles is the same as in other 'partial migrants' (Iack 1943/4).

(ii) The amount the juveniles move varies in different species, in different races, and in individuals of the same race from different areas. No doubt natural selection exerts a fine control on the amount of movement shown by individuals in different areas. In some cases, also, there are marked differences between the amount of migration occurring in different years (e.g. P. a. atricapillus, Wallace, 1941; Boddish, 1938; Odum, 1942: P. ater, Grote, 1913 and 1937; Sevesi, 1934: P. hudsonicus, Bent, 1946). Such differences may sometimes be due to population changes, but presumably are usually due to differences in the proximate factors controlling the migratory behaviour.

(iii) In those species which are relatively sedentary, as well as in those which are migratory, more movement occurs in those months immediately preceding the breeding season than in the winter (e.g. P. caeruleus, Kenrick, 1940: P. a. atricapillus, Wallace, 1941).

G. The Concept of 'Domicile'.

Kluijver (in litt.) distinguishes four areas which have 'special significance in tit biology'. These are: (i) the area immediately surrounding the nest hole; (ii) the territory; (iii) the Domicile (i.e. the part of its range which it frequents most often by day, and in which it also sleeps and breeds. It is measured by calculating the area within which all the breeding and roosting sites used by the bird once it has 'settled down' are included; (iv) the range (i.e. the area in which all the bird's activities take place: it seeks food, sleeps and breeds within the limits of its range). Once a bird has selected a domicile and a range

(vi) seldom changes them.

It would seem that, in the concepts of range and domicile as used by Kluijver, the time factor has not been adequately considered. Thus during a bird's first winter, before it has finally settled, it may feed over a more or less definite range (see p.20) for days, weeks or even months in succession, and then move to a totally different area. (This is, of course, especially the case with migratory birds). Several cases of this were encountered in the present study. Indeed, it is unlikely that all the birds, which were recorded in the area for a week or two and then disappeared, had died: many of them must have changed their range. A distinction must therefore be made between the range during any given period, and the area over which a bird ranges during its life.

Further, the concept of domicile introduces considerable difficulties. Kluijver uses the term to mean the area containing the different successive roosting and breeding sites of one individual. It thus has meaning only in retrospect, and cannot be of any significance to the bird. In Kluijver's study roosting sites were available only in nest boxes, which were scattered more or less evenly through the wood. In Marley Wood, on the other hand, few birds roosted in boxes, the majority roosting in the groups of dead trees. These trees were deserted by most individuals before the breeding season, when the birds scattered to breed in the boxes; these were presumably more suitable than the small holes in the trees. Thus here the domicile, as defined by the roosting sites, was often remote from the next year's territory. Further, Plattner and Sutter, (1946 and 1947) state that in some cases the birds may feed at some distance from the

roosting sites, so that the domicile is not "the part of its range which it frequents most often by day".

It is not denied that individual Great Tits come to frequent one part of their range more than others. This is particularly the case with second year birds, who frequent their last year's territory and its environs more than the other parts of their range. Some first year birds, also, come to prefer a certain part of their range during the winter, presumably because they become conditioned to feed in certain places rather than others. The use of the term domicile for an area which has no existence at any one time is only a way of saying that the birds are more or less sedentary.

H. Homing.

A number of attempts to test the homing abilities of tits have been made, (e.g. P. atricapillus, Butts, 1931; Wallace, 1941; Odum, 1941^b; P. major and caeruleus, Murples, 1932 and 1933; Wenkel, 1935; Delm  e, 1940; Creutz, 1949). All these authorities agree that most birds find their way home over distances up to a few miles, but that very few get home from greater distances. The return seems to depend on the bird coming by chance into known country.

SECTION VI PAIR FORMATION AND THE BEHAVIOUR OF THE PAIR.

A. Pair Formation.

1. Parus caeruleus
2. Parus major
3. Parus palustris
4. Aegithalos ^ucaudatus
5. Other species.

B. Permanency of Mating.

C. Break-up of the flocks.

1. Parus major
2. Parus caeruleus, ater and palustris
3. Aegithalos ^ucaudatus
4. Other species.

D. Behaviour of the Pair after the Break-up of the Flocks.

1. Parus major
2. Parus caeruleus
3. Parus palustris
4. Parus ater
5. Other species.

SECTION VI PAIR FORMATION AND THE BEHAVIOUR OF THE PAIR.

A. Pair Formation.

In most passerine species the males separate out from the flocks before the females and establish themselves on a territory. The females then come to the territories, where pair formation takes place (see e.g. Tinbergen, 1939^a). Often the male at first behaves aggressively towards the female, but then shows other behaviour when she does not respond as another male. Little is known of pair formation in those species which form pairs in the flock. Putman's (1949) observations on Bombycilla cedrorum seem to indicate that in that species the male takes the initiative by making a courtship dance to other birds in the flock, and that the response of the second bird depends on its sex and physiological condition. The exact mechanism of the formation of pairs in the tits has not yet been established, but there is some evidence as to its nature. This evidence is at present stronger for the Blue Tit than for the Great Tit: the Blue Tit is therefore discussed first.

1. Parus caeruleus.

Although the birds in the winter flocks show few indications of sexual behaviour, the fact that some of them are paired is revealed by the study of colour ringed birds, and also by their behaviour at roosting time (see p.267). The members of such pairs show little preference for each others company inside the flock, but on warm days, especially in September/October, and again in the spring, the flocks disperse and the pairs can be more easily recognised. Some of these were second year birds, for permanent

pairing is usual if both individuals survive. In some cases, however, juveniles also became paired during the winter.

It is probable, however, that most pair formation takes place when the flocks break up. On warm days from December onwards there is much aggressive behaviour in the flocks, and although the skirmishes sometimes start as food disputes, food often seems to be irrelevant. Such aggressiveness usually consists in one bird flying up to supplant another, finishing its attack with a short glide, and holding its tail spread and its wings slightly open on landing. The attacked bird may give an aggressive display in return, or it may merely hop aside. In the latter case the attacker may supplant it several times in succession. If the attacked bird flies right away, the attack may develop into a prolonged chase. (cf. Tooby, 1948). The attacks are accompanied by a 'tit tit tit tit' note.

Behaviour similar to the above may be seen between the members of a pair during the first few weeks after the break-up of the flocks. Thus when a pair of Blue Tits is feeding in a tree, the male may suddenly make a series of supplanting attacks on the female, the latter moving away only a short distance after each attack. If the female does fly right away, a chase may ensue. Further, in reproductive fighting, males often supplant (see pp. 123) their adversary's female. The behaviour in the winter flocks described above is so similar that it is reasonable to suppose that it is associated with pair formation. If this is correct, then it would seem that in tits the male takes the initiative in pair formation by making supplanting attacks on other individuals in the flock: the response of the attacked individual no doubt depends on its sex and physiological condition. More observations are needed.

Although some individuals started to sing before the break-up of the flocks, it seems unlikely that song is of any great importance in pair formation. It does function in keeping the pair together at a later stage.

2. Parus major.

In winter the pairs within the flocks are even more difficult to recognise than in the Blue Tit, for the roosting display is less marked, but there is no doubt that the second year birds usually remain paired through the winter, and it is probable that some of the juveniles also form pairs before the flocks break up.

Most pair formation probably takes place when the flocks break up: supplanting attacks and chases similar to those described above for the Blue Tit are common at this time. The supplanting attacks were often followed by head-up posturing. As in the Blue Tit, during the period after the break-up of the flocks males sometimes make a series of supplanting attacks on their females; and in reproductive fighting males often make supplanting attacks on their opponent's mate. Brian (195⁴⁹~~50~~) has described pair formation in one individual Great Tit. The male flew up and supplanted the female and both gave head-up postures. On successive days the posturing became less marked.

After the flocks broke up unmated birds seemed to be rare, though a few wandering individuals were seen. Nevertheless several birds which lost their mates later in the season - even during the nesting season - found new ones in a few days.

3. *Parus palustris*.

In the Marsh Tit it is easier than in the Blue Tit to recognise the pairs in winter. The individuals of the pair show a marked tendency to keep together, even in the flock, and at least most of the paired birds hold territories throughout the year, and rarely leave them.

In June 1949, some individuals of a colour ringed brood were seen by both J. A. Gibb and the writer to keep company with other unmarked juveniles for several successive days after the break-up of the broods. These birds showed aggressive behaviour towards other Marsh Tits in exactly the same way as paired birds in spring, but if these were pairs they were of only a temporary nature: a fortnight later the birds concerned had moved to a different part of the wood and were no longer apparently paired, though still showing aggressive behaviour. In some cases, however, juveniles certainly became paired by November. In late winter, chases, similar to those which have been described for Great and Blue Tits, were common.

4. *Aegithalos caudatus*.

In this species pair formation probably takes place in a similar way to that which has been described for the *Parus* species. Chases were common in flocks from mid-December onwards. These usually started with a supplanting attack; and the chased bird often flicked or shivered its wings between flights. These have also been described by Tooby (1948).

5. Other species.

Odum (1941) found that in *P. a. atricapillus* pairs are formed before the establishment of the territory, and Steinfatt (1938) reached a

similar conclusion for other European species of tits. Odum found that in 60% of cases a paired condition could not have been maintained during the winter, but remarks that mortality could account for this. "If pairs are maintained apparently the bond between them is very weak in the winter flocking period." Verheyen (1947) notes that in P. atricapillus in Europe new pairs form before the end of October. Dixon (1949) found that in P. inornatus, where winter flocking does not occur, but the adults remain and defend their territories all the year round, the juveniles become paired soon after the break-up of the family parties. He also notes that the male of this species often supplants the female: the female may simply shift her perch, or she may fly off, when a chase ensues.

In Remiz pendulinus the mechanism of pair formation is quite different from that in the Parus species, the male starting to build the nest before the arrival of the female. (Burkhardt, 1948).

B. Permanency of Mating.

Odum (1941) has reviewed the literature for the Paridae and has shown that "There is considerable evidence that paired birds of many Paridae maintain an attachment for each other beyond the breeding season and may remain paired/for life". There is indeed strong evidence that permanent pairing is usual, and to Odum's list may be added the observations of Dachy (1946) on P. major and Dixon (1949) ^{See also Kluyver in lit} on P. inornatus. Records of proven divorce are comparatively rare. (P. major and caeruleus, Delmee, 1940; Kenrick, 1940; Schenk, 1929; Verheyen, 1947: P. inornatus, Dixon, 1949). Some of these records refer to changes of mate between the two broods in

one season: similar behaviour in other species has been discussed by Tinbergen (1949^{39a}). Bigamy is also known in the Great Tit (Gooch, 1935).

C. Break-up of the Flocks.

1. Parus major.

In both 1949 and 1950 the break-up of the flocks was a gradual process. Some reproductive fighting was seen in December in both years but it did not become common until January. In late January, 1949, and early February, 1950, the flocks became noticeably less integrated than they had been previously. For instance, individual birds often gave long series of twinks which did not produce an outbreak of twinkling in the flock as a whole (cf. p.30), and when an outburst did occur, the individuals often moved in different directions. Similarly, in Plectrophenax nivalis, Tinbergen (1939)^a noted that just before the break-up of the flocks there was a "higher frequency of repetition of social sounds". ^{Great Tits} Males seemed to have less tendency to flock than females at this time.

In 1949 the flocks in different parts of the wood broke up at different times: well marked flocks persisted in the lower wood when nearly all the birds in the upper wood were in pairs. Paired Great Tits sometimes associated with flocks of Chaffinches (Fringilla coelebs).

In the period between the first appearance of paired behaviour and the beginning of nesting, the Tits were usually on preferred areas of territories in the early morning, but in flocks later in the day. The time of day at which they changed from paired to flocking behaviour was

later in warm weather than in cold, and became later in any weather as the nesting season approached. A few flocks were seen up to the beginning of April. These spring flocks were comparatively loosely integrated, yet more than a mere tolerance for the presence of other individuals was involved in their formation, for up to seven pairs were seen to come together from different parts of the wood to form a flock. Second year birds joined such flocks less often than younger birds. When first formed the flocks would have an explosive quality, short chases and reproductive fighting occurring from time to time. Later in the day they became more like winter flocks, and practically the only aggressive postures seen were those associated with food disputes (see p37). The behaviour of the birds during this change-over period was thus similar to that described by Howard (1920) in his classic studies of Buntings and Finches.

During this period, aggressive behaviour amongst flocking birds seemed particularly likely to occur if the birds were disturbed. Thus on several occasions when the observer approached a flock in such a way that the birds were disturbed but not frightened away, two individuals which had been feeding apparently peacefully on the ground behaved aggressively to each other, giving the head-up posture (p.116) and calling "pit tit churr". Similarly, when the birds in a flock started to fly up into the bushes, preparatory to a flock movement, two birds which landed near together gave head-up postures.

2. *P. caeruleus*, *ater* and *palustris*.

The break-up of the flocks in these species was similar to the break-up of the Great Tit flocks, and took place at about the same time of year. Flocks of varying degrees of integration were seen occasionally up to the beginning of April.

3. *Aegithalos caudatus*.

Similar to that described for other species. Tooby (1948) remarked that the break-up of the Long-tailed Tit flocks took place over a longer period than that of the Blue Tit flocks: this was not the case in either year in the present study, as the flocks of each species broke up at about the same time, and the Long-tailed Tits started to nest much earlier than the Blue Tits. Even after nest-building had started, however, Long-tailed Tits were sometimes seen in flocks in the afternoons.

4. Other species.

Odum (1941) describes the break-up of the flocks of *P. a. atricapillus* as being a gradual process, pairs or single birds separating out a few at a time. The flocks broke up and reformed at each cold spell in April (Odum, 1942).

D. Behaviour of the Pair after the Break-up of the Flocks.

1. *Parus major*.

When the birds are feeding in pairs after the break-up of the flocks, there is a marked difference between the behaviour of the sexes. The females usually feed lower than the males, and spend more time on the

ground: they seem less alert than their mates. The males spend much time keeping watch above their mates: if disturbed they hop up in the bushes and scold the intruder (see p.248), while their females remain silent and often continue feeding in the background. The members of the pair keep in very close contact, and at first wander about together through the whole of the area frequented by the flock to which they previously belonged: some pairs even move outside this area (see p.91). The male is usually but not always dominant to the female, and may drive her away from feeding places. He shows obvious signs of disturbance if he temporarily loses contact with his mate, calling 'twink', 'chich ich ich ich', or 'chip de chip', or singing. Twinks, song and often other calls of the male attract the female, and cause her to fly towards him.

A gliding display flight similar to that described for the Blue Tit (v. in fra) occurs occasionally in the Great Tit, but is not so well marked as in that species. Usually the bird only glides for the last foot or two of a flight, and holds its wings open for a fraction of a second after alighting. More rarely a flight is accomplished in a series of glides, with wing beats in between.

2. Parus caeruleus.

(a) General Behaviour

As in the Great Tit, the pair at first wander over a large area. One of the pairs which was watched closely, however, showed no wandering phase but settled down to occupy a territory of 2.0 acres from the beginning of February on. This territory was held to the breeding season with only slight losses, and the pair bred successfully on it.

The male usually feeds rather higher in the tree than the female and is the more alert and active of the two. Before the establishment of the territory the pair keep close together, and either sex, particularly the male, shows signs of anxiety when separated from its mate, "Der ttt" being the most commonly used call. As in the Great Tit, song plays an important part in keeping the pair together.

(b) Courtship

Certain displays, seen regularly during the pre-nesting period, are not directly related to copulation. They may have significance in pair formation, but it seems more likely that they are associated with 'maintaining the pair bond'. These are:

(1) Flight displays. These consist of the movements of flying in an exaggerated form. The most extreme is gliding flight, in which the male glides very slowly with wings spread and still: the primaries are separated and presumably function as "Handley Page" slots in reducing the stalling speed. Under these conditions the air speed of the bird is very slow, but height is lost. The displaying male can avoid this loss of height in two ways - by making slow strokes of very large amplitude or rapid strokes of small amplitude. Both these types of flight have been observed, but the second is the more common and has been called the 'moth flight'. In both years gliding flight was first seen in early February: it was seen most frequently in March, ~~and only rarely in April~~. Gliding ^{or} as moth flight often precedes a hole inspection display, and it is also often associated with reproductive fighting.

Less extreme forms of gliding flight are very common during the pre-nesting season, especially in the early morning. When pairs are feeding together any flight that the male makes, whether from bough to bough in search of food or from tree to tree when disturbed by the observer, may have a short glide at the end, and the bird may hold the wings widely open for a fraction of a second after landing (cf Great Tit).

Occasionally in such pairs one bird was seen to take a flight almost vertically upward for up to twenty feet, and then to return to the same or a nearby perch. The tail is usually spread. This flight may be performed by either male or female, and also occurs (rarely) in association with reproductive fighting. It has been recorded by Tooby (1948), who also observed it in Long-tailed and Great Tits.

(ii) Other displays. During the intervals between such flights the male usually stands or feeds with a raised crest, spread tail (raised or lowered) and wings slightly open: the lowered spread tail is also associated with a peculiar straddling walk (cf. Turner, 1910). The attitudes may be maintained whilst feeding for long periods even in the absence of the female. There is a gradual diminution in the intensity of such displays as the day progresses.

Wing shivering occurred occasionally in these early displays, but was not common until mid-March, when it apparently represented an incomplete form of the pre-coital display.

3. *Parus palustris*.

As in Great and Blue Tits. The male was usually more conspicuous and more aggressive than the female, though this was not so noticeable as in Great and Blue Tits. Occasionally pairs were seen in which the male was exhibiting postures similar to those described for the Blue Tit - spread tail, raised or lowered, wings held slightly open. Full gliding or moth flight was only seen on a few occasions, and is certainly not common, though a brief glide at the end of a flight is

sometimes seen in the pre-nesting season.

4. Parus ater.

Gliding flight was seen on a few occasions.

5. Other species.

P. a. atricapillus behaves in a similar way to that described for Great and Blue Tits (Odum, 1941); the pairs wander about over a wide area, behaving aggressively towards other pairs, but the establishment and defence of the nesting territory does not begin until "about the time of cavity excavation". In this species and in P. inornatus (Dixon, 1949) it is stated that there is no difference between the behaviour of the male and the female in the pre-nesting period, and they thus differ from Great and Blue Tits in this respect.

Little has been recorded of display in the pre-nesting period for species other than the Blue Tit, but gliding flight or moth flight occurs in P. bicolor (Dickey MS quoted in Bent, 1946), P. cyanus (Kozlova, 1933) and Aegithalos ^Vcaudatus (Day, 1931).

SECTION VII TERRITORY.

A. Establishment of the Territory.

1. Parus major

(a) General

(b) Establishment of territories on the study area.

(c) A comparison with Kluijver's data on P. m. major.

(d) Processes involved in the establishment of territory in the Great Tit.

2. Parus caeruleus

3. Parus palustris

4. Other species.

B. The Area round the Nest-Site.

C. Size of Territory.

1. Parus major

2. Parus caeruleus

3. Parus palustris

4. Parus atricapillus

5. Other species

6. General

D. Relation Between Migration, Permanency of Pairing and Territorial Behaviour in Winter.

E. Function of Territory in the Titmice.

SECTION VII TERRITORY.

In most Passerine species which have been studied, the territory appears to be clearly defined and a more or less rigid area. It is established by the male, who sings from conspicuous points and drives off other males: the female arrives later (see e.g. Howard, 1920). The territory of the Great Tit is often neither rigid nor clearly defined. It appears to be similar to that of Emberiza citrinella, as described by Diess^fhorst (1949), except that it is not established until after pair formation.

In the following section a general description of the territorial behaviour of the Great Tit is given, illustrated by the behaviour of several pairs in the springs of 1949 and 1950. Certain other aspects of territorial behaviour are also discussed.

A. Establishment of the Territory.

1. Parus major.

(a) General

After the pairs separated out from the winter flocks, they at first wandered over a fairly large area, approximating to the range of the flock to which they had previously belonged. When another pair was encountered, the males behaved aggressively. The females usually watched the displaying males from nearby, but sometimes took part in the skirmishes.

Very soon (v. infra), however, each pair showed an increasing preference for a particular part of their range. Certain stations (called here "preferred stations") came to be used regularly as song posts by the male. These might be groups of trees, or conspicuous bushes, or other places providing suitable perches. The pair spent much time in the neighbourhood of such spots, and when intruders approached, they were attacked more vigorously than they were elsewhere. Most pairs had several such stations: usually the distance between adjacent stations belonging to one pair was not greater than 125 yards, and the intervening space was defended. In some cases, however, one male used stations much farther apart than this, and then the intervening space was either occupied by another pair, or else was more or less neutral and unused. Diesselhorst (1949) found a very similar situation in Emberiza citrinella and called the places near which aggressive behaviour was most marked "Schwerpunkte".

Although strange birds of the same species intruding on the area containing the preferred stations were attacked, the area as such was not rigidly defended. In most cases it was so large that it would have been impossible for the owner to drive off all intruders. The area only had precise boundaries in places where there were frequent skirmishes with the neighbouring pair. In such places the boundaries were often highly irregular, one bush belonging to one pair and another to the other in such a way that the areas interdigitated in a complex way: such boundaries might yet be relatively stable for several days. Elsewhere the boundaries were vague, and the areas of neighbouring pairs often overlapped to a very considerable extent. Further, as will be seen later, the areas remained fluid for several

weeks. They can thus hardly be called "territories" (i.e. a defended area), and are therefore referred to as "preferred areas". The difference is, of course, only one of degree.

Different pairs varied greatly in the times at which they started to show a preference for a particular area. As soon as the flocks began to break up the second year birds began to restrict their movements to the neighbourhood of their last year's territory, though the area which they occupied was larger than the territory had been. Most first year birds showed a preference for particular areas a few days after the flocks started to break up, but a few did not do so for a week or more.

The preferred areas were occupied especially in the early morning: as the day advanced the birds wandered more widely. Even in the early morning the area was deserted at intervals, but it was nearly always used for singing. As the season advanced the birds spent more and more time on the preferred area, and flocks became more rare. Males often left their females to sing at one of the preferred stations, or to chase off an intruder. They spent more time patrolling their areas, and some pairs made regular circuits which must have increased their chances of meeting intruders. The areas then became more clearly defined, but the fact that the Great Tits mostly fed below ten feet, and spent only a small proportion of their time singing from conspicuous perches, meant that it was always possible for intruders to trespass unobserved. The boundaries between territories became most clearly defined at the time of nest building, but in many cases they remained vague throughout the season. The preciseness of the boundary depended on the amount of pressure from neighbouring pairs. The further a bird was from its preferred

station, the less it tended to fight and the more it tended to flee.

Boundaries were thus lines along which the fighting abilities of the two rivals were equal. Between two territories there was often an area of toleration, in which the neighbouring pair was not attacked but strangers were.

When a bird disappeared, its preferred area was soon absorbed into those of its neighbours. A bird in the process of occupying a new station sang less loudly than when on its own ground. Even birds which hardly changed their preferred area through the season, sometimes changed their preferred stations - perhaps favouring some groups of trees for several days and then using others. As the nesting season approached, the preferred stations were used much less, and later the nest became the most important point in the territory.

Preferred areas thus changed gradually into territories in the classical sense, but it must not be thought that the change was always a smooth and steady one. The preferred areas of most pairs underwent marked alterations in size and shape: some birds changed their areas gradually, in such a way that the final territory did not overlap at all with the original preferred area, and yet there was continuity between the two through the areas occupied in the intervening stages. In other cases a pair occupied an area for several mornings and then moved to quite a different part of the wood: such changes occurred particularly in the early part of the season and after cold spells.

The results of the present study thus show that the area defended by the Great Tit is by no means rigidly or precisely defined, but consists in the first place of a fluid region round certain preferred stations, its size

depending largely on the pressure from neighbouring pairs. This is in very close agreement with the results obtained by Diesselhorst (1949) for Emberiza citrinella. He writes:-

"Das Revier ist für den Vogel nicht, wie für den Menschen sein Garten, ein in allen Teilen gleichwertiger Besitz, von der Aussenwelt durch einen Zaun abgeschlossen, sondern es besteht eine Art Konzentrationsgefälle in der Intensität der Verteidigung, die wir als Mass für den Grad der Revierbindung des Vogels benutzen müssen, von bestimmten Schwerpunkten nach aussen hin, wo sie allmählich verebbt."

Similarly Lorenz (1938) emphasized that the fighting power of a bird always increases in proportion to how near a certain centre of the territory the fight takes place.

In the present study the establishment of territories was not associated with the selection of any particular nest-site: indeed most pairs displayed at, and built in, several different cavities before the final nest was made. In one case a female built her nest outside her mate's territory in a temporarily occupied area. It must be noted, however, that nest-boxes were very plentiful on the study area.

When the preferred areas were first established, the Great Tits only used them for feeding incidentally, and obtained most of their food outside them. As the nesting season approached they spent more and more of their time in the territory, and thus obtained nearly all their food from it. After the eggs were laid territorial behaviour became less marked - perhaps because little trespassing took place. The greater part of the food for the young was gathered within thirty yards of the nest (5 nests observed), and thus in the

territory. In at least three cases, however, a considerable part of the food was obtained from a strip of more or less neutral ground between two territories, and sometimes actual trespassing took place. There was a recrudescence of territorial behaviour just before the young of the first brood left the nest.

The description given above of the transition from preferred area to territory applies to birds which bred on their winter range. We do not yet know how the birds which winter elsewhere establish their territories, but it is probable that they also pair up before settling on territories.

In spite of the fierce reproductive fighting shown by both Great and Blue Tits, it sometimes happens that two pairs nest in close proximity or even in the same box (Wallis, 1935; Legendre, 1932; Bolam, 1912; Hearn, 1934; Tuckett-Jesson, 1950). The manner in which this comes^{about} is quite unknown.

(b) Establishment of territories on the study area

In order to illustrate the indefinite nature of the boundaries, and the instability of the preferred area of the Great Tit, the histories of the establishment of territories in two parts of the study area in 1949 and 1950 are given below.

(1) 1949. In this year particular attention was paid to a portion of the wood (the Jew's Harp) which jutted out like an irregular peninsula into open country. It was bounded by grassland to the north and by a field of wheat to the south (Fig. 2). By the middle of February it was possible to map preferred areas for ten pairs - though of course the boundaries were by no means clearly defined. By mid-March the situation had changed little except that pair IX, after frequent skirmishes with the neighbouring pairs, moved off to the east. They were seen several times on the area of pair Va in early March, and on that of pair X in mid-March.

Towards the end of March there was an epidemic amongst the tits, and a number were found dead in their roosting holes. Although their bodies were not recovered this was probably the cause of the disappearance of a number of other birds at this time. Both members of pair III and the male of pair Va vanished. The female of pair VI had not been certainly identified, but a female was found dead in a box in the preferred area of the male. The male

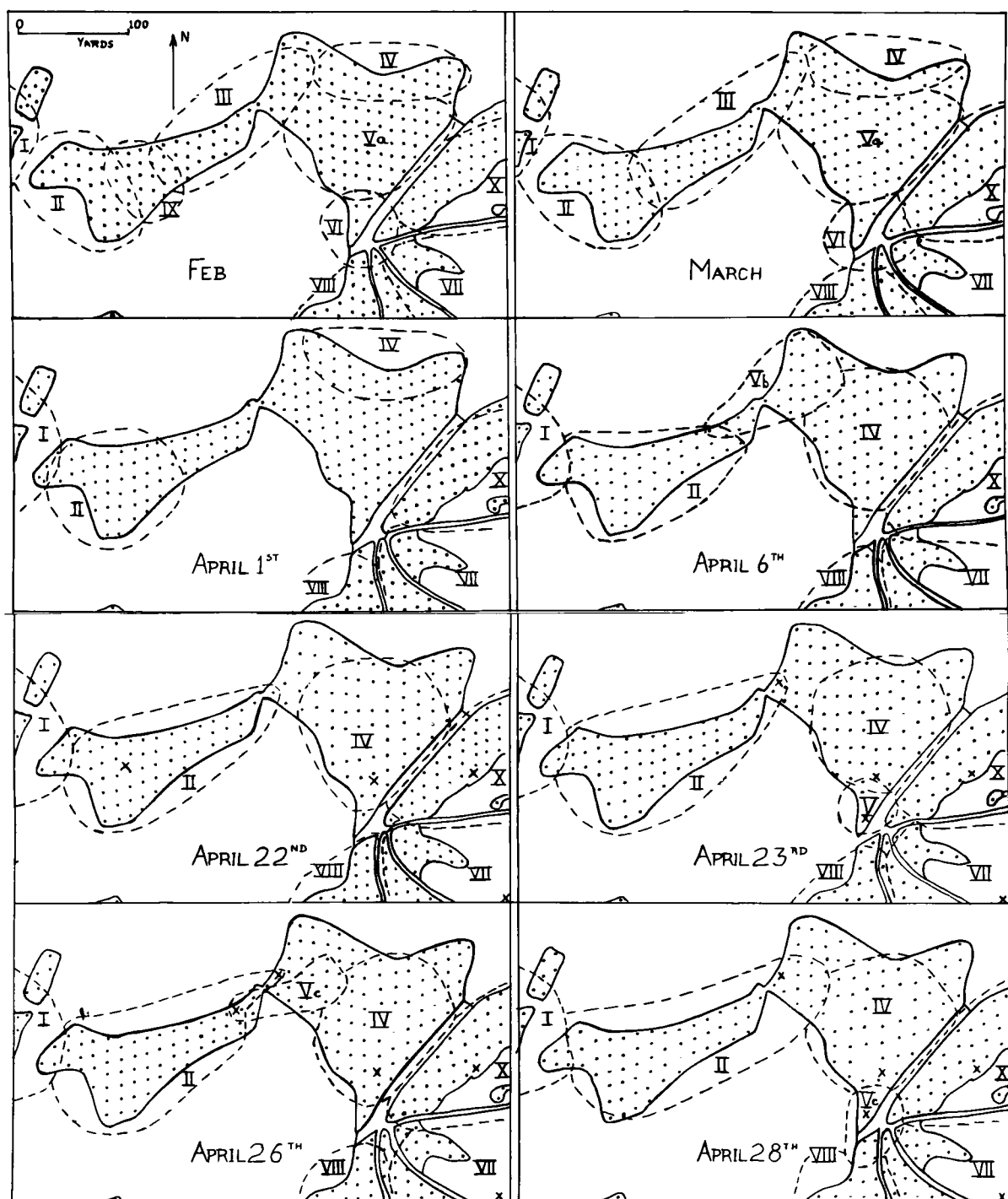


Fig. 2 . Preferred areas and territories in spring, 1949.
Dots indicate wooded area. Crosses indicate nests
under construction.

of this pair also disappeared. This left several areas unoccupied at the beginning of April. The widowed female of pair Va wandered round her old territory, but often went outside its borders. By April 5th she had found a new mate. Meanwhile pair II had extended their boundaries to the east, and pair IV had come down to occupy the whole of the area formerly occupied by pair Va. The female of pair Va and her new mate (pair Vb) were thus confined to an area between pairs II and IV much of which had been outside the territory of pair Va. The female continued to roost on what was now the area of pair IV for several days. Pair II still spent most of their time in the western part of their territory, and in mid-April started at least one and probably two nests there.^{iv} The second of these was still under construction on April 22nd. Pairs IX, VII and X also began nest building. Meanwhile the female of pair Vb had again lost her mate, who was last seen on April 17th. In the evening of April 20th she was seen near the nest of pair IV, and the next morning the male of this pair copulated with her before his own mate emerged. She spent a large part of April 22nd near pair II who were building their second nest. On April 24th and 25th she was still without a mate, but was building a nest in a box at the south end of the territory of pair IV: she also wandered about the territory of pair X. On April 26th she was paired with a third male (pair Vc). This pair was attempting to occupy the territory held by the female when paired with her second mate, and the female was building in a box at the western end of this territory. On April 23rd, however, pair II had started a third nest in the centre of this Vb territory, which was at that time unoccupied, although they continued to feed near their first two nests. This meant that the nest of pair Vc lay between the feeding and nesting areas of pair II. Fierce skirmishes between these two pairs continued for most of the day. No observations were made on April 27th, but by the 28th pair Vc had apparently given up the attempt and were building in the box in which the female had started to build when unmated 20 yards south of the nest of pair IV. This led to considerable skirmishing between these two pairs, but this lasted only for a few days and both pairs bred.

Two points in this account need emphasis. First, many of the complications observed were due to the exceptional mortality in March. Had this not occurred there would certainly have been a smoother transition from preferred area to territory. Second, it must not be forgotten that many more birds were recorded in the study area than actually used if for breeding: even as late as March 18th 7 birds (other than the actual owners) were trapped in the area of pair Va in a single day. Many of these birds must have nested elsewhere, and some may have nested even outside their winter range. The fact that in this particular part of the study area no birds (except the new males in pair Vb and c) nested, which had not used it in late winter, must not be taken to indicate that territories are always established in the way described above: in cases where birds are not able to nest on their winter range the transition through preferred area to territory may be more abrupt.

(ii) 1950. In this season a different portion of the wood was studied. The area consisted of an open space, roughly four hundred yards long, surrounded on the west, north and northeast by woodland and on the south by a tall hedge

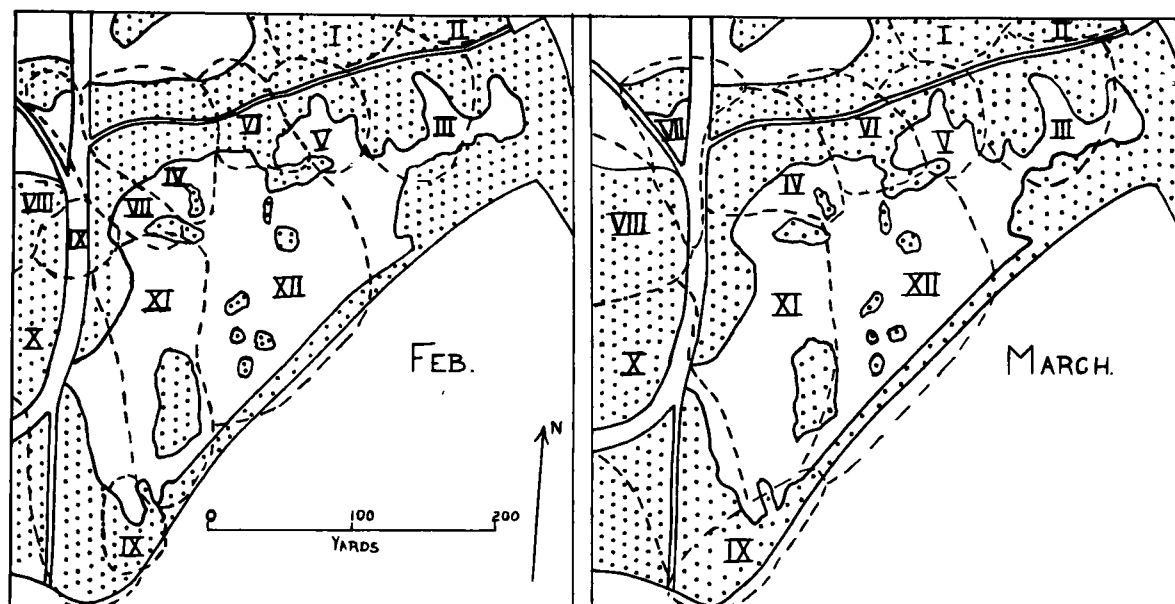


Fig. 3 . Preferred areas and territories in spring 1950.
Dots indicate wooded area.

which separated it from grassland (Fig.³). The preferred areas were fairly clear by mid-February. Pairs, I, II, III and IV were all second year birds, occupying areas approximating to their previous year's territories. Pair VIII had first occupied an area about 300 yards to the west, but moved into the position shown in mid-February. Pair IX was occupying two small separate areas. The male of this pair sang and skirmished in both of them, but was never seen to alight in the intervening space. The three largest preferred areas (those of pairs X, XI and XII) all contained a high proportion of open ground.

By late March pair IX had relinquished the northern-most of its two areas, but had extended the other. Pair VII had relinquished the south-eastern part of its area, but had extended it to the north and west. Otherwise the changes were comparatively slight. The southeastern corner remained unoccupied, although pair III occasionally foraged in it.

Further changes took place during the first three weeks of April, which were not followed in detail. Pair VII relinquished the southern part of its area, but extended eastwards into the northern part of the territory of pair IV. Pair IV extended southwards to occupy the area which had belonged to pair VII in mid-February. Thus whereas in mid-February pair IV occupied an area to the north of pair VII, by the nesting season the reverse was true. In early April a new pair was seen skirmishing with pairs VIII, X and XI on several successive days near the junction of their territories. Pair IX extended its boundaries to the north at the expense of Pair X. In the third week of April the male of pair XI disappeared, and his mate was found with a new male to the west of pair IX a few days later. A new pair (possibly the one referred to above) appeared in the territory of pair XI and occupied most of it: the remainder was occupied by pairs IV and VIII.

(c) A comparison with Kluijver's data on P. m. major

Kluijver (in litt.) states that territories are established in August and September. Since he also says that the "domiciles" (see p.64) of the juveniles are often not established until December, it is presumably the second year birds⁶ which he refers. The assumption that territories are established at this time seems to rest on two facts:- (a) the occurrence of aggressive behaviour at this time of year, and (b) the fact that the "domicile", once established, is rarely changed. In the present study it was also found that aggressive behaviour occurred in early autumn, but there was

no evidence that this was linked with the defence of an area. However the term territory is defined, it must carry the implication of a defended area. Until it is established that the autumn reproductive fighting results in the defence of an area, however, vague, it cannot be assumed that territories are established at this time of year. (It is possible that, during the autumn period of sexual behaviour, birds could become sufficiently conditioned to a particular area, for there to be a tendency for them to establish their preferred areas there, rather than elsewhere, in the next spring).

(d) Processes involved in the establishment of the territory in
the Great Tit

We may now summarize what has been said previously by reviewing the stages in the establishment of the territory. The processes will, of course, be somewhat different for birds which do not winter on their breeding grounds.

(i) Birds in flocks. Each flock forages over a more or less definite area. Song infrequent and of low intensity.

(ii) Flocks begin to break up and pairs are formed. Pairs wander over the whole of the range of the flock, and sometimes even further. Reproductive fighting frequent, but it functions primarily in the defence of the female and not of an area. Song fairly frequent.

(iii) The pair remains in a particular part of its previous range. The male sings only in certain preferred stations to which he quickly becomes conditioned. Singing and fighting become more vigorous near the preferred stations: elsewhere song is rare and the fighting drive weak. The area including the preferred stations becomes the preferred area. It must be

noted that the Great Tits only stay in the preferred area whilst under the influence of the reproductive drive - roughly speaking in the morning and evening. The birds become conditioned to carry out certain activities (song, fighting) connected with the reproductive drive at or near these preferred stations. Other activities, such as feeding, may be carried out inside or outside the territory. This is also true for many other territorial species. The conditioning is not, however, by any means rigid, and the preferred areas remain flexible for some weeks.

(iv) The preferred areas gradually become more stable. Its boundaries become more or less defined in skirmishes with neighbouring pairs, and it takes on the character of a territory.

Eliot Howard (1920) distinguishes two aspects of territorial behaviour -

(i) "The disposition which leads it (the bird) to remain in a restricted area" and, (ii) the disposition which "manifests itself in the intolerance of other individuals". The first of these has two distinct aspects: -

(a) the selection of a suitable breeding habitat. The birds show appetitive behaviour until they reach a suitable habitat which they recognise through a mechanism either innate or learnt in early life. (b) The selection of a particular part of that habitat, i.e. the preferred stations or area.

The mechanism concerned is quite unknown, but a learning process is obviously involved. The relation between the selection of the habitat and the selection of the preferred area is probably similar to that between the recognition of a suitable nest site and the selection of one particular one (see p. 161). In both cases conditioning is probably more rapid when the drive is strong. Tinbergen (1939b) has given a brief description of the

selection of the territory in the stickleback Gasterosteus aculeatus:

the fish gradually restricts its activities to a particular area, a learning process being clearly involved.

The "intolerance^{ance} of other individuals" manifested in reproductive fighting (and song) first occurs before territories or preferred areas have been established. Its function then is the defence of the bird's own female from other males. It is only later, and by a process of conditioning, that it comes to be associated with the preferred area, and thus operative in territorial defence.

The establishment of the preferred stations localises the preferred area, but does not define its borders. These remain vague, unless there is competition with a neighbouring pair. In that case, since the fighting power of each male decreases with distance from the preferred stations, there will be a line where the fighting powers of the two males are equal. This position of equilibrium becomes the territorial boundary.

11. Parus caeruleus.

As in the Great Tit, the pairs show a gradually increasing preference for a particular area, which later becomes the territory. The preferred area usually remains indefinite and has fluid boundaries until the beginning of nest building.

Individuals show great differences in the time at which they start to defend a more or less definite territory, and in the vigour with which they do so. As mentioned above (p.76) one pair held a clearly defined territory from the beginning of February on, and were very vigorous in patrolling it throughout nearly the whole of the spring. The male used the tallest trees

as song posts and kept a look out from them for intruding males: he patrolled his territory frequently and, indeed, showed typical territorial behaviour. On March 23rd another pair attempted to establish itself in the corner of their territory, and vigorous reproductive fighting resulted which lasted intermittently for several days. This fighting was a ding-dong affair, swaying backwards and forwards over a fairly definite boundary. It was intensified by the fact that the female of the resident pair showed great interest in a cleft in an oak tree in the corner which had been lost, and was continually flying into the lost territory to inspect it: this she sometimes did in company with the stranger male. Her own mate was obviously unwilling to cross the new boundary, but always did so if he saw the other male near his mate. On April 27th, at least a week after nest building had started, the male of this pair became interested in the female of the pair on his opposite boundary. Probably this female had lost her own mate. On two successive days he was seen following her out of his own territory, courting her and attempting copulation. This time it was his female who was unwilling to cross the territorial boundary, and she remained, singing vigorously, while her mate courted the stranger.

3. Parus palustris.

No special study was made of this species, but it was apparent that in most cases, at least, the territories were established before the spring. One of the young colour-ringed in 1949, after a short period of wandering, settled down in late June 700 yards from where it was hatched. By August it was clear that it was paired. It may be, therefore, that some juveniles begin to establish territories as early as this.

Southern and Morley (1950) found that the boundaries of Marsh Tit territories are usually quite clearly defined, but this was certainly not the case in the few pairs of Marsh Tits which were observed in the present study, even just before the nesting season.

4. Other species.

Odum (1941) found that in P. a. atricapillus the establishment of territory follows the pre-nesting wandering period. He believes that the finding of a suitable nest site is a determining factor in the selection of territory. This is almost certainly not the case with Great and Blue Tits on the present study area, where the final nest site was not selected until after the start of nest building (see p. 162).

Dixon (1949) found that the territories of Parus inornatus were occupied all the year round, but that fighting was most intense in the spring.

B. The Area round the Nest-Site.

The reproductive fighting of the titmice is directed primarily against individuals of the same species. From time to time, however, individuals of other species are attacked: such attacks are presumably due to the release of the fighting reaction by a normally inadequate stimulus at a time when the threshold of the reaction is unusually low. Near the nest, however, such interspecific skirmishes are quite common. Other Parus species are attacked more frequently than individuals of other genera. The behaviour involved is described on page 136.

C. Size of Territory.

1. Parus major.

The territories of the Great Tits (measured at the time of nest-building) varied in area from 0.6 to about 4.2 acres. The average of fourteen territories measured in the two years was 2.0 acres. The smallest territory measured was that of pair Vc in 1949 (see p. 59) which was established very late, after the pair had been driven out from elsewhere. Apart from this the smallest was 1.1 acres. The largest were those of pairs X, XI and XII in 1950 (3.6, 4.1 and 4.2 acres): these included much open ground. The male of pair X was about average in the amount of time that he spent singing and patrolling his territory: the male of pair XI was above average and the male of pair XII definitely below average.

These figures present an interesting contrast to those given by Kluijver (in litt.) for P. m. major in largely coniferous wood in Holland: here the area of the territories was 2 - 3 ha. (5 - 7½ acres).

2. Parus caeruleus.

Three territories were measured. One of these, that of the pair which showed particularly vigorous territorial behaviour (p. 43) was 2.0 acres. Two others were 0.6 and 0.4 acres.

3. Parus palustris.

Three territories were measured: these were 4.5, 3.8 and 5.5 acres. Southern and Morley (1950), working in Bagley Wood, Oxford, found that Territories varied from 1 to 16 acres, with an average of c. 6 acres.

4. *Parus atricapillus*

The two pairs present in the wood^{in 1949} divided it roughly between them. The boundary between the territories of the two pairs became fairly clearly defined at the time of cavity excavation, but the boundaries in other directions were always vague. Each pair probably moved over an area of at least 20 acres in the period immediately before nesting.

Odum (1941) gives 8.4 to 17.1 acres, with an average of 13.2 acres, for *P. a. atricapillus*. This author also quotes four censuses made in summer in other areas for this race. The maximum population in any of these was 12.3 birds (i.e. 6+ pairs) per hundred acres - allowing about 16 acres per pair.

5. Other Species.

Dixon (1949) gives 3.3 to 12.5 acres, average 6.3 acres, for *P. inornatus*. Hutchinson and Hutchinson (1944-47) in successive years, found one, two, two and three nests of *P. inornatus* in a 17 acre area - thus allowing at least 5 acres per pair.

6. General.

The figures given above seem to indicate considerable differences in territory size between the different species. It is difficult to know whether such differences were due to inherited, specific behaviour factors, or merely to differences of population pressure. In the present study, there were for each species certain parts of the wood which were not occupied, so it seems unlikely that there was much territorial pressure. I am indebted to J. A. Gibb (personal communication) for the information that, in years when the population density was low, the Great Tits were concentrated in certain

parts of the wood. The regions of concentration were not (to the human eye) particularly favourable, and lay in different parts of the wood in the two years concerned. Such a distribution is probably connected with the distribution of the winter flocks.

The correspondence of the results for the Marsh Tit with those given by Southern and Morley (1950), who also had a large unoccupied area, indicates that territories of about 5 acres are at least common in that species. Indeed these authors found that there was no correlation between population density and size of territory, but rather that the latter depended on the individuality of the owner. Similarly the territories of the subspecies of P. atricapillus have been conspicuously large in all investigations so far made: this seems to indicate that for this species the "preferred" territory size is much larger than in the other species.

It may be said, therefore, that there is some evidence for differences in "preferred" territory sizes between the different species, though the sizes are also influenced by other factors, such as the individuality of the owner and environmental conditions: indeed, they must have been selected in relation to the environment in the first place.

D. Relation Between Migration, Permanency of Pairing and Territorial Behaviour in Winter.

In previous sections it has been shown that there are marked differences between species, between different populations of one species, and even between different individuals of one population with respect to the

degree of migration and the extent to which individuals remain on their territories in the winter. Steinfatt (1938) has already suggested that for the different Parus species in his area there is a relationship between the degree of sedentariness and the permanence of the pair bond - a relationship which is to be expected on a priori grounds, and probably also applies to different individuals of one species. Clearly, also, migration is incompatible with the continued defence of the territory. Thus the following types of life cycle occur in the Paridae:-

(a) Permanently paired: juveniles pair mostly in late summer or autumn: remain on territories all the year round: no flocking.

e.g. P. inornatus.

(b) Permanently paired: juveniles pair at any time between one breeding season and the next: second year birds remain on or near territories all the year round, but territories are not usually defended from passing flocks of (mostly juvenile) birds: territory holders join the flocks within the limits of their territories.

e.g. P. palustris in England.

(c) Territories cease to exist in the winter, though second year birds spend most of their time in the neighbourhood of their previous years territory. First year birds wander, but most become more or less sedentary in their first winter.

e.g. P. major in England in mild winters.

(d) As (c), but second year birds may wander away from their breeding areas in hard weather, so that the breeding areas become temporarily totally deserted.

e.g. P. major in England in hard winters.

(e) Paired for the season only. Various degrees of migratory behaviour shown by both juveniles and adults.

e.g. P. major in N. Europe.

Sedentary behaviour such as that shown by P. inornatus is only possible if the territory provides sufficient food all the year round and the winter is not so hard as to prejudice survival unduly. On the other hand such behaviour carries clear advantages - the earlier both territory and mate are claimed, the less difficulty is likely to be experienced in obtaining them. In areas where the winters are usually harder, the advantages derived from flocking may be greater: in such districts the adults remain in touch with, but not necessarily on, their last years territory, unless the food supply there becomes inadequate. In yet colder weather the advantages of total and regular migration from the area may offset the loss of territory and mate.

E. Function of Territory in the Titmice.

In the past a number of functions have been ascribed to territorial behaviour in those species in which it has been studied. The most important of these are (i) that it serves to bring the sexes together and to assist in the formation of sexual bonds, (ii) that it serves to prevent interference in coition, (iii) that it ensures a supply of food for the young, and (iv) that it ensures the possession of a nest-site.

In the titmice the pairs are formed before the territory is established, so territorial behaviour is not of value in bringing the pair together. It is also doubtful if it functions in the maintenance of the pair-bond, for, in the

early stages at least, the pair spend most of their time outside the preferred area. Coition nearly always occurs on the territory, but there is no evidence that territorial practice serves primarily to prevent interference in coition.

Territorial behaviour is not apparently of primary importance in the defence of the nest-site, since potential nest-site competitors are only attacked in its immediate vicinity. However, under natural conditions, the different species of hole-nesters may have slightly different requirements for nest-sites, so that territorial behaviour may keep those individuals most likely to covet the nest-site at a distance.

In all the species of tits which have been observed, only a very small proportion of the territory has been used for food gathering. Indeed Odum (1941) found that P. a atricapillus gathered its food from nearer and nearer the nest as the nestlings grew. Further, the boundaries of the territories tend to break down when the young are in the nest, and some food may be gathered from outside the territory. However, this does not rule out the possibility that territory may be of value in ensuring food for the brood under adverse conditions. Since the fighting in defence of the territory is reproductive fighting, and not food fighting, it would seem that if territory has a food value, then it is at most a secondary development.

Finally it may be said that there is no reason why there should be a single factor in explanation of the function of territory in any bird. Reproductive fighting is an end in itself as far as the bird is concerned, and may have several results, which may be biologically useful, neutral or harmful. Selection may operate to increase the effectiveness of the useful results, so that, for instance, the bird comes to have a nervous structure which causes

it to fight more intensively near the nest-site, or near the mate. Reproductive fighting in tits is comparatively unspecialised in this way, but it does result in the defence of an area. This will have a selective value if pairs which defend a territory are able to leave more offspring than pairs which do not. Many factors may contribute to this increased success, even though none of them would alone seem to be sufficient to provide a selective value for territory.

SECTION VIII SONG.

- A. General.
- B. Parus major.
- C. Parus caeruleus.
- D. Parus ater.
- E. Parus palustris.
- F. Other species.

SECTION VIII SONG.

A. General.

No attempt has been made to review the literature on the songs of the different Parus species, because of the great difficulty of representing bird notes in words, and because representations of the same note made by different ornithologists may differ remarkably, especially when the writers are of different nationalities. Discussion is confined to observations made in the present study, except in so far as other writers have commented on the functions of song.

B. Parus major.

The familiar 'see-saw' song of the Great Tit varies greatly. Each song usually consists of a series of phrases, each of two notes, but there are sometimes one, three or even four notes to a phrase; the relative length and emphasis of each note may also vary. The significance of such variation is obscure: one individual may use several different song types in succession when there has been no apparent change in the external situation. For instance, during egg-laying the male of one pair used at least four variants while waiting for his mate to emerge at dawn.

These variations of the full song are to be distinguished from the seasonal variations which occur as the reproductive drive matures. When the birds first begin to sing in December, song-outbursts consist of only two or three songs, each of which has only about five notes (i.e. $2\frac{1}{2}$ 2-note phrases); and the notes are thin and 'breathy'.

In both 1948/9 and 1949/50 Great Tits began to sing early in December, but there was great individual variation, and the growth of song was halting and gradual. One Great Tit in Oxford began to sing as early as the end of November, 1949, but ceased after a few days. In a warm spell in December, 1948, song became frequent.

The spring of 1949 was an early one, and full song was common from mid-January onwards. In January 1950 it was rather less frequent than it had been in January 1949, but it became common after early February. In 1949 full song continued until the end of the nesting season, dying away at about the time that the young left the nest. No birds reared second broods in the wood, and no song was heard during June, July or August.

While the adults are feeding the fledged young, they use a call rather similar to the song which causes their brood to fly towards them. This call consists of about 7 notes, (i.e. c. $3\frac{1}{2}$ 2-note phrases), uttered rather less decisively and with the phrases less clearly differentiated than the full spring song. It is not considered as song here, because it serves a different purpose, and is apparently the expression of a different drive. Nevertheless there is clearly a relation between the two, for song attracts females in the same way as this call attracts juveniles: many other similarities between female and juvenile behaviour are known (see e.g. p.47).

In 1949, there was some recrudescence of song, together with other activities associated with the reproductive drive in late September and October. This lasted only a few weeks, and then song ceased until December. (No records were made on this point in autumn, 1948).

In order to measure roughly the variations in frequency of song outbursts, a count was made of the birds heard singing in each half hour spent

in the wood from February 1st, 1949, to February 14th, 1950. The song of the Great Tit is distinctive and can be heard from a considerable distance, and so is suitable for this sort of measurement. The records were analysed separately for each half month, and for each half hour period of the day. For each half month, the total number of song out-bursts heard in each half hour period was divided by the number of half hours spent in the field at that time of day. The results are shown in Table 9. Three limitations of this technique must be noted:-

(i) The figures represent the average total of song outbursts in each half hour period: thus if the birds started or ceased singing in the middle of a period, the figure may be low although their frequency of singing during the rest of the period was high.

(ii) The figures give a rough indication of the seasonal variation of song frequency, but must not be used for detailed month to month comparisons because of the effects of population changes. It is probable, however, that the population changes were small during the periods when song was frequent.

(iii) The figures do not give a measure of the total volume of song, because when song outbursts are more frequent, each tends to be both longer and louder: they do, however, give an indication of general trends.

Table 9. shows that there was a marked diurnal variation in the frequency of song outbursts. Typically the peak of song was reached soon after dawn, and was followed by a decline to a minimum in the early hours of the afternoon. There was sometimes a second peak of song in the evening. The morning peak was sharpest in April, when the males were

awakening much earlier than the females and singing outside their roosting places. When song occurred outside the breeding season, it was practically confined to the early morning.

Although this point was not studied in detail, it was evident that the amount of song was profoundly influenced by the weather. With early fog or frost the morning peak was much reduced, while sharp showers brought an immediate cessation of song. The appearance of the evening peak seemed erratic, but in general it was reduced or absent on cold days.

In both 1949 and 1950 song outbursts were more frequent in late February than in March. This was probably due to meteorological factors, for in both years March was colder than late February. In April, however, song was less frequent than in late February although the weather was warmer: this was presumably related to internal changes in the birds, connected with the onset of nest building.

As in many other Passerine species, song has two functions: it attracts females and warns off other males.

During early spring, when the pairs are not firmly attached to any particular area, the song of the male often serves to keep the pair together. If the members of a pair become separated, the male sings and the female flies towards him. Here the situation which produces song appears to be "absence of the female".

During the establishment of the preferred area and territory the male often sings near his mate, or leaves her in order to sing from a conspicuous song-post. Here the stimuli responsible for the song are almost entirely internal, the bird singing when the drive reaches a

certain threshold level. The external situation has some influence, however, for once the birds have preferred stations they rarely sing in other places, and song on unfamiliar ground is usually weak. Also, the frequency of song outbursts is influenced by the weather. As with other instinctive activities in which external stimulation is relatively unimportant, such song does not start abruptly. The first few phrases are given at a low intensity, but gradually become louder and clearer: also the intervals between the phrases gradually decrease. (A fact not yet clear is that song is often preceded by a long series of twinks, which change gradually into song. See also Howard (1920) for a discussion of the relation between call notes and song).

Although, as has been said, the release of territorial singing is often largely independent of new external stimuli, this is not always the case. Song is often provoked by the singing of another individual, and neighbouring males often have prolonged song duels. An intruder singing on the preferred area causes the owner (if in reproductive mood) to move towards him by stages, singing from positions successively nearer to the intruder. The latter usually flies off, but if he does not a skirmish ensues. The use of song in territorial defence is thus similar to that in other Passerine species. (cf. Lack 1939, for Erithacus rubecula).

Although some males preferred conspicuous song posts near the tops of tall trees, many sang from only eight or ten feet above the ground. On a few occasions Great Tits were even seen singing from the ground, or whilst in flight. Usually a singing male sits still throughout a song outburst, or at most hops a foot or two to a new perch between songs. Occasionally, however, birds were seen singing in intervals between

opening a nut, searching for food, or preening. The birds heard singing on the ground were, at the same time, hopping about searching for food: it would therefore seem that singing and food-searching behaviour are not necessarily absolutely mutually exclusive.

Song is often heard during reproductive fighting, especially during lulls in a skirmish and just after a skirmish is over. Although such singing may be functional as a threat, it is apparently a displacement reaction, caused by the thwarting of the fighting drive through the disappearance of the adversary.

During the nesting season the male sings particularly vigorously outside the female's roosting hole before she emerges at dawn. The female's emergence is often followed immediately by copulation. It is not certain whether such singing should be regarded as due to "absence of the female" or as due primarily to internal factors.

Singing by female Great Tits was rare, but was heard fairly often when the females were taking part in reproductive fighting, and twice in situations which could be interpreted as "absence of the male". One female often gave a short see-saw phrase when leaving the box during nest-building and incubation. Thus the nervous mechanism necessary for singing is present in both sexes, but there are great differences in the strength of the motivational factors. Nice (1943) has reviewed the literature on the song of females of other species.

C. Parus caeruleus.

The song of the Blue Tit is very different from that of the Great Tit, being "a rapid liquid trill introduced by two or three single notes" (Witherby et.al. 1938). It is, however, subject to the same kinds of variation. Several pairs used variants of the normal song, or even more or less distinct phrases, in situations apparently similar to those in which they used the normal song. A particularly frequent variant was similar to the normal song, but had the final notes ascending instead of descending. On rare occasions a Blue Tit was heard giving a 'see-saw' similar to that of a Great Tit, but whether this is part of its normal repertoire or mere imitation is unknown.

The times of year at which song was heard were very similar to those given above for the Great Tit, except that song in late summer was more frequent. At this time juvenile Blue Tits were often heard singing, the singing being associated with aggressive behaviour. Song was heard more frequently in the morning than later in the day at all times of year.

Female Blue Tits were heard singing on a number of occasions, especially when engaged in sexual fighting. One Blue Tit female sang when her male was courting with a strange female over the territorial boundary.

The functions of song are the same as those in the Great Tit. If the pair become separated during the pre-nesting period the male soon started to sing. Song often occurred during lulls in skirmishes, the rival males singing vigorously in competition from either side of the territorial boundary. Colquhoun (1942) describes a case in which a copulation was followed by song from the male. In one case in the present

study a Blue Tit sang whilst in a trap, and on several occasions one sang when released from a trap.

D. Parus ater.

The song of the Coal Tit is similar to, but clearer than, that of the Great Tit. For the most part it was heard during the same periods of the year. During the late summer, however, there were a number of juvenile Coal Tits in the wood who produced a considerable volume of song, apparently associated with aggressive behaviour (cf. Blue Tit above).

E. Parus palustris.

The variability of the song of the Marsh Tit is well known. The usual bubbling song is itself subject to considerable variation, and there is also a mono-, di- or tri-syllabic call of the same type as the song of the Great Tit. One male, whose nesting box was often passed in the early morning, often used the di-syllabic see-saw song whilst waiting for his female to emerge at dawn.

The song period was similar to that of the Blue Tits, starting in mid-December and increasing through the spring, dying away soon after the beginning of May. After the young became independent, they were often heard singing: this singing was usually associated with aggressive behaviour.

Females were heard singing on several occasions.

P. Other species.

Odum (1941) notes that the 'phoebe' song of the American P. a. atricapillus both attracts females and intimidates males. It may be heard in two or three note versions, but both seem to serve the same purpose. Both sexes sing, but the males sing more often than the females. Odum states that song may be used to "establish dominance" in the late summer flocks. Jouard (1932) states that in Switzerland this species continues to sing during incubation, and records young singing soon after becoming independent.

P. inornatus typically has a di-syllabic song. Here again the song is subject to variation, and Dixon (1949) says that the two basic types are used indiscriminately. Here, also, the song (or a call like it) is used by the male to lead the brood.

SECTION IX REPRODUCTIVE FIGHTING.

A. Intra-specific Reproductive Fighting.

1. Parus major.

- (a) Display types
- (b) Behaviour during skirmishes
- (c) Low intensity skirmishes
- (d) displaying parties of males
- (e) Behaviour of females during the skirmishes
- (f) The nature of the displays
- (g) Variation in the intensity of reproductive fighting.

2. Parus caeruleus.

- (a) Display types
- (b) Behaviour during skirmishes
- (c) Behaviour of the female

3. Parus palustris

4. Parus ater

5. Other species.

B. Inter-specific Reproductive Fighting.

C. The Functions of Reproductive Fighting.

D. Conclusion.

SECTION IX REPRODUCTIVE FIGHTING.

Tinbergen (1926) used the term "Sexual Fighting" for that fighting "before and during the formation of sexual bonds" which "serves to secure objects or situations which are indispensable for reproduction". The term "Reproductive Fighting" is preferable, as the fighting is associated with the major Reproductive Drive.

Reproductive fighting in the tits usually occurs between members of the same species, in which case it usually serves for the defence of the mate or of the territory. It may also occur between members of different species, in which case it is usually in defence of the nest site, (see p.139).

A. Intra-specific Reproductive Fighting.

This occurs mainly during the pre-nesting period, when the pairs are wandering widely, and during the establishment and maintenance of the territory. In the fights the combatants show a number of display postures which are remarkably similar in the different Parus species: these are described below.

1. Parus major.

(a) Display types

The following behaviour patterns are used in the displays. Some of them have been previously described by Tinbergen (1937).

(i) Supplanting attack. This appears to be exactly similar to the supplanting attack seen in winter flocks in food disputes, the attacker flying directly at his opponent. When a supplanting

attack is made on a stuffed bird, the attacker usually lands on its back and pecks at its head or eyes: normally an attacked bird takes some avoiding or defending action (see below). Occasionally the attacker does not land on his opponent, or his opponent's perch, but a few inches away. This occurs under two different conditions:-

(a) When the attacked bird resists by staying in position, and showing the head-up posture: (b) In reactions of low intensity - one gets the impression that the fighting drive was not sufficient to carry the attack through to completion.

The attacked bird responds in one of four ways:- (a) It flies right away: the attacker then flies after it and a chase ensues. (b) It shifts its perch a few inches: the attacker lands in its place, and both usually show head-up postures (see below). (c) It remains where it is, but ^oad^opts a head-up posture: the attacker usually then shows upright flight (see below). (d) It may fly up and meet the attacker in mid-air: in that case an actual combat may ensue, or both combatants may show upright flight.

(ii) Up-and-down supplanting attack. This is an elaboration of the simple supplanting attack, in which the attacker flies up and then down on his opponent from a height of about 2 feet. The attacker often descends with half-open wings, so that there is ample time for his opponent to fly clear. This is not so common in the Great Tit as in the Blue Tit.

(iii) Head-up posture. In this the bird stands with the body nearly vertical, bill pointing upwards, so that the breast is exposed:

in addition the neck is craned upwards and the body is swayed from side to side so that the cheeks are exposed alternately. The tail is often spread. In very intense reactions the birds may perch on the sides of twigs, so that the body is more nearly vertical. Occasionally the posture is given by birds hanging upside down beneath twigs, so that the bill points to the ground. Sometimes two individuals will posture thus at each other for as long as ten or fifteen seconds. Although the effectiveness of the posture apparently depends on the exposure of the black breast and white cheeks, it is quite common to see two birds posturing thus but not facing towards each other. Nevertheless the posture is certainly orientated towards the opponent more often than can be accounted for by chance alone.

During skirmishes the posture is given under four sets of circumstances:- (a) By the aggressor when it has landed just after making a supplanting attack. (b) By the attacked bird when it has landed after a flight of a few inches made to avoid an attack. (iii) By the attacked bird when it does not shift its perch on being attacked. (iv) Occasionally during the course of a skirmish, when the birds are hopping about near each other, one may give an incipient head-up posture. Incipient postures may also occur when a male is moving towards a skirmish which he can hear but not see. In such postures the bill is pointed upwards, though sometimes only momentarily: craning movements are seldom involved.

The head-up posture may have a marked effect on the rival. When an attacked bird does not fly off but gives this posture it is often sufficient to make the attacker hold off in mid-air. Once a male was seen to fly towards an intruder singing on his territory, land about six inches in front of it, and posture vigorously: the intruder flew off immediately.

(iv) Upright flight. In the supplanting attack the males often fly with the body in an almost vertical position: the wings are moved in a peculiar manner, consisting of several rapid beats followed by a momentary closure, so that the flight is in a series of upward ^wseeps. In this way the breast is exposed to the opponent even during flight. Upright flight only occurs in at least moderately intense skirmishes in which the antagonists are fairly evenly matched.

(v) Chases. Chases occur often in skirmishes. The stimulus is apparently the sight of another bird flying away, and thus they often follow the supplanting attack when the opponent flies right away instead of just shifting his perch. The chasing may be released merely by another Great Tit (or even a Chaffinch Fringilla coelebs) flying past.

(vi) Displacement Pecking. During the skirmish the birds often show an activity which appears at first sight to be quite irrelevant - they peck vigorously at the branch or twig or at a bud. This is a displacement activity (cf. Tinbergen and van Iersel, 1947), presumably produced by the conflict between

the drive to fight and the drive to flee. The pecking movements may be quite gentle, but are often very vigorous, so that a shower of fragments falls to the ground. The more intense the skirmish the more vigorous the pecking. Sometimes two males will remain a few inches apart, displacement pecking vigorously for ten seconds or more.

It is often difficult to distinguish displacement pecking from the real pecking which forms part of the food-seeking behaviour, especially as the displacement pecking is often directed at buds in the same way as real pecking. Apart from this it must be noted that there is no proof that the movements are derived entirely from feeding movements, for they are also similar to the movements which the bird would make if it was successful in landing on its opponent's back and attacking its head, and they are often much more violent than normal feeding movements. Perhaps components of both activities are involved. There is also no proof that the movements have a display function, though it seems likely: in any case it seems that no conspicuous structures have been especially evolved to emphasize it.

(vii) Wings-raised and head-forward postures (see p. 40-1). These are seen in reproductive fighting but are rarely so marked as in food fighting. They occur when the birds are hopping round near each other during lulls.

(viii) Combat. Sometimes the skirmishes develop into actual combats. These usually occur after a supplanting attack. (Only once has a chase been seen to develop into an actual combat). The birds fall together to the ground, striking with their beaks and sometimes claws: more

usually their claws become interlocked. Actual combat is not common, and, when it does occur, it rarely lasts for more than a few seconds.

It is, of course, difficult to follow the movements of the birds, but the experiments with stuffed birds show that the attacks are usually directed at the eyes, or at least at the head. The dummies^u usually lost their glass eyes after they had been attacked a few times. Once a trap was left unattended for as long as an hour during the autumnal period of reproductive behaviour: two male^s Great Tits were found in the trap, one of them killed by a small hole through the back of the skull. There are several similar records in the avicultural literature. Hollom (1934) reports a case of a Great Tit pecking out both the eyes of a House Sparrow (Passer domesticus). Crested Tits (P. cristatus) also aim for the eyes in fighting (Hildebrandt, 1937).

(ix) Wing-flicking. This is seen sometimes in Great Tit skirmishes, but it is neither so common or so well-marked as in the Blue Tit.

(x) Other displacement activities. Displacement bill-wiping occurs fairly often in low intensity skirmishes, but its significance is difficult to assess. It is difficult to understand why a displacement activity should occur when the drive is low, but other cases are known. Thus Tinbergen (1936b, cited after Lorenz) states that the Whitethroat (Sylvia communis) shows displacement preening when injury feigning has been performed a few times.

In two skirmishes the males were seen to turn leaves (an activity used in looking for food on the ground), throwing the

leaves over their backs with exceptional vigour: this was at least an irrelevant activity.

(xi) Calls. Several different calls are uttered during the skirmishes. Owing to the great apparent variability of the calls, and to their complex nature, it has not yet been possible to analyse them in detail. The following are the most important:-

a. "Pit tit tit churrrr". A scolding note, used during lulls, and in low intensity skirmishes. It is rarely heard at the height of battle.

b. "Dit tit tit dur dur dur". Also used in low intensity reactions. Perhaps merely a variant of the above.

c. "Chich ich ich ich ich". Heard at various intensities according to the strength of the reaction, and thus varies from quite a gentle sound to a harsh scold. Usually used almost continuously by the attacker. A twanging note, like that of a vibrating guitar is probably a derivative of this call.

d. "Chat chat". Often used in intense skirmishes.

e. "Twink". Often heard - used more by the subordinate bird than by the attacker. Sometimes c. and e. are combined to give "Twink twink chich ich ich ich".

f. Song. The birds sing during lulls in the skirmish, and nearly always after it is over. Probably a displacement activity arising from the disappearance of the adversary.

(b) Behaviour during skirmishes

The sequence of events in a skirmish is usually of the following type (variations are described later). As the males approach each other, the

feathers of each become sleeked against the body. One bird, A, makes a supplanting attack on his opponent, B. B. flies a few inches away, and A lands in his place. Both birds then posture with the head up. After a few seconds the posturing dies away and the birds remain perched a few inches apart calling loudly. Then A makes another attack, and the process is repeated. This procedure may vary in any of the ways indicated above. The attack may be simple or up-and-down, and may or may not involve upright flight. The attacked bird may fly off, so that a chase results, or may resist the attack by head-up posturing, and so on. From time to time both birds may start displacement pecking. We shall see later that such variations can be explained if we postulate variations in the drives of fighting and fleeing in the two males.

Usually one male appears to be the attacker throughout the skirmish, and initiates all the supplanting attacks. The roles may change, however, thwith distance from mate or territory. Sometimes such changes are very dramatic. One bird may chase another vigorously from one bush to another, where both perch a few inches apart: then the roles are reversed and the previous aggressor is chased back again. The change is often related to the proximity to the mate, rather than to a territorial boundary: each male is the attacker near his own mate and is attacked near his opponent's.

(c) Low intensity skirmishes

At times, particularly in cold weather and in the afternoon, reactions of very low intensity are seen. The actual form of such skirmishes varies with the level of intensity reached, but typically the males hop round each other with sleeked feathers, calling and sometimes flicking their wings.

Supplanting attacks are infrequent and lacking in vigour: often they are not followed by the head-up posturing. Sometimes the head-forward posture (p.41) is adopted.

(d) Displaying parties of the males.

The noise of a skirmish attracts other males to the vicinity, so that ^{Several pairs are often seen. Sometimes} skirmishes involving three or four males can be seen sitting within a few feet of each other, all giving head-up postures. Similarly three or four males may chase each other through the wood. Such parties were seen particularly in the February/March cold spell, and so are perhaps most likely to occur when the birds are showing a tendency to flock, during the pre-nesting season.

(e) Behaviour of females during the skirmishes

Although the female may be the object of a skirmish, she usually plays a comparatively passive part in it. If she is supplanted by the rival male she may just hop aside, or she may fly off and become involved in a chase. Usually the female continues feeding, or sits nearby, occasionally calling with twinks ^y of which ich ich calls. Occasionally, however, females play an active part, especially in the weeks immediately preceding nest building. They sometimes give definite head-up postures, though these are never so vigorous nor so prolonged as those of the males. More frequently they follow behind the male-male chases. They often sing.

It is known, for many territorial species, that the males usually attack other males, and the females attack females. When one pair of Great Tits trespasses on the preferred area of territory ^y of another pair, the owning male usually attacks the intruding male rather than the female, but males also usually (not always) drive off solitary females. On one occasion only, a female was seen to drive off another female while her mate remained passive.

(f) The nature of the displays

Collias (1944) writes that "It seems doubtful if the details of a vigorous and active combat can readily be segregated into mechanical stimulus-response chains": he goes on to point out some of the difficulties involved. Lack, however, in 1939, showed that the reproductive fighting of Erithacus rubecula can be analysed into "three motor patterns, each with a corresponding visual element". He points out that the separation is not complete, because of the complexity and variability of the displays, and, after rejecting various explanations, writes "one is left with a confused picture of complex inter-action between the visual and auditory situation, the motor pattern and the internal driving factors". More recently the fighting of the Herring Gull (Larus argentatus) and of the Three-spined Stickleback (Gasterosteus aculeatus) have been analysed by Tinbergen (personal communication), and it is possible to make some analysis of the casual chains underlying the fighting of the Great Tit by using a method similar to that used by Tinbergen.

During reproductive fighting two subdrives of the main reproductive drive (see Tinbergen, 1942) are aroused: these are the fighting and fleeing drives. These drives, like others, are subject to fluctuations due to changes in the physiological condition of the animal, relations with other drives, and to the external stimulus situation (see e.g. p. 246). Tinbergen and van Iersel (personal communication) have analysed the fluctuations of various drives in Gasterosteus aculeatus. (Räber, 1948, has pointed out that in Meleagris sp. fleeing from males of the same species differs from escape from males of hostile species in that it does not occur during the moulting season, and is subordinate to the major mood "readiness for procreation").

The fighting drive is expressed primarily in the supplanting attack.

The fleeing drive is expressed in escape, but in a fight escape must be suppressed. During a skirmish the fighting and fleeing drives are of almost equal strength - the former preponderating to a greater extent in the attacking bird than in the attacked. If the fighting and fleeing drives are not approximately in equilibrium, then of course no skirmish can occur. This is most clearly seen in skirmishes near a territorial boundary: as each male enters its opponent's territory the fleeing drive predominates, and it is only on the boundary itself that intense skirmishing takes place. The head-up posture occurs in circumstances in which the two drives are very nearly equal - i.e. when fighting is inhibiting fleeing or fleeing is inhibiting fighting.

Thus:

- (i) After a supplanting attack - the fighting drive, formerly predominant, has been partially dissipated.
- (ii) When a bird shifts a short distance in order to avoid an attack, The escape drive, formerly predominant, has now been partially dissipated.
- (iii) In resisting an attack. Escape is inhibited.

Head-up posturing does not occur, or is at most limited to incipient movements, if the rival shows no resistance, however vigorous the attack may have been in the first place.

Further, it seems highly probable that there is a close connection between head-up posturing and upright flight, for the same structures are displayed in both. Upright flight occurs during supplanting attacks when the rival shows some resistance, particularly when the attacked bird stays in its place and gives a head-up posture. Often supplanting attacks start with normal flight,

and the attacker changes to upright flight when his rival does not fly off. In such cases the attacker dances in the air, hovering with intermittent bursts of rapid wing beats before his adversary. Sometimes an attack is started with upright flight: such attacks are rarely pressed home. Upright flight is not used when the dominant bird attacks vigorously and the other bird shows no resistance.

Whether the head-up posture is derived from an inhibited attacking movement or an inhibited fleeing movement is not clear. The evidence given above would support either alternative, and it is possible that the distinction is not a real one, for the situation is one of equilibrium between the two drives. In the Blue and Marsh Tits the head-up posture is not so elaborate as in the Great Tit, and often appears merely as an alert postural set similar to that adopted by many small birds immediately before flying off when alarmed. This seems to favour the suggestion that the head-up posture is an inhibited fleeing movement. In any case, in the Great Tit it has become highly elaborated as a display, and a colour pattern has been evolved to make the display more conspicuous.

Displacement pecking is also probably caused by inter-action between the fighting and fleeing drives - apparently when the two drives are of such intensity that the internal conflict can be resolved in no other way except by means of a dissipation of the energy through a totally different channel. It does not occur in obviously one-sided skirmishes when the attacked bird shows little resistance.

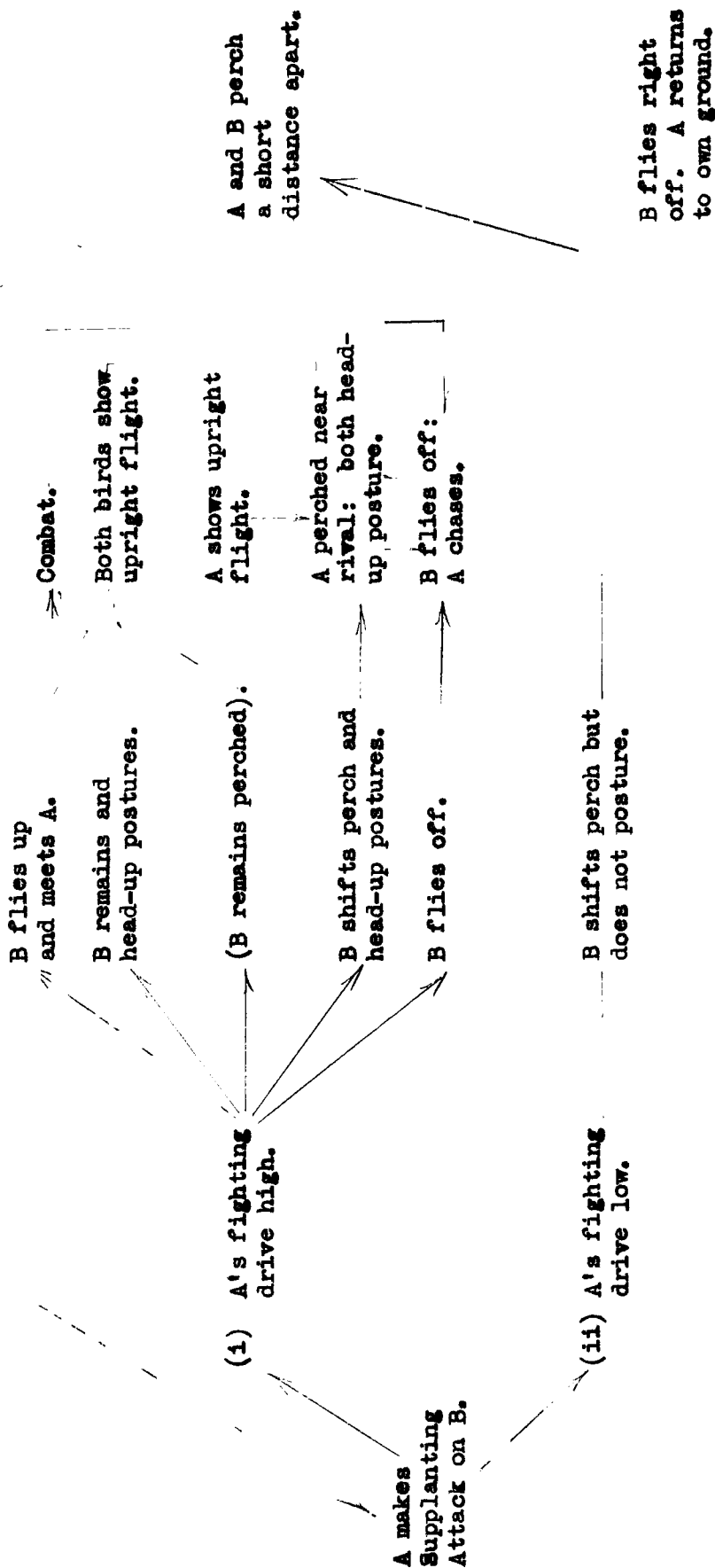
We can now consider the casual chains involved in a skirmish of moderate intensity. Each skirmish can be divided into a number of cycles each of which starts with one bird, A, making a supplanting attack on the other

bird, B, and finishes either with B flying right away or with the start of another attack. Most skirmishes are made up of many such cycles. (Of course, the roles of the two birds may change during the course of the skirmish, so that B becomes the attacker. In the following account the letter A always refers to that bird which is the aggressor at the moment). *Figure Diagram 1* illustrates some of the courses which such a cycle may take. It must be emphasized that the figure is not complete, and is intended only as a suggestion of the mechanisms involved.

The sight of the intruding male on his territory brings the owner into the fighting mood, and he flattens his feathers and approaches the intruder, calling as he does so. He then makes a supplanting attack on B. This may be made with rapid normal flight (fighting drive high and fleeing drive low), with upright flight (fighting and fleeing drives at least moderately strong and almost in balance) or with slow normal flight (fighting drive predominates over fleeing, but neither is high). In the latter case B usually merely hops aside, so that the two birds perch a short distance apart with practically no further display. A usually then makes another attack, either almost immediately, or after the birds have been hopping through the bushes near each other for a few seconds.

If, however, the attack is made when the fighting drive in A is strong (i.e. either with rapid normal flight or with upright flight), B may respond in one of five ways: which course he actually takes depends on the intensity of the attack and on the strengths (and relative strengths) of his own fighting and fleeing drives. We will consider the five possibilities, starting with the one in which B shows the least amount of resistance to the attack.

Diagram 1 . Illustration of some of the possible causal chains which may occur during reproductive fighting. For explanation see text.



(i) B flies right away. The situation "other-bird-flying-away" releases flying-in-pursuit in A, and a chase ensues. A chase may end in three ways:-

- a. It may lead to combat: this is rare (see below).
- b. B may perch again, in which case either A may continue the chase into a supplanting attack (and thus the start of a new cycle), or may perch near him and use a head-up posture (see below).
- c. B may fly right away: A returns to his own mate or territory (end of skirmish).

(ii) B shifts his perch a foot or two: A then lands near him and gives a head-up posture. Thus both birds are perched a short distance apart giving the head-up posture. This situation may lead to two possible results:-

- a. If the fighting drive in A is strong, then he may proceed immediately to another attack.
- b. If it is of only moderate strength, then the posturing dies away, and the two birds are left perched close together. They may hop about in the bush a little before another attack is made, or B may fly off, whereupon a chase follows, (see above).

(iii) B remains perched, but does not posture. A presses home his attack and a combat results. This probably never happens in nature, though of course it does if B ^{is} a dummy. A similar situation arises however, if B is caught unawares. A combat usually ends in B flying off and A chasing it: sometimes, however, A flies off and leaves B on the ground.

(iv) B may remain, and adopt a head-up posture. Then A may do one of three things, depending on the strength of his fighting drive:-

a. A may press home his attack. A combat ensues (see above).

b. A may hold off his attack and show upright flight.

This is not usually sustained for more than a few seconds, and then A perches near his rival, so that both are perched a short distance apart giving the head-up posture, (see above).

Rarely A may still press home his attack, though still showing upright flight. In fact all degrees of "upright" flight, from an almost normal attacking flight to flight in which the attacker is almost perpendicular and hovering, may occur.

The exact nature of the flight depends, of course, on the relative strengths of the attacking and fleeing drives of A.

c. A may perch near B, and posture. Then we again have the situation in which both birds are perched a short distance apart giving the head-up posture (see above).

(v) B may fly up and meet A. Then either:

- a. The birds strike each other and a combat ensues (see above),
 - or, b. They dance round each other showing the upright flight,
- but soon perch a short distance apart giving the head-up posture.

It must be noted that the above scheme is not complete, and omits many of the complexities. Displacement pecking occurs if the fighting and escaping drives are fairly strong and in equilibrium - thus it is often seen after both birds have shown upright flight, or head-up postures.

It may occupy much of the time between successive supplanting attacks, and may be shown by one or both birds. It may lead to (i) another supplanting attack (A's attack drive builds up faster than it is dissipated in the pecking, and faster than the escape drive), (ii) B fleeing (B's escape drive builds up faster than its attack drive), (iii) A more or less neutral situation in which the birds hop around until another attack is made.

Some examples of other possible variations are as follows:

If the fighting drive in A is low, he may not follow in a chase when B flies off. When A and B are perched close together, whether or not B flies off depends in part on the distance between the two birds. Changes in the internal state of either bird may occur without any change in ^{the} external situation, as when the fighting drive of A builds up and leads to an attack. Females may become involved in the skirmish, and the roles of A and B may become interchanged. It is clear, however, that all such variations occur as a result of processes similar to those which have been outlined above. The whole of the skirmish can thus be interpreted on the assumption that each individual is subject to the opposing drives - fighting and fleeing - and that the relative strengths of these two drives determine which of the several possible responses is made to each stimulus situation. The differences which are observed between skirmishes depend largely on differences in the strengths of the two drives in the birds concerned.

In the next section some of the causes of variation in the strength of the fighting are considered.

(g) Variations in the intensity of reproductive fighting

(i) Seasonal variation. As will have become clear already, the intensity of reproductive fighting shows a marked seasonal variation.

It is first seen shortly before Christmas, rises to a maximum during the weeks before the breeding season, and dies away while the young are in the nest. There may be a new outburst of reproductive fighting related to the rearing of a second brood. It also occurs amongst newly independent juveniles, and during the autumn recrudescence of sexual behaviour.

(ii) Diurnal variation. Table shows the frequency with which skirmishes were seen at different times of day between March 1st and April 15th, 1949. In the calculation of the table, each day was divided into four quarters, and the number of skirmishes seen in each quarter was divided by the number of hours spent in the field at that time of day. Fighting was most frequent (and most intense) in the early part of the day, and rare in the afternoon.

Table . Diurnal variation in frequency of skirmishes (Reproductive fighting). Number of skirmishes seen in each quarter of the day, per hour spent in the field, between March 1st and April 15th. Skirmishes of high intensity only included.

	<u>Quarters of the day.</u>			
	<u>I</u>	<u>II</u>	<u>III</u>	<u>IV</u>
No. of hours in the field.	59	71	31	62
Great Tit skirmishes per hour.	0.22	0.16	0.00	0.05
Blue Tit skirmishes per hour.	0.37	0.43	0.10	0.06

- (iii) Weather. This affected reproductive fighting in the same way as other reproductive activities (see p. 108).
- (iv) Presence of the mate. Full skirmishes, as opposed to incipient head-up posturing, probably never occur between birds without mates. Throughout the spring the females may influence the course of the skirmishes without taking an active part in them, for each male fights more vigorously in the presence of his own mate.
- (v) Territory. After the establishment of preferred stations and preferred areas, each male fought more vigorously on his own ground than when on strange ground.
- (vi) Proximity to the nest-site. As will be seen later, in the neighbourhood of the nest not only other Great Tits, but also birds of other species are attacked. This is presumably due to a lowering of the threshold of the fighting drive near the nest-site, so that an otherwise inadequate object is sufficient to release attack.
- (vii) Effect of repeated skirmishes. Each male fought more vigorously against strangers than against known and established neighbours. On several occasions when two males were skirmishing and a stranger arrived on the scene, both the first two males attacked the stranger. Skirmishes across established territorial boundaries were usually not very vigorous. Tinbergen (personal communication) suggests that this may be due to a type of negative conditioning. The aim of fighting is to cause the opponent to flee: if continued fighting against a particular opponent fails to produce this result, then the bird 'learns' not to fight him.

(viii) Even when all other known causes of variation had been considered, there still remained a marked degree of variation which could not be accounted for. This indicates the presence of other causes of temporal fluctuations in the strengths of the drives which are not yet known. Further, there may exist innate differences in the strength of the aggressive drive between individuals.

2. Parus caeruleus.

(a) Display types

These are very similar to those of the Great Tit.

(i) Supplanting attack.

(ii) Up-and-down supplanting attack. As in the Great Tit.

Sometimes the attacker hovers for a moment before descending on his rival.

(iii) Head-up posture. This is not so marked as in the Great Tit, and is often difficult to distinguish from an alert postural set. One male, who was watched during numerous skirmishes, never used a proper posture of this type. Other individuals, however, sometimes used postures which were sustained for several seconds, and were accompanied by a swaying movement of the body and a craning upwards of the neck. Sometimes the bird perched on the side of the twig, the body thereby becoming absolutely vertical, or even over the vertical. The head-up posture is given immediately after a supplanting attack, and by birds which have just avoided an attack, but rarely on other occasions.

(iv) Upright flight.

(v) Chases. Often very prolonged. In one pair which held a territory in a narrow strip of wood the sight of another bird flying past twenty yards away in the field was sufficient to release chasing.

(vi) Displacement pecking. Very common in intense skirmishes.

(vii) Calls. The notes most often heard are "pit tit churrrr", "Drrrrrt tit tit tit" and "Drich ich ich". Singing in lulls or after the skirmish is common.

(viii) Wing flicking. During the course of a skirmish the ^{attacked} ~~subordinate~~ bird always appears to the human observer to be more "agitated" than the attacker. This impression arises largely from the fact that ^{it} ~~the subordinate bird~~ often has a raised crest and flicks his wings. The wing flicking may be only spasmodic, or it may be so frequent that it resembles the wing-shivering seen in epigamic displays. Since the wing-shivering is more common or more marked in the attacked bird than in the attacker, and since it increases in intensity if the attacker ~~bird~~ approaches, it seems probable that it is an inhibited intention movement of fleeing. Such wing flicking is often associated with a spread tail.

(ix) Gliding flight. This is usually associated with epigamic display, but it also occurs fairly frequently in reproductive fighting. One bird may glide down to supplant its rival, or, during a lull in a skirmish, a bird may leave the scene using the gliding flight.

(x) Up-and-down flight. A brief flight up into the air for two or three feet and down again occurs occasionally in skirmishes. It may be derived from the up-and-down supplanting attack. Once a male gave a series of such flights just after the end of a skirmish - flying up about 20 feet, turning with a stall turn and fluttering or gliding to another bush.

(xi) During lulls in skirmishes, Blue Tits often hop through the bushes near each other with the wings ^{raised} ~~elevated~~ and with the cheek feathers elevated. When the wings are raised to a considerable extent the tail is usually spread. (See food fighting, p.40). The contrast between the white cheeks and the blue head is emphasized by the elevation of the cheek feathers.

(b) Behaviour during skirmishes

The general pattern of the skirmishes is similar to that which has already been described for the Great Tit. They usually take place rather higher in the trees than in that species, and indeed height seems to be a factor of great importance. The supplanted bird usually flies up and perches above his rival.

(c) Behaviour of the female

The female may remain feeding or passively watching the encounter. She is often the goal of the opposing male, who tries to supplant her. Often, however, the female plays an active part in the skirmish - she is in fact much more vigorous in this respect than the Great Tit female. She may merely call or sing whilst the males skirmish, or may make active supplanting attacks, chases, head-up postures and so on. In a series of experiments

in which stuffed Blue Tits were presented near Blue Tits' nests during incubation and the feeding of the young, the females often attacked more vigorously than the males.

3. Parus palustris.

All the display types recorded for the Great Tit have also been recorded for the Marsh Tit. Head-up posturing is, however, even less marked than in the Blue Tit, and although seen occasionally in a well marked form and accompanied by craning of the neck, it is often only a momentary posture. On one occasion wing-shivering was seen in a skirmish. The most usual notes are "pit chur" and "dur dur dur". Both sexes take part in the skirmishes, the females sometimes displaying as vigorously as the males.

4. Parus ater.

Only a few skirmishes have been seen, but these included supplanting attacks, upright flight, and head-up posturing. The latter was more marked than in most Blue Tit skirmishes, but not so marked as in the Great Tit. This furnishes us with yet another example of the correlation between structure and display, for the ^{Coal Tit has a} black patch on the throat and upper breast which is exhibited in the head-up posture. In the Blue Tit the markings in the same region are much less conspicuous.

5. Other species.

Only one skirmish between Willow Tits was witnessed, and few details were seen, but the up-and-down supplanting attack, upright flight and

display pecking were all used. Odum (1941) divides the skirmishes of P. a. atricapillus into challenge, chase and fight, and mentions that the male stands very straight in the challenge: both sexes took part when the skirmishes were intense. Dixon (1949) states that in P. inornatus posturing is lacking, but action consists of scolds, calls or song, often in combination with wing vibrations. He adds "A threatening posture in titmice appears to be an attitude of potential movement towards the intruder, and may be accompanied by wing vibrations. The pursuit which follows may be a flight towards the perched bird or to a position beside it, the objective being to drive the bird from its perch". (In a description of one encounter, the wing-shivering seemed to be limited to the subordinate birds.). From these descriptions we can recognise behaviour closely similar to that which has been described for the Great, Blue and Marsh Tits.

B. Inter-specific Reproductive Fighting.

One of the results of the territorial behaviour which has been described in the previous section is that there is little fighting between birds of the same species over actual nest sites. There is, however, no territorial exclusiveness against tits of other species except in the immediate vicinity of the nest-hole. It thus often happens that birds of different species become interested in the same hole. Interspecific reproductive fighting over nest-sites between Great, Blue, Marsh and Coal Tits have been seen in nearly all possible combinations. (There were one or two records of a bird carrying nest material attacking birds of other species while still many yards

from the nest. This suggests that such fighting may be linked to the nest-building mood, as well as to the actual nest-site.).

These interspecific skirmishes are not usually accompanied by the types of display which have been described above as occurring in the intra-specific encounters. Head-up posturing is rarely seen, is never sustained, and appears to be quite irrelevant to the skirmish and not functional as a display. The wings-raised posture, which is used commonly in food disputes (p. 40), and is rare (at any rate in the Great Tit) in the intra-specific skirmishes, is common in all species in the inter-specific encounters. For the most part, however, these encounters consist of direct supplanting attacks, often ending in fierce combat.

It is interesting to compare the frequency with which actual combat occurs in these encounters with its frequency in the intra-specific skirmishes. The figures are given in Table // for the two seasons (1949 and 1950), only high intensity skirmishes being included. It will be seen that fights occur very much more often in inter-specific skirmishes than in intra-specific ones. This is presumably due to the exceptionally intense fighting which often occurs where nest sites are concerned. Both birds are on their own territory, and so in both the fighting drive is much more strongly activated than the fleeing drive. Possibly the fleeing drive can only be activated to a degree comparable with that to which the fighting drive is activated by the pattern characteristic of the species; and it is for this reason that the head-up posture and upright flight (which depend on approximate equilibrium between the two drives) do not appear.

Species of other genera rarely elicited aggressive behaviour except in the immediate vicinity of the nest-hole. Great Tits were seen to drive a Hedge Sparrow (Prunella modularis) and Blue Tits a Robin (Erithacus rubecula) away from the nest box. Other observers have recorded several other species of small birds being driven away from the nest. Such species are apparently not attacked when on the ground, but only when moving about near the nest-hole.

Table II . Number of skirmishes involving actual combat.
(Skirmishes of high intensity only included.).

	<u>No. of skirmishes witnessed.</u>	<u>No. involving actual combat.</u>
Great Tit intraspecific skirmishes.	68	10 (15%)
Blue Tit intraspecific skirmishes.	62	6 (10%)
Marsh Tit intraspecific skirmishes.	18	6 (33%)
Interspecific skirmishes (all species).	16	12 (75%)

C. The Functions of Reproductive Fighting.

Tinbergen (1936) has emphasized that the function of reproductive fighting is to secure "objects or situations which are indispensable for reproduction". In the Great Tit these are: (i) the mate, (ii) the territory, and (iii) the nest-site. (For a discussion of the values of territory, see p. 100).

D. Conclusion.

In the preceding sections we have seen that the behaviour involved in the reproductive fighting of the Tits can be understood if we make assumptions similar to those made by Tinbergen in analysing the reproductive fighting of other species - namely that during the skirmish the fighting and fleeing drives are aroused in each combatant, and are normally in approximate equilibrium. Some actions are the direct expression of one of these two drives - thus attack is the expression of the fighting drive, and escape is the expression of the fleeing drive. Other actions must be interpreted as due to the conflict between the two drives. Which of the several possible responses the animal makes to each stimulus situation depends on the strengths, and on the relative strengths, of the two drives. Published descriptions of the reproductive fighting of other Passerine birds also seem to fit this hypothesis (e.g. Erithacus rubecula; Lack, 1939; Motacilla flava; Smith, 1950. Both of these species display the breast in fighting).

We have also seen that the displays involved in reproductive fighting are very similar in the different Parus species. The head-up posture has been elaborated to a much greater extent in the Great Tit than in the other species, and, parallel with this, a broad black ^{ventral} ~~vertical~~ stripe, which is displayed in the posture, has been evolved. Thus we seen the parallel development of a display and of a conspicuous structure which accentuates it. Many other examples of this are known (Tinbergen, 1948). The parts played in reproductive fighting by the two sexes are more nearly equal in the Blue and Marsh Tits, where the colour patterns of male and female are very similar,

than in the Great Tit, where the male has a much broader ventral band than the female.

Although the displays used in intra-specific reproductive fighting in the different species are closely similar, they are not all ^{evoked} ~~worked~~ in inter-specific encounters. In each species the displays, with their innate releasing mechanisms, have undergone a long period of evolution so that the pattern exhibited by one species no longer releases the movements typical of intra-specific reproductive fighting in the other.

SECTION X COPULATION AND COURTSHIP FEEDING.

A. Parus major.

1. Copulation
2. Courtship feeding.

B. Parus caeruleus.

1. Copulation
2. Courtship feeding.

C. Parus palustris.

1. Copulation
2. Courtship feeding.

D. Parus ater.

E. Parus atricapillus.

1. Copulation
2. Courtship feeding.

F. Other species.

1. Copulation
2. Courtship feeding.

SECTION X COPULATION AND COURTSHIP FEEDING.

A. Parus major.

1. Copulation.

Copulation is preceded by a wing-shivering display performed by both birds. It may be initiated by either sex. It usually takes place in thick bushes, so that it is seldom possible to see the whole sequence of movements in any one case. Typically the male, slightly crouched down on a ^{branch} bench, starts shivering his wings and calling as he does so. The note used seems to vary considerably, but it might be written as "zeedle-zeedle-zeedle-zee" or "zee-zee-zee-zee-zee". He usually, but not invariably, holds his head down and his tail up. This initial display may occur in bursts of increasing intensity with pauses between. The male flies to a perch near the female. If she is receptive, she too starts shivering her wings, calling, and crouching. The birds display thus for several seconds before the male mounts. One or both birds may continue to shiver their wings after they have separated, and this may lead to another mounting; or, more usually, gradually dies away. After an apparently successful copulation the birds usually fly apart with little after-display; but on occasions bill-wiping, wing-shivering and courtship-feeding have each been seen to follow attempted copulation. If the female initiates the display, the male flies close to her and then mounts as above.

It sometimes happens that one bird (of either sex) starts shivering its wings and calling, and then flies near to the other, who pecks at it:

this may develop into a brief fight. The significance of this behaviour is not clear, but it is possibly due to one bird not being in a receptive state. 'Sexual chases' are occasionally seen at this time of the year.

Incomplete wing-shivering displays by the male may be seen for some weeks before nesting. They are accompanied by a very faint seedling call, inaudible at a range of more than a few yards. This was first seen on March 16th ~~in~~ 1949, and March 8th in 1950. In 1949 intensive observations were made on one pair during nest-building. The first copulation was seen on April 16th, five days before the laying of the first egg.

'Reversed mating' (i.e. mounting of the male by the female) was seen once. It took place between a female who had lost her mate and a male who was waiting for his own mate to emerge at dawn. After an apparently unsuccessful copulation of normal type the birds separated but continued wing-shivering and calling, the female more vigorously than the male. The female then momentarily mounted the male, but they quickly separated and sat side by side, both still displaying and the female still the more vigorous. The female then crouched slightly and the male mounted, but only momentarily. The female continued wing-shivering, but the male sat still and then flew off.

Although no precise observations were made, copulation seemed to follow a similar diurnal rhythm to that shown by most other activities associated with the reproductive drive - i.e. it occurred most often in the early part of the day, rarely in the afternoon and occasionally in the evening (see p.22). During the appropriate season, copulation nearly always occurs just after the dawn emergence of the female - sometimes within a few seconds of her leaving the box. At one nest the pair used a particular bush for copulation

at dawn on at least six out of seven successive mornings. On several of the following mornings the male, while waiting for the female to emerge, flew away from the nest box and gave a wing-shivering display in this bush. On some mornings he repeated this several times before the female emerged.

2. Courtship feeding.

The display preceding courtship feeding is very similar to the pre-copulatory display and often, in an incomplete form, impossible to distinguish from it. The first complete courtship feeding pattern by 207 pair, who were watched intensively at this time, was seen on April 21st, the day that the first egg was laid. Courtship feeding continued throughout egg-laying and incubation, and ceased soon after the eggs hatched; though throughout the whole period when the young were in the nest, the female was often seen to pursue the male, begging (see p. 210).

In typical courtship feeding the female displays by crouching, shivering her wings, slightly raising her tail and giving a zeedling call. The male feeds her either without display, or with slightly shivering wings. Sometimes the female hardly begs at all, or does so only as a response to the sight of the male with food: on other occasions she begs before the male finds the food. For several days during the egg-laying period the female seems to beg almost continuously, following the male around: the male feeds her at intervals, sometimes several times in quick succession. The female's wing-shivering usually increases, but sometimes decreases, on the approach of the male: the calling usually ceases temporarily while the male³ actually is feeding her.

No doubt the amount of wing-shivering and calling shown by the male and the female depend on the strengths of the drives in the two individuals. In the early stages the male's drive is usually stronger than the female's, and he feeds her although she hardly begs at all. Even before nest-building starts, however, females sometimes beg unsuccessfully from males. The female's begging becomes well-marked just before egg-laying, and in the next few days she begs almost continuously. This, of course, is also the time at which copulation occurs. During the early part of incubation the male often feeds the female either on or off the nest, but courtship feeding becomes less common towards the end of this period. Courtship feeding again becomes common just before the young leave the nest. No doubt this is correlated with the potential start of a second brood. At some nests only one of the pair shows a recrudescence of courtship display at this time (see p.210).

Verheyen (1947) states that in the Great Tit feeding precedes copulation, but this was not the case in any of the copulations observed in this study.

As courtship feeding becomes common at the time when copulation is occurring, and as the associated displays and calls are closely similar, it seems likely that there is a close relationship between them. The exact nature of this is as yet uncertain. The begging display^{used} by the young when out of the nest is also similar to the displays used in copulation and courtship feeding (see p.221). It seems likely that in all three cases the wing-shivering is a ritualised intention movement of flight.

B. Parus caeruleus.

1. Copulation.

The pre-copulatory display is closely similar to that of the Great Tit. On two occasions when the whole sequence of the display was seen, its beginning was very gradual. The presumed male first shivered his wings for a few seconds and then resumed feeding. A minute or so later he shivered his wings again and gave the 'zeedle' call. After two or three repetitions his mate flew over to perch near him and both birds shivered their wings for a few seconds before copulation. The call seemed to become rather deeper at the moment of copulation. In one case the pair made two mutual flights - as if one were chasing the other, except that the rear bird did not seem to be trying to catch up - accompanied by excited calling: each of these ended with mutual wing-shivering.

Brief scuffles have sometimes been seen to follow the pre-copulatory display, as in the Great Tit. Colquhoun (1942) describes a copulation in which the after-display consisted of wing-fluttering and a deliberate pecking by each bird at the other's body and bill. Wing-shivering was seen to follow (probably unsuccessful) copulations on several occasions in the present study. Once, one of the pair fluffed out its feathers and preened very briefly before flying off.

2. Courtship feeding.

The display associated with courtship feeding is similar to that of the Great Tit, and to the pre-copulatory display. At two nests courtship feeding was first seen two or three days before the laying of the first egg: it

became common during egg-laying and incubation, and was also seen during the period of feeding the^s young. Further examples are given in correspondence to British Birds Vols. 40 and 41.

C. Parus palustris.

1. Copulation.

Incomplete wing-shivering displays were seen from mid-March in both 1949 and 1950. At this time, and during early nest-building, it is not unusual for one bird of a pair (sometimes, at least, the female) to perform a wing-shivering display without evoking any response from the mate.

The full pre-copulatory display is very similar to that described for the Great and Blue Tits. On the four occasions when the whole sequence was seen, it was initiated by the male with a series of bursts of wing-shivering of increasing intensity, accompanied by "zeah-dee zeah-dee" calls. Usually the male increased the shivering of his wings until he floated up and then down onto the female. At the moment of copulation the "zeah-dee" calls changed to a full "Koo Koo Koo Koo". Scuffles similar to those recorded for the Great Tit and Blue Tit were also seen.

Excellent descriptions of five complete and two abortive copulation are given by Morley (1949). The performances show considerable differences in detail; for instance, sometimes the male flew straight onto the female's back, and at other times he floated on with a sailing flight; sometimes the copulation was initiated by one sex and sometimes by the other. On one occasion copulation was followed by courtship feeding.

2. Courtship feeding.

This was recorded a few times in Marsh Tits believed to be in the nest-building stage. It became exceedingly common during egg-laying and incubation, when males were often seen to feed their mates several times in quick succession: some females seemed to beg almost continuously from their mates during the egg-laying period. The associated displays were apparently identical with those already described for the other species. During the period when courtship feeding was at its height, the begging call of the female was a rather coarse "ze-ak, ze-ak". As the male approached the calls became rather more rapid and ^{more highly} pitched. In the intervals between feedings the female either held her wings slightly raised or shivered them a little: the shivering increased greatly as the male approached with food. Sometimes a high trilling sound, resembling the copulation note, is heard at the moment of feeding. As the male turns away the shivering stops momentarily. He usually hesitates a second or so before flying off. One male habitually hovered in front of his mate whilst feeding her.

Morley (1949), in a detailed discussion of courtship feeding in this species, distinguishes four ^{stages} ~~styles~~ of display shown by the two birds. In the first stage neither individual shivers its wings, and the whole process is extremely rapid. In the second, the male shivers and the female twitches the wings, and in the third, both shiver. In the fourth stage the female's begging becomes very pronounced and almost continuous, and 'her desire to be fed eventually outstripped the male's wish to feed her'.

The results of the present study are in general agreement with these conclusions, but do not indicate that the "stages" are as distinct as

Morley implies. Variations in the intensities of the displays used may occur at any stage, correlated, no doubt, with short-term changes in strengths of the drives (see p.294). For instance, even before nest-building had started females were occasionally seen to beg unsuccessfully from males, though in general the drive was apparently stronger in males than females at this time.

D. Parus ater.

Only one Coal Tit copulation was seen. The initial display was similar to that which has already been described for the other species. After the birds separated they both continued to shiver their wings for about 20 seconds, the female more vigorously than the male. Then the male fed the female four times in quick succession.

E. Parus atricapillus.

1. Copulation.

Witherby (1934) has described a copulation of P. atricapillus kleinschmidtii. It occurred after a chase, and after it the male flew away with a 'butterfly-flight'. It has also been seen by Odum (1941), who mentions the shivering of the wings of the female and the high pitched twitter.

2. Courtship feeding.

Odum (1941) records the male feeding the female with no display on the part of the latter during the early part of hole digging. This apparently

corresponds to the first stage described by Morley for the Marsh Tit. In his 1943 paper Odum states that courtship feeding starts gradually during nest construction and reaches its peak during incubation. He does not mention the continuous begging of the female during the period of egg-laying, which has been described for other species above. Courtship feeding is also described by Bacmeister (1917), Jouard (1926, 1932) and other writers.

F. Other Species.

1. Copulation.

This has been described as follows:-

P. inornatus. Dixon (1949); Thompson (1930).

P. hudsonicus. Kennard in Bent (1946).

P. bicolor. Johnston (1944).

2. Courtship feeding.

This has been described as follows:-

P. cristatus. Gengler (1910); Smith (1941). The latter author notes that it continues after the young have hatched.

P. hudsonicus. Kennard in Bent (1946); Walkinshaw (1948).

P. inornatus. Dixon (1949). Most marked just before and during incubation.

In all cases of both copulation and courtship feeding quoted above, the associated displays seem to be closely similar to those already described for other Parus species; though ^{there} is yet no species in which a sufficient number of either have been described to permit generalisations on the significance

of the variation in details between different performances.

Wing-shivering has also been described in P. gambeli (Bent, 1946), P. bicolor (Thompson, 1930), and P. albiventris (Newton, quoted by Bannerman, 1948).

SECTION XI THE NEST SITE.

A. Nest Site.

1. Parus species.

- (a) Parus major
- (b) Parus caeruleus
- (c) Parus ater
- (d) Parus cristatus
- (e) Parus palustris
- (f) Parus atricapillus
- (g) General

2. Other genera.

B. The Genus Parus as Hole-nesting Birds.

C. Nest Site Selection.

- 1. Parus major
- 2. Parus caeruleus
- 3. Parus palustris
- 4. Other species.

SECTION XI THE NEST SITE.

A. Nest Site.

1. Parus species.

All members of the genus Parus typically nest in holes. There is however, much variability in the types of holes used - both between species and between individuals of the same species. In the following discussion, considerations of habitat are omitted except where directly relevant, and little mention is made of the preferred heights of nest sites since few reliable data are available.

(a) Parus major

P. m. newtoni typically nests in a hole in a tree or wall, but holes made by rats, sand martins, etc., are occasionally used. Many of the earlier handbooks of ornithology list many strange sites such as letter boxes, cupboards and the interiors of pumps. The height of the nest is very variable, but the preferred height is probably between 5 feet and 20 feet, and seems to be rather lower than in P. caeruleus. Nests in holes in the ground are known (e.g. Ticehurst, 1932; Jourdain, 1906): in the present study area one bird nested in a petrol can with the hole about one foot above ground level. The interior dimensions of the hole seem to matter little, as large holes are filled up with moss. Similar considerations hold good for P. m. major (see e.g. Lebourier et Rapine, 1941; Verheyen, 1947). Nests placed in the open (i.e. not in a hole) are recorded from time to time, mainly in the deserted nests of other species (e.g. Nelson, 1907; Proctor, 1910; Colthrup, 1910; Gurney, 1916; Headley, 1919; Hills, 1934;

Jouard, 1936; Walpole-Bond, 1938; Verheyen, 1947). In some of these cases, however, the nests appear to have been built by the tits themselves, and one of those found by Walpole-Bond had a roof (which a nest in a hole never has). Nests are sometimes found in the interstices of squirrels' dreys or of the nests of Magpies or Rooks, and some of the earlier writers state that nests found in such situations are much more closely woven than nests in true holes, and are sometimes domed. (Seebohm, 1883; Dixon, 1893; Hudson, 1902).

Other subspecies typically nest in whatever holes are suitable and available locally, (see e.g. Stuart Baker, 1932, for the Indian subspecies). P. m. alancorum (Jourdain, 1937) and P. m. cinereus (Hume, 1889) have occasionally been recorded as laying in open nests.

Most subspecies of Parus major do not excavate their own hole, though they may enlarge the cavity or the entrance. Stuart Baker (1932), however, states that P. m. cinereus usually excavates its own hole. There are a few records of other subspecies excavating in rotten wood (P. m. major; Legendre, 1932; P. m. newtoni; Riddell, 1939 and Walpole-Bond, 1938).

(b) Parus caeruleus.

In general the sites chosen are similar to those chosen by P. major, though the cavities are as a rule rather smaller. It occasionally nests in holes in the ground (e.g. Dixon, 1893; Sharpe, 1896; Jourdain, 1906). Occasionally nests have been recorded in deserted Wren's nests (British Birds and Zoologist), and very occasionally birds have been found nesting in open nests (e.g. Owen, 1915; Corlett, 1929; Chandler, 1943). In the latter case there is good evidence that the nest

had been built by the Tits themselves, and the young were probably reared successfully. Butler (1907/8) records a nest built in an exposed position behind lattice work which was "over arched".

There is no record of the Blue Tit excavating its own hole, though Verheyen (1947) states that they sometimes enlarge natural cavities.

(c) Parus ater

This species nests in a hole in the ground or in a bank much more frequently than do the other species. Cases of ground nesting have been recorded for many of the subspecies, and in some districts the habit is common (e.g. Legendre, 1932; Klaas, 1934; Lynes, 1920; Jouard, 1932; Durango, 1946; Verheyen, 1947; Laurent et Mouillard, 1939). This preference for ground nesting is probably connected with the fact that the species is usually found in coniferous woods, where natural holes in trees are less common than in deciduous woods. Holes in trees are usually used when available. Stoney (1928) found a nest of P. a. hibernicus between the matted ivy and stem of a sycamore tree. Newmann (1861) quotes a description of a nest "on the branch of a fir, close to the bole, very like a Long-tailed Tit's but much rounder", and Butler (1907/8) states that when the nest is partially exposed it is "over arched". Bond ~~(1861)~~ also ~~describes a roofed nest.~~ It sometimes nests in the cavities of old Magpie's or squirrel's nests. There are doubtful records of the Coal Tit nesting in open nests of other species. It often enlarges natural cavities (Verheyen, 1947; Atkinson, 1886).

(d) Parus cristatus

This is another species which typically nests in coniferous woods where natural holes are often scarce. Whereas P. ater nests in holes in

the ground, P. cristatus typically excavates its own hole wholly or partially. Such excavated nests are typically in rotten stumps: their form is often irregular and the sides of the hole not smooth. When natural holes are available, they are often used. Nests have occasionally been found in squirrel's dreys, Rook's nests, or in old nests of Wrens or Long-tailed Tits, (e.g. Dixon, 1893). It also occasionally nests among roots or in other situations on or very near the ground (Verheyen, 1947). Verheyen also states that this species sometimes builds in an open nest. Roofed nests similar to those of a Wren have been recorded by several observers (Fatio and Studer, 1893; Dresser, 1881).

(e) Parus palustris

Typically nests in natural holes in trees; these holes are often touched up, and there are a number of records of complete excavation, (Noble, 1913; Walpole-Bond, 1931; Musselwhite, 1931; Mohr, 1938; Morely, 1936; Verheyen, 1947). As in the Crested Tit, such holes are very irregular. This species sometimes nests in holes in the ground (e.g. Legendre 1931 and 1932).

(f) Parus atricapillus

This species typically excavates its own hole in rotten wood. The holes are often started where there is a fault or depression in the wood, or where a woodpecker has been digging for insects. Several writers have given records of P. atricapillus nesting in ready-made holes where these were available, (de Balsac, 1929; Jouard, 1932; Odum, 1941; Verheyen, 1947), and all intermediate stages from completely self excavated holes to those in which practically no work is done may be found. The holes excavated by the bird are in general smoother inside than those of

Crested Tits, but are not so competently excavated as those of Woodpeckers.

(g) General

The species reviewed above are sufficient to demonstrate that although each species shows remarkable catholicity of taste in the requirements of the nesting site, yet there are definite differences between the 'preference' of the different species. These differences were shown clearly in Marley Wood, where ~~e~~very nearly all the Great Tits, but only about half the Blue Tits, used the artificial nest boxes provided, although many boxes remained unused, (cf. Cadger, 1909-14; Enemar, 1948).

Clearly, it is essential that the characteristics required in a nesting hole should not be too rigid, for 'suitable' holes may be scarce. Nevertheless the differences between the 'preferences' of the different species seem to have selective value: thus Blue Tits prefer smaller holes to Great Tits: and species which nest in areas where natural holes in trees are scarce, nest in the ground (Coal Tits), or excavate their own holes (Crested Tits). We do not know whether these preferences are innate, but it seems highly probable that they are. If so, a selective balance between preference for a particular type of nest site and catholicity of taste must exist in each case. Perhaps the differences are brought about by a process of Organic Selection (Baldwin, 1896; Morgan, 1900). Tinbergen (1946) and Kluijver (in litt.) have shown that the availability of nest sites may influence the size of the population, at least locally. Further study of the degree to which the different species overlap in their nesting requirements would be of great interest.

The occurrence of excavation in the genus Parus is shown in Table 12. Although most, if not all, species enlarge holes to some extent if necessary,

it appears that the habit of excavating the hole has been developed or retained to a greater extent in the subgenus Poecile than elsewhere.

Table 12 . Occurrence of excavating behaviour in the
genus Parus

<u>Species.</u>	<u>Occurrence of excavating.</u>	<u>Authority.</u>
P. (Lophophanes) dichrous.	2 out of 3 nests excavated.	S. Baker, 1932.
P. (Lophophanes) cristatus.	Usually.	
P. (Baecolophus) inornatus.	Occasionally.	Bent, 1946.
P. (Parus) major.	Very rarely in <u>P. m. major</u> and <u>P. m. newtoni</u> . Usually in <u>P. m. cinereus</u> .	Legendre, 1932. Riddell, 1939. S. Baker, 1932.
P. (Poecile) carolinensis.	Usually.	Bent, 1946.
P. (Poecile) gambeli.	Occasionally.	Bent, 1946.
P. (Poecile) sclateri.	One out of 2 nests excavated.	Bent, 1946.
P. (Poecile) rufescens.	Usually.	Bent, 1946.
P. (Poecile) atricapillus.	Usually.	v. supra.
P. (Poecile) palustris.	Sometimes.	v. supra.

Although tits are normally considered to be hole-nesting birds, there are records of nesting in the open for several of the species. These records are too numerous to be attributed to faulty observation. The evidence for the occasional building of domed nests is less reliable, but there are several independent records. In other genera in the family domed nests are the rule.

2. Other genera.

Other genera build domed nests, placed usually amongst the twigs of bushes or trees. Those of Auriparus are built of thorns and the supporting twigs are woven into the structure; forming a support from underneath. Those of Aegithalos are similarly placed in thick bushes and supported from underneath: they are sometimes placed in the forks of trees. Psaltiriparus and Remiz build hanging nests which are suspended from branches or twigs.

B. The Genus Parus as Hole-nesting Birds.

It has been suggested (e.g. by Csörgey, 1913; Berndt, 1936; Jouard, 1936) that tits (Parus spp.) have only comparatively recently become hole-nesting birds. If any transition from open-nesting to hole-nesting did take place, it did so very long ago; and such speculations are of little value in the absence of any but circumstantial evidence.

C. Nest Site Selection.

In this section the processes of nest site selection in Parus species are first discussed. The Hole Inspection Display, which may be relevant to the early stages of nest site selection, is then described.

The Nethersole-Thomsons (1943) have summarised data on nest site selection for many species. For all British Parus species they state that both sexes examine possible nest sites together, and of the Great and Blue Tits they remark that the males "suggest" several possible sites, one of which is chosen by the hen. It would indeed seem that, in such a species, the female, who alone is responsible for the building of the nest, must select the site. In tits, as in most other birds, actual building is preceded by a period in which the birds pick up and 'play' with nesting material and start to build in several different sites. Indeed it sometimes happens that one nest is almost completed, and is then abandoned, and another started elsewhere. In such cases it could be argued that the final selection does not take place until well after the start of building.

In fact, nest building may be divided into (i) looking for nest material, (ii) picking up material, (iii) flying with material to the nest site, (iv) placing the material in the nest and the various actions associated with the actual building. There must, in the first place, be a general recognition of a suitable site (innate, or possibly learnt in early life) which causes a Great Tit to carry the material to a hole and a Long-tailed Tit to a bush. In the early stages of building the chain of reactions is often incomplete, and the material may be dropped at random, as well as in one or more suitable sites. The final selection would seem

to be a process of conditioning to one particular site which takes place in this period of incomplete building. The rate of conditioning may vary in different species and in different individuals, and also with the intensity of the drive. When the drive is high the chain of nest-building activities occurs frequently, and there is ample opportunity for conditioning to one site: when the drive is low nest-building only occurs at long intervals, and the material may be carried to a different site on each occasion. This suggestion regarding the processes of nest site selection in Parus species does not, of course, rule out the possibility that in other species the site may be selected long before building is started.

The behaviour which the Nethersole-Thomsons describe as the male "suggesting" holes to the female is, in fact, a form of display, referred to here as the "Hole inspection display". This display is often seen in an incomplete form, and does not really involve selection. In certain instances, the pair may confine themselves to one particular site for all their display, either because suitable sites are scarce, or for other reasons; but in many pairs the display is performed at several different holes in turn. It is possible that the display may make the birds familiar with the holes in the area; or that repeated performance of the display at one particular hole may later result in that hole being selected for the nest, but of this there is little evidence. The hole inspection display is described below.

(a) Parus major

The hole-inspection display consists in the first instance of the bird perching outside a hole, crack or crevice, so that its head is on a

level with the hole. The body is usually vertical and below the hole. Although such behaviour occurs at all times of year, it is seen much more often at those times of year when the birds are sexually active than at others. The actual number of times that such behaviour was seen at different times of year in 1948/9 is shown in Table 13.

Table 13. Total number of records of Great and Blue Tits inspecting holes between Sept. 1st, 1948 and April 30th, 1949, in half-monthly periods. All records made both in Marley Wood and elsewhere are included.

Period.	Sept.		Oct.		Nov.		Dec.		Jan.		Feb.		March		April	
	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Great Tit.	1	1	1	9	3	6	2	2	0	6	9	11	8	16	22	12
Blue Tit.	0	1	1	2	2	1	0	0	0	2	0	3	1	14	25	2

Hole inspection is more frequent in autumn than in summer. This may be related to the general return of sexual behaviour at this time, or perhaps to the claiming of winter roosting sites, for it is at this time of year that many tits change over from roosting in foliage to roosting in trees. Both male and female Great Tits were seen inspecting holes at this time of year. They did not usually remain long outside the hole, and only rarely entered. Frequently, when one tit was inspecting a box, another flew down on it and supplanted it at the hole: sometimes the aggressor remained inspecting in the other's place, and at others the two fell fighting through the air. On one occasion in November a Great Tit was inspecting a nest box when a Blue Tit arrived nearby. The Blue Tit fluttered around nearby, hopping from perch to perch,

peering at the box and showing obvious signs of disturbance. It then inspected a neighbouring ventilator for a few seconds. Then the Great Tit entered, the Blue Tit inspected the box while it was inside.

In December and early January this inspection of holes became relatively infrequent, but in late January, as soon as the flocks had broken up and most of the birds were feeding in pairs, it was seen more often. At this time of year inspection of holes is certainly to be regarded as part of the breeding behaviour.

In its complete form the display takes place as follows. The male flies to the hole, leaving the female feeding nearby. He often perches first for a second or two above the hole, and then inspects the hole with his body vertically below it. As the male perches outside, he sometimes taps at the hole, and sometimes turns his head round so that the white cheeks are exposed to the female. Perhaps the tapping has been ritualised from movements made in attempts to enlarge the hole, and the turning of the head from movements made in looking round at the female; certainly both now have a display function. They are not functional in any other way, since the male may tap persistently at wood far too hard for him to chip, and often turns his head round to look at the ground when the female is above him. If the female does not respond, the male may leave the hole, but he usually returns in a few seconds. This happens most often when the female is in a position from which she cannot see the hole, and may serve to attract her attention. Sometimes the male enters the hole and pecks at the entrance from inside, so that his head keeps on appearing and disappearing at the entrance. In cases where the female responds, she

moves in stages towards the hole. At first her body is simply in an alert upright posture, but as she approaches she starts to shiver her wings. The intensity of the shivering increases as she gets nearer the hole. Sometimes the female perches within a foot of the entrance while the male is still inspecting. It is not uncommon for the male to inspect the hole for as long as three minutes continuously before the female comes right up to him. If the display gets to this stage the female usually enters, but the exact manner in which she does so varies. At times the male flies off the hole and the female enters directly. Sometimes the male enters first and the female follows him inside after a few seconds; the male emerges as soon as the female enters. Occasionally the male enters and the female waits until he comes out again before she goes in. The female may remain inside the box for several minutes, during which she can often be heard hammering at the entrance. On the other hand she may enter for only a few seconds, or enter and emerge several times in quick succession. It must be emphasized that the display is subject to considerable variation with the intensity of the reaction, and with other factors, which await elucidation. In particular, one feature which cannot at present be explained is that on several occasions the female gave a momentary head-up posture when arriving at the box, apparently identical with the head-up aggressive posture used in reproductive fighting.

The above description applies to the complete display as it is performed in the week or two before nest-building, but it is seen in various degrees of completeness from the time that the winter flocks break up. In 1949 the flocks started to break up in late January, and

there was a noticeable increase in the frequency with which tits were seen inspecting holes. At this time it was principally the males which were seen to inspect. Sometimes they clung outside the holes for as long as half a minute, and sometimes put half their bodies inside; if they entered completely they rarely stayed in for more than a few seconds. The female was usually nearby, but took little or no notice of the male's behaviour and continued feeding. (At times females inspect holes independently of their mates). In late February females sometimes approached when their mates were inspecting a hole, and rarely inspected after them, but this did not become common until late March and April. During the first half of April a more or less complete form of the display was seen frequently, especially in the early morning. One pair which was watched closely, often performed the display three or more times in an hour. This pair displayed at three different boxes, often using all three in a single hour. Other pairs showed a similar indifference to the actual hole used - though it is perhaps significant that in all cases where the complete display was performed it took place at a potential nest site, whereas mere hole inspection sometimes took place at quite unsuitable nooks and crannies.

Table 4 . Diurnal variation in frequency of hole-inspection.
Number of hole-inspections seen in each quarter of the day per hour
spent in field, between March 15th and April 15th.

	<u>Period of day</u>			
	I	II	III	IV
No. of hours in field.	43	60	23	43
Great Tit hole inspection per hour.	6.44	0.20	0.06	0.04
Blue Tit hole inspection per hour.	0.34	0.32	0.02	0.08

In Table 4 is shown the number of times hole-inspection was seen in each quarter of the day per hour spent in the field, for the period March 15th - April 15th, 1949. Hole-inspection was much more frequent in the early hours of the day than later on. Most of the records of hole-inspection for the earlier part of the season were in the second quarter of the day.

Hole inspection was seen on a few occasions during nest building in one pair which was watched intensively at this period. Hole inspection by the male during the early part of nest-building caused the female to shiver her wings and seemed to cause her to resume building after a long period away from the nest. Hole inspection by the female sometimes occurred about five hours after dawn, at the end of the day's nest building activity. The male of one pair inspected another, nearby, nest on the day on which his own mate laid her first egg.

Hole inspection was seen on a number of occasions out of its usual functional context. Once a Great Tit inspected a hole from which it had just seen a Wren emerge. Several times hole inspection occurred during a lull in sexual fighting, and at other times, the male of a pair which had been feeding on the ground flew up and inspected a hole when slightly disturbed by the observer.

From before nest-building until incubation the male usually inspects the female's roosting hole several times after she has gone to roost in the evening and before she emerges at dawn. Similar behaviour may occur less frequently at other times of year. It is described in the section on roosting behaviour.

Hole inspection has also been described by Gibb (in litt.) who remarks particularly on the conspicuousness of the head of the male, as, perched inside the hole, he pops his head in and out. There are also numerous incomplete records of birds inspecting holes. It may be taken as certain that the display occurs in all subspecies of Parus major. For instance, Hume (1889) quotes the following record: "When I was in Poona, in the hot season of 1873, the Grey Tits (probably P. m. mahrattarum R.A.H)..... became exceedingly busy about the end of May, courting with all their spirit and examining every hole they could find. One was seen to disappear up the mouth of a cannon at the arsenal."

(b) Parus caeruleus

As with the Great Tit, inspection of holes became fairly common during a period of a few weeks in the autumn. It was seen with increasing frequency from late January, becoming very common in late March and April. The earlier inspections represented incomplete forms of a hole inspection display similar in all respects to that described for the Great Tit. The complete display occurred commonly in April.

Female Blue Tits were often seen inspecting holes in the absence of their mates - this seemed to occur most often when a female was showing interest in a particular hole. In March 1949 one female inspected a cleft in an area which had previously been in her territory, but which had recently been usurped by another pair: her behaviour caused much fighting between the two pairs.

Inspection of the nest hole by the male during nest-building occurred more often amongst the pairs of Blue Tits under observation than in the Great Tits. It is referred to in the section on nest-building.

Several other writers have mentioned hole inspection by Blue Tits (e.g. Kenrick, 1940; Lebourier et Rapine, 1941; Colquhoun, 1942; Pullen, 1946) but few details are given.

(c) Parus palustris

Hole inspection was seen several times, but only once was the sex of the birds known: on this occasion it was the male which was inspecting, while the female fed nearby. Steinfatt (1938), on the other hand, recorded that the female inspects while the male remains hunting or on watch nearby.

Morley (1942) mentions that hole inspection is sometimes stimulated by the presence of a known "bait-giver" or by other "emotional level raisers such as fights with neighbours on territory boundaries, or scraps with Blue Tits."

(d) Other species

It is probable that this, or a similar display, is widespread if not universal amongst the other Parus species, though the references to it in the literature are brief. Records which probably refer to this display are given for P. cristatus (Ross, 1935), P. niger (Bannerman, 1948), P. atricapillus (Jouard, 1932; Forbush, 1912 quoted by Bent, 1946) and P. inornatus (Dixon, 1949). Odum (1941) states that in P. a. atricapillus the female apparently takes the lead in site selection.

SECTION XII. THE NEST.

A. Parus Species.

1. Materials
2. Share of sexes
3. Start of nest-building
4. Size of nest
5. Behaviour during building
 - (a) Parus major
 - (b) Parus caeruleus
 - (c) Parus palustris
 - (d) Other species
6. Variation in nest-building activity through the day.

B. Other Genera.

SECTION XII . THE NEST.

A. Parus species.

1. Materials.

The great majority of species, in all parts of the world, usually use moss as a foundation to the nest: the few exceptions seem to be birds nesting in rather dry regions, e.g. P. ater atlas (Lynes, 1920), P. afer (Stark, 1906), P. lugubris (Legendre, 1932; Jourdain, 1906). Moss is also usually absent in nests of the European subspecies of P. atricapillus (e.g. Meares, 1932; Musselwhite, 1932; Legendre, 1932), though some is usually present in nests of P. a. atricapillus (Odum, 1941). In this case the small amount of moss used is probably connected with the fact that the species usually excavates its own hole: in other species the moss largely serves to reduce a large hole to manageable proportions, but a self-excavated hole is usually of a suitable size already.

The nature of the lining depends largely on availability, but hair, wool, or feathers are used most frequently. Differences may exist between the preferences shown by different species in this respect. Thus in the present study area Great Tits lined their nests almost entirely with fur, only occasionally using feathers, whereas Blue Tits usually used feathers, and only occasionally fur.

2. Share of sexes.

At all nests of Great, Blue and Marsh Tits watched by the present writer, the building has been performed entirely by the female, who was

usually accompanied on her visits to and from the nest by the male. This is undoubtedly the usual procedure. On one occasion, however, a male Marsh Tit was seen to pick up and drop a piece of moss early in nest-building, and a number of authors have recorded cases of males playing a more active part, (e.g. *P. major*; Zollinger, 1930, Pike, 1932: *P. caeruleus*; Pullen, 1946; Witherby et.al., 1938: *P. ater*; Selous^a, 1905; Ussher and Warren, 1900: *P. cristatus*; Ross, 1935; Witherby et.al., 1938; Smith, 1941: *P. atricapillus*; Johnston, 1936; Verheyen, 1947: *P. palustris*; Verheyen, 1947). In the majority of these cases the activities of the male were limited to picking up material and dropping it, or to carrying it to the nest - that is, to the early stages of the chain of behaviour which constitutes nest-building. There are few records of males actually building. This is typical of incomplete activities. We must conclude that the nervous mechanism necessary for nest-building behaviour is present in both sexes, but that the motivational factors are normally much stronger in the female.

In those species which excavate their own holes, it is usual for the male to play a part in the excavation, though even here the female does the greater part of the work. In *P. atricapillus* most authors agree that excavation is the work of both sexes (e.g. Steinfatt, 1938; Witherby, 1934; Odum, 1941), though it is usual for the female to do more than the male, and Temperley (1934) watched a nest where only the female excavated. In *P. cristatus* Ross (1935) believes, and Smith (1941) states, that only the female excavates, but Bailly (1854)³ states that both sexes take part. Dingle (in Bent 1946) records that in *P. carolinensis* both sexes excavate but only the female builds.

3. Start of nest-building.

Gibb (in litt.) has shown that the time between the start of nest-building and the laying of the first egg (see p. 189) varies in different years. It was particularly small in a year when a warm spell followed a cold period and apparently precipitated nest-building: in this year the nests were less substantial than usual.

It is noticeable that species of those genera which construct elaborate nests begin building very early and often take several weeks over it - e.g. Aegithalos and Psaltriparus.

4. Size of nest.

In Passerine birds which build open nests, the nests of different individuals may vary to some extent in weight and in solidity of construction, but it is usually clear whether or not the nest is complete. This is not the case with the Tits, where the basis of the nest consists of a more or less untidy heap of moss and where building continues after egg-laying has begun. No experimental work aimed at discovering the factors which determine the size of the nest has yet been done, but circumstantial evidence permits us to draw certain conclusions. In the first place the size of the hole has an important influence. We have already noticed that in P. a. atricapillus which excavates its own hole, the cavity is often not much larger than the nest, and that the nest is thus usually small. The opposite is found in individuals of other species which choose capacious nest sites, and fill them up with a mass of material. Instances of this are common in the literature: we may cite for example Herr (1927), who described P. palustris filling up the inside of

a pump with moss; Hume (1889) who found half a cubic foot of moss in a nest of P. melanopus; Verheyen (1947) who describes a nest of P. caeruleus 3 cms. in thickness extending over an area of 6 sq.dcms., and states that nests of P. major in large holes are often 50 cms. in depth; and Stevenson (1866) who describes a nest of P. major in a three cornered cupboard (length in front 15", height 9", depth from front to back measured to the angle of the cupboard 10"). The size of the nest is also, however, influenced by the readiness of the female to lay eggs. In the present study one female who was very late nesting, because of the death of two mates, eventually laid her first egg on the bare boards of a nest box with only a little moss round the sides: she continued to bring moss after this, but the nest was never as large as those of other individuals. This bird, however, had already started other nests elsewhere, and it is not impossible that the smallness of her nest was due to the fact that she had already expended some energy in nest-building.

5. Behaviour during building.

(a) Parus major

Fairly intensive observations were made at three nests in 1949, and casual observations at other nests. During the early part of nest building the female visited the nest at intervals carrying large beak-fulls of moss: sometimes the beak-fulls were so large that she could enter the hole only with difficulty, and had to turn round when inside and pull in some of the material after her. On most visits she stayed in the cavity for less than a minute, but on occasions for as long as ten minutes. The first few scraps of material were dropped loosely on the floor of the box, but

there was soon discernable a tendency for the material to be pushed to the sides of the box, leaving the centre of the floor bare or only shallowly covered in material. In this way the beginning of the cup was formed. The material was almost invariably pile higher on the side of the entrance hole than on the other sides, and the cup eventually came to be nearer the side remote from the entrance.

The female often called 'chich-ich-ich-ich' softly before she entered with material, and the female of 207 nest often sang a see-saw song of 4 or 6 notes on emergence. Occasionally the female pecked at the entrance of the box from inside: this may represent a genuine attempt to enlarge the hole.

The male usually escorted the female to and from the box. He often sang ^{or} ~~or~~ called 'Twink' outside. If the female spent unusually long inside the box he showed obvious signs of impatience - calling 'twink' or 'chich ich ich' and looking at the entrance. Occasionally he inspected the hole while the female was inside. When not building the pair spent the time feeding in close company, usually at some distance from the nest.

The time elapsing between the start of nest building and the laying of the first egg is variable, but may be taken as usually rather over a week. Gibb (in litt.) gives more precise figures. Lining is usually started just before the laying of the first egg, and continues for the greater part of the egg laying period. If the nest is examined just after the female emerges in the morning, the eggs are usually uncovered[^]; but the female brings fresh material to cover them during the first hours of the day: when the nests were examined after about eight o'clock in the morning the eggs were invisible. In some cases the female continued to bring

material for some days after the start of incubation. Nests were lined with fur, and occasionally a few feathers were incorporated. Some individuals decorated the completed cup with torn fragments of leaves: the leaves chosen almost invariably had an uneven edge (e.g. Nepeta hederacea).

When they were gathering material, females often held it under the foot while perched on a branch and teased it out with the beak - perhaps making it into a ball which was easier to carry.

When not building each pair usually stayed well away from the nest, but the female sometimes visited the vicinity of the nest without bringing material - perhaps merely inspecting the hole or calling 'chich ich ich' in the tree. This was especially apt to occur towards the end of the morning period of building activity.

(b) Parus caeruleus

One nest was watched intensively during nest building, and casual observations were made at others. The behaviour of the birds was very similar to that of the Great Tits. The nests were lined with feathers and often decorated with fragments of leaves. Lining continued during the period of egg laying. The males often accompanied their mates to the nest: while the female was building the male usually sat nearby, and drove off intruders if necessary. The way in which the moss was arranged in the box was closely similar to that which has already been described for the Great Tit.

At one nest the female collected all the moss for the main structure of the nest from the base of the nest tree. The male inspected the box on a number of occasions: sometimes he actually entered the box, in which

case the female invariably also entered immediately afterwards, though without the wing shivering characteristic of the earlier hole inspection displays; and often then began a period of nest building activity. Occasionally the male inspected while the female was actually inside, and sometimes the female inspected the hole without entering. At another box, to which a female was bringing moss very frequently, the male often flew to the entrance hole with moth- or gliding flight and inspected it. He also flew in this way from tree to tree near the hole, and perched with wings drooped and tail spread. After each flight he held the lateral breast feathers out, so that his body appeared to be dorso-ventrally flattened.

Blue Tits were not seen to tease their nest material in the manner described for Great, Marsh and Willow Tits before carrying it off, but this was probably because the nests are lined with feathers which cannot be treated in this fashion. A Blue Tit female who was interested in a hole occupied by Marsh Tits repeatedly pulled out some of the hair brought by the Marsh Tit and teased it on nearby branch before letting it drop.

Further details of behaviour during nest building have been given by Pullen (1946).

(c) Parus palustris

One nest was watched fairly closely during nest building. The general behaviour was very similar to that which has been described for the Great Tit, and the nest was formed in the same way.

The male often fought with a pair of Blue Tits, who were interested in the hole, while the female was building. On several occasions he inspected the hole after the female had left. Once he was seen to pass

something to the female while she was inside the hole, but unfortunately it was not possible to be certain whether this was food or nesting material.

(d) Other species

Nest Building behaviour seems to be remarkably similar throughout the genus, and will not be further discussed here. It is interesting to note that the teasing out of material, which was seen in the present study in Great, Blue, Marsh and Willow Tits, has also been recorded in the Crested Tit (Ross, 1935) and is probably widespread. A similar action is mentioned by Addicott (1938) in Psaltiriparus minimus.

In the case of those species which excavate their own holes, the chips are often carried to a branch several feet from the nest and dropped there, though there is considerable variation in this respect. The carrying away of chips seems to be rather more common in P. a. atricapillus (Jouard, 1925²⁶, 31, 32; Meares, 1932; Mayr, 1928; Temperley, 1934; Johnston, 1936; Odum, 1941; etc.) than in P. cristatus, (Ross, 1935; Smith, 1941; etc.).

There are numerous records of the covering of the eggs during laying in Parus spp., and it is probably universal. It does not occur in Aegithalos caudatus, (Brown, 1924).

(b) Nest 207 (Visual).

<u>Hour beginning</u> <u>G.M.T.</u>	<u>15th</u>	<u>16th</u>	<u>17th</u>	<u>19th</u>	<u>APRIL</u>		<u>24th</u>	<u>26th</u>	<u>27th</u>	<u>28th</u>	<u>29th</u>	<u>Mean</u> <u>April</u> <u>15th-29th</u>
					<u>20th</u>	<u>21st</u>						
0300		-	-	-		-	-		-			
0400		0	0	0		0	0		0		0	0
0500		7	7	0		2	0		1		1	2.6
0600		1	1	1		3	2		0		1	1.3
0700		7	4	2		0	1		1+		1	2.3
0800		1	1	1		0	1	1	0		1	0.8
0900	4		3	0		0			0	1	0	1.1
1000	4		2	0		1				1	0	1.3
1100				0		0				1	0	0.3
1200				0		0						0
1300				0		0					0	0
1400	0		0	0		0	0				0	0
1500	0		0	0	0		0			0	0	0
1600	0		0	0	0		0			0	0	0
1700	0		0	0	1+		0			0	0	0.1
1800			0	0	0		0			0	0	0

6. Variation in nest-building activity through the day.

In the Great Tit the female visits the nest most frequently in the morning, and only comparatively rarely in the afternoon. There is sometimes a period of activity in the late evening. This is shown for nest 207 (where the records were made visually) and nest 132 (to which a drum recorder was connected) in Table 15. It will be seen that little building was done after mid-morning on most days. Pike (1932) also records that little building is done after 10.a.m. in this species. (It must not be thought that the visits to the nest are always so infrequent as at the nests shown. One Great Tit was seen to bring material over twenty times in an hour, and others have been seen building in the late evening)

Observations made at nests of Blue, Coal and Marsh Tits confirmed that a similar diurnal variation occurred in these species, though no precise data were obtained. Pullen (1946) on the other hand, states that in the Blue Tit the greatest building activity occurs at midday, but no details are given. Ross (1935) writing of excavation in the Crested Tit, says "Work was carried on most actively all the morning, and again in the evening between 5 and 7, while in the afternoon the bird would work for 5 or 10 minutes and then be away for three-quarters of an hour or more". In P. a. atricapillus Odum (1941) records that digging is most intense in the morning. In Aegithalos caudatus Brown (1924) says that building never continues after 3.p.m.: Gait and Tuckett comment that it does sometimes continue after 3.p.m., but at a reduced rate. It thus seems that this sort of diurnal variation in building activity, with building most intense in the early morning, is widespread in the family.

Within this broad daily rhythm of activity, another shorter rhythm can

be distinguished. There is a tendency for the visits to occur in bursts, each of several visits made in quick succession. Between these bursts are occasional visits, or pairs of visits. The subject is discussed in more detail on p. 274.

B. Other Genera.

The details of the nests and nest building behaviour of the other genera of the Paridae can only be given passing mention here. In all cases the nest is domed, but the details of its construction vary greatly.

Members of the genus Aegithalos build a domed nest, whose exterior is woven principally from moss and hair, and covered with spider's webs, lichens, small pieces of bark, etc. The inside is closely lined with feathers, (Savage, 1923; see also Astley, 1923). The form of the nest appears to be very constant for different members of the genus, (La Touche, 1906; S. Baker, 1932; Whitehead, 1907; et al.). Both sexes take part in building, but the female plays a greater part in the shaping of the nest than the male (personal observation). The nest is started as a small platform, the sides being built up all round. The bird stamps material into the platform and shapes the growing walls by turning round and round inside the cup, its tail almost vertical. The entrance is near the top. Occasionally there are two entrances. Further details of nest building are given by many writers, notably d'Abadie (1926), Lintia (1905), Loos (1913), Owen (1945) Tinbergen (1942), Verheyen (1947).

Addicott (1938) has given an excellent description of nest building in Psaltriparus minimus. The nest consists of a bag hanging from twigs with its top covered by a hood. The entrance is near the top, but may be either above or below the supporting twigs. The first stage in building is the construction of a circular horizontal rim supported between the forks of a twig, or between two adjacent twigs. Then a small, loosely woven bag, about 1" in depth, is hung from the rim. This bag is stretched and extended from within, and new material is added to the thin parts. Most of the work is done from inside. Then the hood and final entrance are built. The nest is constructed of "mosses, lichen, oak leaves and spider's webs". The lining is of down or feathers. In some cases, after the building of the rim, a loose bag as much as 8" in depth is added on the second day, and is then stretched and filled in as before: Addicott states that nests built towards the end of the season are usually constructed in this manner. ^{The strength of the nest depends largely on the spider's webs} These are bound into the nest by an up and down movement of the head which seems to be similar to the movement used for the same purpose by Aegithalos spp. Both sexes share equally in the construction of the nest.

The genus Auriparus builds domed nests with an entrance near the bottom and facing downwards. There seem to be some differences between the nests of different races of Auriparus flaviceps: Au. f. ornatus builds its nest principally of thorned twigs, so placed that the nest has the appearance of a hedgehog (Brandt, 1940, quoted in Bent, 1946), whereas that of Au. f. flaviceps is built of fine weed twigs or grass stems, and not protected on the outside by thorns or larger twigs (Bancroft, 1930; Bent, 1946). The nests are typically lined with feathers. The only account of nest-building which has been

found was given by Bancroft (1930) and refers to Au. f. flaviceps.

Unfortunately the description does not make it clear if the initial circle is a horizontal or a vertical one. Brandt (1940) suggests that in Au. f. ornatus the male builds several nests, and the female chooses one of these and lines it, but the account given by Bancroft (1930) of Au. f. flaviceps seems to infer that both sexes take part from the start.

The processes of nest building in the Penduline Tits have most recently been described by Burkhart^c (1948). He shows that in Remiz pendulinus the male first covers a thin forked twig with material, and extends this into a vertical circle, which forms the basis of the nest. Related species, and even the same species in other areas, build nests which differ considerably in appearance, and which are apparently constructed in a different way; though the details of the construction are not yet known. The nest is built of animal and vegetable fibres, but the exact nature of these seems to vary in different areas. The nest is started by the male, who sings in intervals of building and attracts a female: the female may help in the later stages of building.

Although only a brief outline of nest building in these genera has been given, it will be clear that they exhibit great divergences in the type of nest constructed, the technique of construction, the materials used and the parts played by the sexes. Within each genus there is usually great uniformity, though in some cases there are divergences in detail which have not been mentioned above. At first sight it may appear that no homologisation of nest building activities is possible between birds which build their nests from the bottom upwards (Aegithalos) and birds which build from the top downwards (Psaltiriparus); or, amongst the genera which build pendant nests,

between birds which start with a vertical circle (Remiz) and birds which start with a horizontal one (Psaltriparus). Unfortunately we have as yet practically no knowledge of the details of nest building in these genera - that is of the stereotyped movements (instinctive acts in Lorenz' sense) which are used in building. It is at this level that we may hope to see homologies between the different genera. It is, however, already clear that the genera Aegithalos and Psaltriparus show certain similarities in the parts played by the sexes, in the materials and lining used, in the first stage in the building, and in the relation of nest building to environmental factors; although the ways in which the nests are supported are very different. These two genera are already known to be closely related on morphological grounds.

SECTION XVI: EGG-LAYING AND INCUBATION

A. Eggs and Egg-laying.

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3. Time of laying.
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SECTION XIII EGG-LAYING AND INCUBATION

A. Eggs and Egg-laying.

1. Eggs.

The eggs of all members of the Paridae are extremely similar, being white or whitish, with little gloss, and speckled with red brown spots which are usually denser at the larger end. In some cases there is a tendency for the spots to be reduced: thus P. gambeli abbreviatus lays eggs which are usually pure white, but sometimes have a faint speckling of reddish brown, and P. gambeli grinnelli lays pure white eggs (Bent 1946). Similarly in P. inornatus, P. wollweberi and Psaltriparus minimus the eggs are often unmarked. The eggs of Aegithiliscus cocinnus iredali vary from pure unmarked white to pink with a dense dark ring of reddish brown (S. Baker, 1922). The actual shade of white varies from grey-white to pinkish-white in the different species. Similarly the spots vary in size, shape and shade, and some species (e.g. P. cinctus, P. minor; La Touche, 1906: P. varius; Ingram, 1908: P. venestulus; La Touche, 1925-30) have spots of more than one shade of red on the same egg. In the genus Auriparus the ground colour has a greenish or bluish tinge (Bent, 1946).

2. Sequence of laying.

All species normally lay an egg a day. In the Great Tit departures from this rule are unusual: Delm   (1940), Mocek (1939) and Verheyen (1947) found that such gaps as do occur to be commoner after the first egg, or at

least early in laying, than later. Moock says that the same is true of Blue and Coal Tits. Gibb (in litt.), on the other hand, found that gaps may occur at any stage. Kluijver (in litt.) found that gaps are rather more frequent in Blue than in Great Tits. Cases of more than one egg laid in one day are rare, but have been recorded in the Great Tit (Verheyen 1947) and Blue Tit (Gibb, in litt.). Gibb remarks that one of the eggs was a marked runt.

3. Time of laying.

Eggs of Great and Blue Tits are nearly always laid before the dawn emergence of the female. When the female first emerges the eggs are exposed, but are soon covered up with lining material brought by the female in the early hours of the day (personal observation). Zollinger (1930) also noted that the eggs of the Great Tit are laid in the early morning, as did Odum (1941) in the case of P. a. atricapillus.

4. Season of laying.

In the Great Tit there is much variation in the stage of nest building at which the first egg is laid. In the present study it was usually found that the nest-lining had either just been started or nearly completed, but sometimes there is a gap between the completion of the nest and the laying of the first egg. (cf. also Zollinger, 1930). It is thus clear that egg laying does not invariably follow nest building after a fixed interval. It would thus seem that nest building is, at most, only one of the factors influencing the start of egg-laying. Similar considerations apply to the Blue Tit. Information on other species is meagre, but Odum (1941) records

an interval of two days between the completion of the nest and the laying of the first egg at one nest of P. a. atricapillus.

The influence of the season on the date of egg-laying is discussed in detail by Kluijver (in litt.) and Suomalainen (1937). Gibb (in litt.) found that laying was so timed "that the period with the maximum number of tit nests with young corresponded very closely with the period of greatest abundance of moth larvae, Chaematobia brumata and Hibernia defoliara".

5. Behaviour during egg-laying.

Great, Blue and Marsh Tits seldom visit their nests during egg-laying except to bring lining material during the early part of the day. From about 1100 hours on, it is rare to see the pair near the nest. The female roosts on the nest, and the behaviour of the male at the nest at dawn and dusk is described on page 267. During the day the pair keep in close company, feeding in the territory. Sexual fighting is less common than in the previous weeks, as most pairs are already settled and the territories are established. The male sings from time to time, and courtship feeding is common.

Similar behaviour is recorded for P. inornatus by Dixon (1949) and for P. a. atricapillus by Odum (1941), though the latter author describes courtship feeding as being less common than it is during incubation.

B. Incubation - General.

1. Share of the sexes.

In the genus Parus incubation is carried out by the female alone. The only possible exceptions to this rule are P.atricristatus where a male is said

to have been taken on the nest, and males are said to have brood patches (Sennett, 1879, in Bent, 1946); and P. carolinensis (Bent, 1946). Other records of males incubating are inadequately substantiated.

The same is true of the genera Remiz and probably of Auriparus, but in Psaltriparus (Skutch, 1935; Addicott, 1938) and Aegithalos both sexes incubate, though the female takes a greater share than the male.

2. Behaviour during incubation.

Incubation may start before ^{or} after the clutch is complete (Zollinger 1930; Gibb, in litt.). In the Great, Blue, Coal and Marsh Tits the female incubates for periods of about 20-30 minutes and then leaves the nest for periods of about 8 minutes (see p. 117). When sitting on the nest the female holds the tail vertically, not spread: the tail is often pressed against the side of the cavity, but it is held vertically even when the bird is well away from the walls. During the periods on the nest the female is fed periodically by the male, either on the nest, at the entrance hole, or nearby. The food which she receives in this way is quite inadequate to sustain her, and she also feeds herself during her periods off the nest. During these periods off the nest, the female is also fed by the male; she begs with the zeedling call and shivering wings described above (see p. 146).

(a) Parus major

During the first few days of incubation the male remained fairly close to the nest, but later he ranged widely over the territory while the female was sitting. When the male approached the nest to feed the female he did not enter directly, but hesitated outside and called. The actual call used varied greatly - usually a few 'twinks', sometimes (especially later in

incubation and during brooding) a few notes of song, sometimes a 'chich ich ich', a soft 'zee zee zee', or sometimes a soft call which was inaudible to the observer ten yards away. These calls sometimes caused the female to leave the nest, in which case the male fed her outside, but on other occasions she remained inside the box and the male fed her at the entrance or inside. It usually happened that if the male arrived with food soon after the female had commenced a period on the nest, she did not leave but was fed on the nest; if, on the other hand, the male arrived later, the female emerged and was fed outside. Owing to the difficulty of being certain on all occasions whether or not the female had been called off the nest, an exact analysis of this point is not possible. The male often sang just after the female had entered the nest-box.

In Table 16 are shown, for two nests, the number of times that the male fed the female inside the box or at its entrance. Occasions when the male fed the female outside the box are not included as it was impossible for a stationary observer to follow the movements of the female in the open all the time. The figures for nest 207 were obtained by direct observation. Those for nest 132 were obtained with the automatic recorder, each visit of less than one minute's duration being assumed to be a visit of the male. This latter assumption was found to hold good over several hours visual observation. It will be seen that:-

- (1) There was a marked difference between the two males in the frequency with which they fed their females on the nest. The existence of such variability between individuals was confirmed by casual observation at other nests.

(ii) At nest 132 the male visited most frequently on the third day of incubation, and thereafter the frequency of his visits decreased. No such tendency was apparent at nest 207.

(iii) At both nests the greatest number of visits occurred in the early part of the day, with a peak at about 0600-0700 hours. This peak could be due either to greater feeding activity on the part of the male, or to greater unwillingness on the part of the female to leave the nest, so that a higher proportion of feedings took place inside the box. It will be shown (p.199) that the length of the periods-on of the females in one case increased, and in another decreased, in the afternoon; but in neither case were the differences sufficiently great to account for this result. It must thus be concluded that the differences are due to differences in the strength of the drive of the male during the day. It will be noted that there is an indication of a second peak during the afternoon at nest 132.

Kluijver (in litt.) gives figures for P. m. major very similar to these, and states that feeding is "most frequent in the morning, with a second but smaller peak between 2 and 4 p.m."

At both nests the visits of the male with food occurred most frequently just after the female had entered to start a period-on: a similar observation has been made for the Blue Tit by Pullen (1946). This is presumably due to the 'after-reaction' (see p.297): the male is stimulated to feed the female while she is off the nest, and the feeding drive does not die away as soon as the female starts to incubate.

Table 16. Great Tit. Visits of the male to the nest during incubation.

(a) Nest 207. (Visual).

<u>Hour beginning.</u>	<u>April</u>		<u>1st</u>	<u>2nd</u>	<u>May</u>		<u>10th</u>	<u>Mean</u>	
	<u>29th</u>	<u>30th</u>			<u>4th</u>	<u>7th</u>		<u>April 30th to</u>	<u>May 10th.</u>
0400	0	0		0	0	0	0	-	
0500	0	0		2	0	0	1	0.6	
0600	0	2		0	1	0	2	1.0	
0700	0	1		2	2	1	0	1.2	
0800	0	0		0	0	0	1	0.2	
0900	0	0	0		0	0	0	0	
1000	0		0		0	0	0	0	
1100	0		1					-	
1200				0				-	
1300	1		1	0	0	0	0	0.2	
1400	0		0	0	0	0	0	0	
1500	0		0	0	0	0	0	0	
1600	0		1		1	0	0	0.5	
1700	0		0		0	0	0	0	
1800	0		0		0	0	0	0	

(b) Nest 132. (Recorder).

<u>Hour beginning.</u>	<u>April</u>		<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>May</u>		<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>	<u>Mean.</u>
	<u>29</u>	<u>30</u>						<u>6</u>	<u>6</u>						
0400								1		0	3	1	0	1.0	
0500		3	2	1	6		0	0		0	1	1	2	1.6	
0600	2	6	4	2	3		3	4		0	1	3	0	2.5	
0700	2	1	2	0	1		1	1	0	0	1	0	1	0.8	
0800	1	2	6	1	6		1	2	0	1	0	0	1	1.8	
0900	2	2	0	1	1		0	0	0	0	1	0	0	0.6	
1000	0	0	0	0	1		1	0	1	1	0	0	0	0.3	
1100	0	1	0	1	1	1	0	1	0	0	1	0	0	0.2	
1200	1	0	2	1	0	2	1	1	2	0	0	0	1	0.9	
1300	1		1	0	0	0	3	0		0	0	0	1	0.5	
1400	0		3	0	0	0	2	0		1	1	0	0	0.6	
1500	0		4		4	1	0	0		1	0	1	0	1.1	
1600	0	1	3		0	0	0	1		1	0	0	0	0.5	
1700	2	2	2		1	0	0	1		0	0	0	1	0.8	

The female usually entered the nest silently, but rarely she called 'twink' or 'chich ich ich' or sang a few notes before entry. On emergence the female usually called in some way: often she sang a four or six note song outside the box before flying off, which occasionally seemed to serve as a directive call to the male, but more often caused him to answer with 'twinks', towards which she flew. Often the female 'twinked' as she emerged: this had a similar effect on the male. Occasionally she called with a soft 'chich ich ich'.

Incubation of the eggs passed smoothly into brooding of the young and both should be regarded as manifestations of the same drive.

(b) Parus caeruleus, ater and palustris

Casual observations were made at two nests each of Blue and Marsh Tits and at one nest of a Coal Tit. The general behaviour was very similar to that which has already been described for the Great Tit. In all species the male usually accompanied the female to the vicinity of the nest at the beginning of a period-on, and fed her most frequently just after she had entered. The male Blue Tit called 'Drrrrtttt' as the female entered the nest. On the occasions when the male was heard to call the female off, he used a soft 'tsit tsit' call. Pullen (1946) records that a female Blue Tit started to incubate on the afternoon of the day before the last egg was laid. The amount the cock fed the hen on or near the nest decreased as incubation progressed.

Morley (1949) states that, in the Marsh Tit, the visits of the male to feed the female on the nest become less frequent in the second week of incubation, though fairly rapid feeding of the female on emergence continued.

Morley describes the behaviour of the male whilst approaching the nest and feeding the young. A similar description is given by Steinfatt (1938)

(c) Parus atricapillus

The behaviour of this species during incubation is closely similar to that which has been described above. Odum (1941) remarks that the male plays only a limited role in controlling the behaviour of the female: if the female has been on the nest only a few minutes when the male returns, she is usually fed at the nest and returns to incubate, but if she has been sitting for ten or fifteen minutes or more, she may leave the cavity before or immediately after receiving food from the male. (See also Jouard, 1926, 1932, 1933; and Temperley, 1934).

(d) Other genera

In Aegithalos and Psaltriparus both sexes incubate. The female often takes a rather larger share than the male (personal observation; Loos, 1913), but Addicott (1938) states that in Psaltriparus the shares of the sexes are about equal, though the female develops a brood patch and the male does not. The periods on the nest seem to be shorter in Psaltriparus minimus than in the other genera - Addicott gives an average of ten minutes, and Skutch (1935) records that the sitting bird is sometimes relieved as often as every three or four minutes, and on warm days the birds often leave the nest unoccupied for quite long periods: these observations, however, were made in the tropics.

In Remiz the female alone incubates, the male starting to build another nest. Little seems to be known of incubation in the genus Auriparus. Kozlova (1933) state that the male of Remiz pendulinus stoliiskae feeds the incubating female.

C. Incubation: Periods on and off the Nest.

1. Parus major.

(a) Method of study

One nest (Box 207) was kept under visual observation for c.130 hours, while the female was sitting. The greater part of this time was during the days immediately following the onset of incubation, and those following the hatching of the eggs. An automatic recorder was attached to another nest (Box 132) and gave a reliable record for c.185 hours (excluding the hours between roosting and morning emergence) between the onset of incubation and the hatching of the first egg. The automatic recorder was also used at a third nest for c.35 hours (Box 148). Scattered observations, made both visually and with the recorder, were made at a few other nests. At the nests where the recorder was used, a trigger was fitted to the entrance of the nest box in such a way that a contact was made every time that the bird entered or left: at each contact a mark was made by one of two pencils (in and out) on the drum of the recorder.

(b) Normal incubation

Incubation during the period between the time when the incubation rhythm became fully established and the hatching of the first egg will be considered first. The average periods on and off the nest during this time are given in Tables 17 and 18 .

Table 17. Incubation: periods on the nest.

<u>Box</u>	<u>Period of observation</u>	<u>Total of periods-on. mins.</u>	<u>No. of periods.</u>	<u>Average period-on.</u>	σ
132	April 30th to May 11th.	6838	191	35.8	11.75
207	May 4, 7 and 10."	1432	46	31.2	14.5
148	May 12th to 15th.	1628	53	30.7	13.0

Table 18. Incubation: periods off the nest.

<u>Box</u>	<u>Period of observation</u>	<u>Total of periods-off. mins.</u>	<u>No. of periods.</u>	<u>Average period-off.</u>	σ
132	April 30th to May 11th.	1593	200	7.96	3.60
207	May 4, 7 and 11th.	261	46	5.7	1.54
148	May 12th to 15th.	536	59	9.1	2.5

The high values of σ (the standard deviation) show that the lengths of both the periods-on and of the periods-off were highly variable. In fact, the periods-on varied from 4 to 98½ minutes, and the periods-off from 2 to 22 minutes.

The periods-on of the females of Boxes 148 and 132 are significantly different; and those of the females of Boxes 132 and 207 are just not

significantly different. Both differences between the periods-off of the females are significant. Kluijver (in litt.) gives an average period-on of 27.6 mins (1st brood) and 26.2 (2nd brood) and average periods-off of 7.9 mins (1st brood) and 10.9 (2nd brood) for P. m. major.

These figures have been analysed in more detail in order that the change in incubation through the day might be studied. In the cases of Boxes 132 and 148 the day was split into four periods; dawn to 0800 G.M.T., 0800 to 1100, 1100 to 1400 and 1400 to roosting time. The records for Box 207 had to be subdivided rather differently to coincide with the periods of observation, and the day was split into the periods dawn to 0800, 0800 to 1000, 1300 to 1600 hrs. At all nests the periods-off were longer in the afternoon than in the morning, but the periods-on showed different trends at different nests.

The average period-on of the female of Box 132 decreased to a minimum in the afternoon and rose again in the evening; her periods-off rose to a maximum in the afternoon and decreased in the evening (see Table 192b). The differences are, however, in no case significant. At nest 148 the periods-on decreased to a minimum in the afternoon, and the difference between the dawn to 0800 and 1100 to 1400 periods is significant. The periods-off increased to a maximum in the afternoon, but the differences are not significant. The female of Box 207, however, showed a different tendency. The average period-on at this nest increased throughout the day, the difference between the first and second part of the day being significant and that between the second and third just not significant. The periods-off at this nest also increased in length throughout the day, but the differences are not significant.

Table 19. Incubation; periods-on through the day.

<u>Nest</u>	<u>Period of day</u>	<u>No. of periods.</u>	<u>Average length.</u>	<u>T</u>
132	dawn-08	50	37.7	11.6
	08-11	45	34.4	13.5
	11-14	47	33.7	10.9
	14-Rst.	49	37.3	13.6
148	dawn-08	12	35.5	6.2
	08-11	9	33.8	7.6
	11-14	12	27.1	6.2
	14-Rst.	20	28.6	7.1
207	dawn-08	20	23.2	7.7
	08-11	14	32.3	10.5
	13-16	12	42.9	18.1

Table 20. Incubation: periods-off through the day.

<u>Nest</u>	<u>Period of day</u>	<u>No. of periods.</u>	<u>Average length.</u>	<u>T</u>
132	dawn-08	51	7.6	3.7
	08-11	45	7.8	3.4
	11-14	46	9.0	4.6
	14-Rst.	58	7.7	2.9
148	dawn-08	12	8.3	1.1
	08-11	11	9.0	1.3
	11-14	13	9.2	2.4
	14-Rst.	23	9.4	3.1
207	dawn-08	20	5.1	1.4
	08-11	14	5.6	1.7
	11-14	12	6.8	0.82

Table 21. Minutes per hour spent on nest by female during early part of incubation. Squares left blank indicate times when no observations were made. In cases where only part of the hour period was covered, either because the female was roosting or for other reasons, the square is divided with the minutes incubated in the top left corner and the minutes of observation in the bottom right.

(a) Nest 132. (Recorder).

Hour beginning G.M.T.	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18
April 27th	$\frac{0}{2}$	0	0	0	0	0	4	0	0	0	0	0	0	$\frac{0}{27}$	
28th	$\frac{0}{17}$	0	5	0	0	0	0	0	0	30	30	21	0	$\frac{0}{35}$	
29th	$\frac{0}{5}$	0	0	0	45	31	13	0	51	13	0	0	0	$\frac{15}{26}$	
30th	$\frac{25}{27}$	45	46	41	44	42	44	40	34	47	-	-	51	51	$\frac{7}{13}$
May 1st	$\frac{0}{9}$	43	48	53	40	49	51	39	-	50	45	38	-	51	$\frac{18}{23}$
2nd		50	47	49	46	47	48	43	54	41	44	-	-	-	

(b) Nest 207. (Visual).

Hour beginning G.M.T.	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18
April 28th					0	0	0	0				27	0	$\frac{6}{51}$	
29th	$\frac{2}{19}$	$7\frac{1}{2}$	0	0	0	0	0	0	$\frac{21}{30}$	31	42	36	25	$\frac{32}{48}$	
30th	$\frac{16}{21}$	24	43	36	37	$\frac{13}{30}$									
May 1st					$\frac{16}{30}$	41	50	-	44	51	48	51	$\frac{31}{50}$		
2nd	$\frac{1}{7}$	54	45	36	49	$\frac{17}{30}$	-	-	$\frac{22}{30}$	38	49	35			

Kluijver (in litt.) found a significant correlation between the minutes incubated per day and the temperature.

(c) Onset of incubation

Kluijver (in litt.) found that incubation in the Great Tit starts in the afternoon, and that the greater part of the incubation takes place in the afternoon for the first few days. Exactly the same conclusion was reached in the present study. In Table 21 are shown the minutes incubated per hour by the female during the first six days after the onset of incubation at two nests. The record for nest 132 is reasonably complete, and shows the point clearly. The visual observations at nest 207 are less complete but also illustrate the point.

Incubation did not start gradually, with the periods-on the nest gradually increasing in length, but more or less abruptly with the early periods-on averaging as long as those later on. The actual lengths of the periods-on for the first two days are shown in Table 22.

Table 22. Length of periods-on at start of incubation.

<u>Date.</u>	<u>Nest 132.</u>		<u>Nest 207.</u>	
	<u>Period-on began.</u>	<u>Duration.</u> <u>(in mins.)</u>	<u>Period-on began.</u>	<u>Duration.</u> <u>(in mins.)</u>
April 28th	0622	5	1527	27
	1330	44		
	1444	37		
	(Average)	(29)		
29th	0405	18	0458	9
	0833	29	1238	21
	0918	29	1307	31
	1027	13	1400	32
	1200	33	1450	22
	1242	31	1524	22
	1700	15	1558	13
	(Average)	(24)	1613	14
			Av 1703	22, 32

(d) Cessation of Incubation

The automatic recorder trace could not be used to assess incubation during this period as the entries of the female for brooding could not be distinguished from the visits of the male with food. Thus the records from Box 207 only are available.

In Table 23 are given the minutes incubated per hour on successive days after the hatching of the eggs. On each day the minutes incubated in any one hour are in general less than those in the corresponding hour on the previous day. For each particular day there is less incubation per hour in the early afternoon than in the morning or evening.

Table 23 . Mins incubated per hour. First egg hatched in early morning of May 12th.

Hour beginning.	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19
May 12th		54	54	54	51	53	47			47	39	48	54	48		
13th		46	47	46	50	46	40		39	41	33	44				
14th	38	32	42	29	55	36	15			34	24	43	23	14	42	
15th		43	34	28	32	31					23					
17th		19	17	7	12	6	1		8	8	6	22				

The reduction in incubation could be due to shorter periods-on the nest, longer periods-off the nest, or both. In order to investigate this, each day's observations were divided into four periods, and the average periods-on and -off the nest for each period of the day calculated. These are shown in Table 24. Since the periods on and off varied greatly, too much reliance cannot be placed on averages, but the following relations appear. The average periods-on the nest decrease and the periods-off the

nest increase on successive days for all portions of the day. There is no regular difference between the periods-on during the different portions of the day, but the periods-off are regularly longer in the early afternoon than in the morning or evening. It thus seems that the reduction in incubation in the early afternoon is due primarily to an increase in the lengths of the periods-off, whereas the reduction in the amount of incubation on successive days is due both to a decrease in the lengths of the periods-on and an increase in the lengths of the periods-off, the former being the more important. In this respect it may be noted that Kluijver found a greater coefficient of correlation between temperature and the lengths of the periods-off than with the periods-on.

Table 24. Brooding. Average periods-on and -off at Nest 207.

(a) Average periods-on.

Date.	<u>12th</u>	<u>13th</u>	<u>14th</u>	<u>15th</u>	<u>17th</u>	<u>18th</u>
Dawn-08	34.7	25.1	13.7	12.0	5.1	
08-11	37.7	28.0	18.4	10.3	3.4	
13-16	33.2	17.6	22.6	8.1	6.8	
16-Rst.	35.0		9.3			3.8

(b) Average Periods-off.

Dawn-08	3.8	7.5	9.5	8.9	17.0	
08-11	7.4	9.0	12.5	10.6	25.5	
13-16	9.2	10.3	14.0	15.0	28.4	
16-Rst.	8.3		13.0			21.5

2. Other Species.

The observations of other authors on the rhythm of incubation in Parus species are summarised in Table ~~XXI~~ 25

Table 15. Observations on rhythm of incubation in other species of Parus.

<u>Species.</u>	<u>Periods-on</u>			<u>Periods-off</u>			<u>Authority.</u>
	<u>No.</u> <u>recorded.</u>	<u>Range</u> <u>(mins).</u>	<u>Average</u> <u>(mins).</u>	<u>No.</u> <u>recorded.</u>	<u>Range</u> <u>(mins).</u>	<u>Average</u> <u>(mins).</u>	
<i>P.a. atricapillus</i>	15	15-36	26	16	2-10	5.6	Odum 1941
<i>P.a. atricapillus</i>	7	6-48	23	9	3-23	9.6	Odum 1941
<i>P.a. atricapillus</i>	7	11-61	22	8	7-11	8.3	Odum 1941
<i>P. palustris</i> (12th day of incubation).	17	5-73	37.9	17	2-15	7.1	Steinfatt 1938.
<i>P. palustris</i> (young 1 and 2 days old).	26	1-46	17.4	26	1-8	3.2	Steinfatt 1938.
<i>P. inornatus</i>	6	-	28.5	9	-	8.5	Dixon 1949.
<i>P. caeruleus</i>	-	8-37	15	-	7-14	5	Pullen 1946

SECTION XIV CARE OF THE YOUNG.

A. Hatching of the Eggs.

1. Hatching.
2. Removal of addled eggs and dead young.
3. Brooding.

B. Feeding the Young in the Nest.

1. Parus major.
 - (a) General behaviour
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 - (a) General behaviour
 - (b) Daily variation in feeding activity
3. Parus palustris.
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5. Other genera.

C. Eggs or Young of more than one Species in the Nest.

D. Nest Sanitation.

1. Parus major.
2. Other species.

E. Fledged Young.

1. Leaving the nest.
2. Second broods.
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 - (a) Parus major
 - (b) Parus caeruleus, ater and palustris
 - (c) Other species
 - (d) Other genera
 - (e) General

SECTION XIV CARE OF THE YOUNG.

A. Hatching of the Eggs.

1. Hatching.

Two nests of Great Tits were under observation during the period of hatching of the eggs. In each case the first egg hatched in the early morning: both parents showed great activity soon after the dawn emergence, flying in and out of the nest hole. Most of these visits were without apparent purpose and nothing was brought or taken away; but on some of them portions of egg-shell were removed. Nethersole-Thompson (1942) states that all the British Parus species carry away the large portions of egg-shell. At another nest, to which an automatic recorder was attached, the first eggs hatched at about 1500 hours. The male increased the frequency of his visits as soon as the first eggs hatched.

Hatching of the eggs was normally spread over about two days. Steinfatt (1938) states that in P. palustris the egg-shells are eaten.

2. Removal of addled eggs and dead young.

Addled eggs and dead young are sometimes removed from the nest by the adults in the Great Tit (Ryves, 1929, 1930; Musselwhite, 1931; Buxton, 1945; Gibb, in litt.), Blue Tit (Alexander 1929; Ryves, 1929 and 1930; Dagley, 1929) and Long-tailed Tit (Owen, 1945b). Sometimes however, eggs or dead young are merely trampled into the bottom of the nest (personal observation).

3. Brooding.

(a) Parus major

Incubation changes smoothly into brooding. The female continues to brood the young for about a week after the hatching of the first egg - occasional brooding may last even longer than this (see p.203).

Although the female is mainly responsible for bringing food to the young at this stage, the female sometimes, but not always, brought food at the beginning of a period-on. As the amount of brooding decreased, the female brought food without staying to brood.

During the first few days after the hatching of the first egg at Nest 207, and especially just afterwards, the male frequently pecked at the ^{nest} ~~entr~~ hole when bringing food. Sometimes he spent several minutes inside working at the entrance. The female was not seen to do this. Throughout nesting the male experienced a certain amount of difficulty in getting through the hole, whereas the female slipped through easily: thus this behaviour may have been a real attempt to enlarge the hole.

(b) Other species

Odum (1941) records that in P. a. atricapillus brooding stops almost entirely during the final week of nest life.

Table 26 . Feeding of young in nest. Share taken by male at Nest 207. Only visits to the nest with food are included. The number of visits refer to the number during the period of observation only, not to the number during the whole day.

Age of oldest nestling in days.	$\frac{1}{2}$	$1\frac{1}{2}$	$2\frac{1}{2}$	$3\frac{1}{2}$	$5\frac{1}{2}$	$6\frac{1}{2}$	$12\frac{1}{2}$	$13\frac{1}{2}$	$17\frac{1}{2}$	$18\frac{1}{2}$
Visits by male.	122	134	199	114	187	76	67	166	31	90
Visits by female.	0	3	12	6	32	15	12	23	10	29
% by male.	100	98	94	94	85	84	85	88	76	76

B. Feeding the Young in the Nest.

1. Parus major.

(a) General behaviour

During the first few days after the young hatch, the female is primarily concerned with brooding, and the male brings nearly all the food for the young. As the amount of brooding decreases the female starts to bring food to the nest during her periods-off, and the amount of food she brings increases on successive days after this. At nest 207, however, the male continued to play the predominant part in the feeding of the young up to the time of fledging: at no time was the female recorded as visiting the nest more than seven times in an hour. Table¹⁶ shows the percentage share of the male on different days at this nest. Casual observations at other nests confirmed that the male plays a greater part than the female, but there is undoubtedly much individual variation in this respect, and several factors are probably involved. Zollinger (1930) noted that a male of P. m. major fed more zealously than the female. Kluijver (in litt.) gave details of the shares taken by the sexes at two nests and showed that that of the male decreased during the first few days after the eggs hatched. At one nest the share of the male decreased from 96 to 35%: at the other it was apparently only about 59% on the first two days but increased to 78% on the third, and thereafter decreased to a minimum of 37%. An individual of either sex may take over the complete care of the young if an accident should befall its mate.

When visiting the nest whilst the female was brooding, the male usually sang or called before entering, and could be seen looking into the

entrance of the nest from an adjacent bough, presumably to see whether or not the female was sitting (cf. incubation). This behaviour continued throughout the whole of the period for which the young were in the nest, though later the amount of hesitation grew less and he often entered without calling. The female rarely hesitated just outside the nest, but flew straight in from 6 feet or more away. If the male did arrive whilst the female was brooding he usually took the food into her just the same, but on occasions waited outside until the female had emerged.

Although the female did not hesitate immediately outside the hole, she often sat for quite long periods near the top of the tree, several feet above the nest, where she gave the seedling call and shivered her wings from time to time. Sometimes she sat thus, with food in her bill, while the male came and went several times, before she entered. On such occasions she would shiver her wings and seedle each time the male approached, just as she did when begging for food in courtship feeding. On only one out of the many occasions when this behaviour was seen did the male show any reaction, and then only a slight wing-shivering: usually he entered the box with his food directly and flew straight away on emergence. Even if the female was actually moving towards the hole when the male arrived she would sometimes turn and pursue him with begging cries. When the male entered the hole the intensity of the female's begging diminished: it usually increased slightly when he emerged and then died away again rapidly: the female then usually entered with her food. Towards the end of the period when the young were in the nest the female's hesitancy increased. On one occasion she sat above the hole for 16 minutes holding a caterpillar: during this time

the male visited the nest four times and the female begged at each visit: on another, the female hesitated for 32 minutes but was out of sight for much of the time and it was not possible to see if she begged each time the male came. Sometimes the female sat outside for several minutes with food and then flew off. During this latter part of the period the reaction of the hesitating female to the male seemed to change, and although she still begged, she sometimes flew off a little way when he approached. The female at nest 207 continued to beg from the male until at least the day on which the young flew. This begging on the part of the female was presumably due to the return of a readiness to mate for a second brood, although this readiness was not shared by the cock, and no second broods ^{was} were, in fact, laid. A few other instances of wing-shivering were seen in the next few weeks. Thus another female shivered her wings a little when scolding a stuffed Sparrow Hawk five days after her young left the nest, and the same bird, seventeen days later, was again seen to give a shivering display - though in this case the shivering was not very vigorous and the bird sometimes preened her breast at the same time as she shivered her wings. A male was seen to shiver his wings near a stuffed Sparrow Hawk about a week after his brood flew.

The begging cries of the young in the nest can often be heard from a distance of several yards, but they cease immediately in response to the 'chick & chick' alarm call of the parent.

The young were fed predominately with caterpillars. Before the parents brought the caterpillar to the nest they held it with a claw against a bough and opened the skin. Each parent brought only one caterpillar at a time. Promptov and Lukina (1938) say that one caterpillar may be shared between several young.

Table 27 . Number of feeding visits per hour by both parents.

(a) Box 148. Young hatched May 17th-18th.

Hour beginning G.M.T.	18th	19th	20th	21st	22nd	23rd	24th	25th
0300	-	1.5	0.5	1.5	5.5	-	-	-
0400	5	11	12.5	15	14.5	-	23	37
0500	10	10	6	15.5	12	28	30	40
0600	9.5	5.5	10	12	9.5	7.5	-	31
0700	4.5	9	10	13.5	19.5	-	-	31.5
0800	3.5	6.5	12	24	15	-	21.5	19.5
0900	8	5.5	12.5	12	14	29.5	33.5	37.5
1000	6	9	15	16.5	19	17	25	37
1100	8.5	11	7	10	12.5	16.5	31.5	30
1200	1.2	11.5	5.5	16	10	15.5	20	26
1300	7.5	6	11.5	13	3.5	20	24	23
1400	11.5	16.5	9	10	16	13	19.5	34
1500	13	18	16	5	7	15	38	-
1600	16.5	14	13	19	12	33	22.5	-
1700	15.5	6.5	15	22	17.5	15	18	-
1800	9.5	12	21	7	24.5	10.5	37.5	-
1900	1	-	-	0.5	1.5	-	5	-

(b) Box 179. Young hatched May 19th-20th.

Hour beginning G.M.T.	26th	27th	28th	29th	30th	31st	1st	2nd	3rd	4th
0300		-	-	-	12	-	-	1.5	-	-
0400		16	-	22.5	20	20	-	21	12	12
0500		22.5	-	33	26	27	-	20.5	10	16
0600		20.5	-	22	28	15.5	-	27.5	36	17
0700		29.5	-	26	20	21	-	25	24	11
0800		18.5	-	25	37	36	-	16	35	42
0900		19	-	17	37	40	-	36	29	25
1000		22	-	20.5	29	38	-	14	20	52
1100	23	25	-	29.5	15	24	19.5	24	24.5	39
1200	29	21.5	33.5	33	30	17	28	29	20	30
1300	13	-	20	26	11.5	20.5	20	23.5	23.5	22
1400	25	-	24.5	27	23	7	20	15.5	26	40
1500	18	-	26	15	32	18	24	21.5	22.5	35.5
1600	31.5	-	32.5	26	16	-	33	38	17.5	30.5
1700	24.5	-	21	23	45	-	11	35	20	15
1800	16.5	-	36	17	36	-	25.5	23	4.5	34
1900	3.5	-	-	6	8	-	7.5	6	-	6

(b) Daily variation in feeding activity

Records ~~were~~^{fe} obtained from two nests of Great Tits with the drum recorder. This does not, of course, differentiate between visits of the male and the female, and so only totals of visits by both parents are available. These are shown in Table 27. There were only slight indications of regular diurnal variation in feeding activity. At nest 148 the rate of feeding was usually below average in the early morning, reached a peak at about 0700 hours, decreased somewhat in the afternoon and reached a second peak in the evening. During the first few days after the first young hatched more food was brought in the evening than in the morning, but later this was reversed. At nest 179 the rate of feeding was again below average in the early morning, and above for the next few hours, but there was little regularity in the variation in the rest of the day.

Kluijver (in litt.) found that in all pairs studied the maximum activity occurred in the morning, before 1200 hours. This was followed by a definite minimum in the afternoon and a second maximum in the evening which was always smaller than the morning peak. The present study thus presents less clear-cut but generally similar results to those obtained by Kluijver, except that at nest 148 the evening peak was often higher than the morning one, and at nest 179 this was the case on some days, whilst on others the evening peak was almost non-existent. Kluijver also states that the time of the minimum may vary on different days, even for the same brood, and this was also borne out by the present results. Kluijver, however, found that the feeding activity at the afternoon minimum was always about 60% of the morning maximum: this was not the case at either of the nests studied here, where the minimum frequency (in feeds per hour) was sometimes as low as 18% of the maximum.

2. Parus caeruleus.

(a) General behaviour

Casual observations at a few nests indicated that the general behaviour of the adults when feeding the young was closely similar to that which has been recorded for the Great Tit. Detailed observations are given by Pullen (1945 and 1946).

(b) Daily variation in feeding activity

MacGillivray (1839) quotes the results of a day's watch on the nest of a Blue Tit by a Mr. Weir, who counted the number of feeding visits per hour at a nest containing six young. A first peak of 40 was reached between 0500 and 0600; between 0700 and 0800 the rate of feeding was depressed to 20 and in the two succeeding hours rose to 36 and 46. During the afternoon the rate of feeding was rather slower, ranging from 18 to 34. A similar all day watch was made by Bergman (1946): the feeding frequency reached a peak in the late morning.

Similar data is given by Pullen (1946), who found that the morning hourly rates were usually above the average for the day, with low figures in the afternoon and evening; the highest rate was usually reached three or four hours after sunrise. His figures show indications of an evening peak on some, but not all, days.

Verheyen (1947) quotes some observations of Briede and van Gogh who found that the visits of the parents were at first most frequent in the evening, and only became equal in the morning and evening later in the fledging period. This agrees with the observations made on P. major at Box 148 in the present study.

3. Parus palustris.

A few observations made in the present study showed that both sexes fed the young, but further details were not obtained.

Steinfatt (1938) gives details of an all day watch on a nest containing 7 young of 8-9 days old. The female fed 85 times to the male's 110. A first peak of 17 feeds per hour was reached in the fourth hour of the day, but there was a second peak of 21 between 1200 and 1300 hours, though during the rest of the afternoon the adults only visited 9-13 times per hour.

Morley (1949) mentions that a female of this species brought practically no food to the nest during the first few days of the nestling's life.

4. Other Parus species.

In all other Parus species for which data are available both parents help to feed the young, but there is little reliable information on the shares of the sexes. The only case where there seems to be any doubt on this point is P. cristatus scoticus, where the observations of Smith (1941) that both sexes share more or less equally, contradict those of earlier authors that the female is mainly or entirely responsible. No doubt other species are subject to a variability in this respect similar to that which has been shown to exist in the Great Tit.

In P. a. atricapillus Odum (1941) found a similar hesitancy on the part of the male on entering the nest during the early days of incubation, to that which has been described above for the Great Tit. In the days after hatching the male brought food more often than the female, but later the

shares became equal.

Wing-shivering displays by the parents during the feeding of the young are known in P. gambeli (Bent, 1946), P. ater (Ruttledge, 1947) and P. a. atricapillus (Odum, 1941).

5. Other genera.

In Psaltiriparus (Addicott, 1938) and Aegithalos (personal observation) both sexes feed the young. In Auriparus Wheelock (1902, quoted by Bent, 1946) states that in a nest which she watched the feeding was carried out largely by the female during the first few days, but the male helped later. The pair bond in Remiz usually breaks down soon after egg laying, and the male plays no part in the feeding of the young.

C. Eggs or Young of more than one Species in the Nest.

There are a number of records of tits of various species incubating eggs, and even rearing young, of species other than their own. These records commonly refer to birds incubating eggs of a congeneric species, and are usually due to one pair usurping the nest and part of the clutch of a second pair, while the latter were in the process of egg-laying. In many of these cases the foster parents reared the young successfully. Examples are:- P. gambeli and P. inornatus (Jenson, 1923 in Bent, 1946), P. major and P. caeruleus (Temple, 1908; Pike, 1932; Marples, 1934; Verheyen, 1947; Amman, 1949), P. ater and P. caeruleus (Butler, 1931). Ryves (1929) records a Great Tit laying in the nest of a Nuthatch (Sitta europaea) and Tutt (1910) a Blue Tit nesting in the nest of a Redstart (Phoenicurus^u phoenicurus).

A very remarkable record of a slightly different nature is given by Lonsdale (1935). A pair of Blue Tits nested inside, and a pair of Robins on the lid of, the same nest box. After the Tits had laid 3 eggs they ceased laying for the time being and fed the young robins in the nest on the roof. When the young robins flew the Blue Tits laid seven more eggs in their own nest, which they hatched. Russel (1947) found a pair of P. gambeli feeding young Sapsuckers (Sphyrapicus thyroideus).

There are a number of records of more than two adults attending the same nest. The majority of these refer to Long-tailed Tits, where this appears to be fairly common, but it has also been recorded in Psaltiriparus minimus (Addicott, 1938), Psaltiriparus melanotis (Skutch, 1935), Parus ater (Legendre, 1932), Parus major (Pässler, quoted by Dresser 1871-81) and Parus palustris (Fatio et Studer, 1889).

D. Nest Sanitation.

1. Parus major.

During the first few days after the young hatched at nest 207, faecal sacs were usually swallowed by both parents. The adults could often be seen making swallowing movements as they emerged from the nest, and sometimes the faecal sac did not disappear until the bird was flying away. Even on the day of hatching, however, the faecal sacs were occasionally carried away, and this happened more and more frequently on successive days.

Swallowing of sacs was seen up to at least the fifth day after hatching. Because of the impossibility of determining on all occasions whether or not a sac had been swallowed, exact counts of the number of sacs removed could not be made. It is estimated that a sac was removed on about one in seven visits.

2. Other species.

Observations summarised by Blair and Tucker (1941) indicate that with the Blue Tit, as well as the Great Tit, faeces were not carried until the fourth day, but there is no indication that the sacs were not swallowed before this. Heinroth (1924-26) has described the peculiar stance adopted by tit nestlings about to defaecate which brings the cloacal opening on to a level with the beaks of the other birds: the opening is surrounded by a circle of white feathers. Nest sanitation behaviour in the Blue Tit is further described by Blair (1941) and Pullen (1945). The latter states that faeces are carried away about once in 8 or 10 times. In P. inornatus (Dixon, 1949) and P. palustris (Steinfatt, 1938) also, both sexes are known to remove faeces. In the latter case faeces were removed on about one in four visits at a nest with 8-9 day old young.

E. Fledged Young.

1. Leaving the nest.

At the three nests for which accurate data were obtained all the young left the nest within three quarters of an hour. It is possible that at some nests the flying of the young may be spread over more than one day.

On May 31st, 1949, at Box 108, a brood of 16 young were seen actually leaving the nest. For the first few hours after dawn the parents brought food at the rate of about 50 visits per hour for the first few hours after dawn. The young were usually fed at the entrance, and between the visits of the parents there appeared to be a continual struggle between the members of the brood for the position at the hole. When the young were fed at the entrance, the parent often went inside after the feeding to fetch a faecal sac. The begging calls of the young were almost continuous. By 0700 the struggles of the young had become very vigorous, and several times individual young came three-quarters of the way out of the hole, and then returned inside. At 0804 one of the young emerged and perched 6" from the hole. The female arrived a few seconds later and took no notice of it, but fed the next one at the entrance. The male evidently noticed the emerged young and gave a see-saw call, like a thin song: the young flew over towards him. This call of about seven notes was subsequently used frequently by adult Great Tits to summon their broods. *The young continued to emerge at about one a minute*
 The male sang in the same way several times and some of the young flew straight off towards him, while others perched outside the box for a short while before doing so. When about four young had emerged, and two of them were still near the entrance, a Grey Squirrel walked down the trunk within about two feet of the box. Neither parents nor young took any notice of it. The female continued to feed the young remaining in the nest, though her rate fell off considerably. The emerged young continued the 'zi zi zi zi zi' begging call from near the nest. At 0832 the last young bird, after many fruitless attempts to get out of the hole, emerged and fluttered off. The

whole of the brood thus emerged in 28 minutes. Half an hour later the brood had moved 80 yards down the wood and were being fed in an oak tree by their parents.

Legendre (1932) and Pike (1932) also state that the young leave the nest in quick succession. In the latter case the whole brood left within 20 minutes, and the author states that the parents seemed to entice the young out by perching at the hole and then flying off. This was not noted in the departure of the brood described above, but it was evident that the young were perching at the entrance and coming half out in their efforts to be first for the food when the parents returned.

Descriptions of the young leaving the nest have also been given for P. a. atricapillus (Odum, 1941), Saltriparus minimus (Finlay, 1905; Addicott, 1938) and Aegithalos caudatus (Verheyen, 1947). All agree very closely with the account given above for P. major. Hendy (1943) gives a case where the fledging of a brood of Blue Tits was spread over several days, and Bailey (1854)³ says that this may occur in the Long-tailed Tit.

2. Second Broods.

In 1949 none of the Great Tits in the study area attempted second broods, though there were indications of a recrudescence of sexual behaviour. The proportion of pairs which attempt second broods varies from year to year, but is apparently always smaller in England (Gibb, in litt.) than on the Continent (see e.g. Kluijver in litt.). When a second clutch is laid, it is usually started shortly before the first brood leave the nest. It is usually laid in a different hole, and the nest is at first very sketchy (Delmee, 1940; Dachy, 1946).

3. General Behaviour.

(a) Parus major

The young remain in the care of adult birds for 2-4 weeks after leaving the nest, although they are entirely dependent on the parents for food for only about a week. During this early period after leaving the nest, the young beg almost continuously with a similar begging call to that used in the latter part of the nestling period. This call I recorded at different times as 'zicker zicker zicker zid' and 'zi zi zi zi zi zi zi zid'. The begging calls of the young Great, Blue, Coal and Marsh Tits are all closely similar though probably distinguishable by means of the differences in pitch, etc. The young also shiver their wings when begging in a similar manner to that which has been described for courtship feed^{ing} and pre-copulatory displays.

The intensity of begging varies greatly, apparently according to the degree of hunger. At times each parent is pursued by a group of young which call continuously and settle near it with wings shivering whenever the parent pauses in its search. On the other hand, at times when the young are apparently more satisfied, they beg only when an adult approaches with food. It is usually possible to tell which of a brood^d young will be fed next by the intensity of its begging. If an adult with food settles near a juvenile which does not beg immediately, it flies off elsewhere. If one young is fed several times in succession the intensity of its begging decreases with each feeding. Both the begging calls and the wing shivering increase on the approach of a parent: they die down a fraction of a second before the food is passed but are usually resumed again immediately afterwards.

It should be noted that fighting between the young occurs at most very rarely during the first few days out of the nest, so that competition for food seems to take the form of competition in ability to keep near the parent, and in ability to stimulate the parent to feed. Occasionally, when a brood is begging very vigorously, one juvenile may knock another off a twig in its efforts to get near the parents.

The begging of the young is stilled immediately by the alarm calls of the parents. The adults use a thin see-saw song of about seven notes to summon the brood. This call is used particularly when the young are moving about the wood, but a female with food in her beak, but out of sight of young, was also heard to give it.

The parents usually remain on or near their own territory, although territorial aggressiveness is rare at this time. The young remain with their own parents for the first few days, but after about a week from when most young had left the nest it was found that many of the "broods" did in fact consist of young from more than one nest, although they were being fed by only one pair of adults. In some cases a pair of adults were feeding young from at least three nests. The way in which this mixing of broods could come about in a wood where the population was fairly high and the adults did not keep strictly to their own territories, is easy to understand. In one case two mixed (ringed) broods were seen to come together and intermingle: when one pair of adults moved off giving their see-saw call those young which happened to be near them followed.

By the second day out of the nest the young can often be seen looking with apparent interest at the leaves around them. Within a day or so they begin to make pecks at surrounding objects, and are soon able to get at least

some of their food for themselves. Their efforts are at first clumsy, and they often peck at objects beyond their reach, or lose their balance and topple of the twig. When they have been out of the nest a week they can feed themselves quite competently, hanging upside down with apparent ease and treating caterpillars in the adult fashion before eating them; but nevertheless they still get the greater part of their food from the adults. From this time the amount of food which they obtain from the adults decreases. The adults go off to feed by themselves for increasingly long periods, and the young seem content to feed alone. Nevertheless the sight of an adult produces an immediate begging response, and young which have been feeding themselves at one moment may be begging furiously the next. Some feeding by adults goes on for at least three weeks after the young have left the nest. Verheyen (1947) gives 15 days as the period for which the young are fed by the parents.

The young preen in the normal fashion immediately after they have left the nest, and possibly before. One juvenile was heard to call 'chich ich ich' within half an hour after leaving the nest. The first 'chich a chich a' alarm call by a juvenile was heard from a bird ten days out of the nest.

The first fights between juveniles were seen about 17 days after fledging, and became increasingly frequent thereafter. They are discussed further in Section XV.

(b) Parus caeruleus, ater and palustris

The begging of the young and the general behaviour of the brood are very similar to those of the Great Tit. I got the impression that the Blue

tit broods moved farther than those of the Great Tits, so that mixing of broods may have occurred at an earlier stage than in that species. On the other hand the large territories of the Marsh Tits delayed the mixing of the broods. Colquhoun (1942) also noticed association between broods of Blue Tits, but stated that the broods kept distinct in the flock. No mixing of broods of different species occurred while the young were still being fed by adults.

In one Marsh Tit brood, which was followed closely, the young started to feed themselves on the third day out of the nest, though the first attempts were very incompetent. The first flight between juveniles was seen on the eighth day. The brood remained closely associated and in the parental territory until the sixteenth day, after which the young suddenly scattered to all corners of the wood. On one occasion one young Marsh Tit was seen to beg from another. Steinfatt (1938) says that the young of P. palustris longirostris are fed by the parents for 8 - 14 days.

The Blue Tit young, as well as using the begging call, also sometimes called 'tis si si si seep'. This call seemed to be used particularly in the absence of the parents. The 'Drrrrrrrrt' call seemed to be used by the adults to summon the young.

The young Marsh Tits were heard to give the 'chirrup chirrup' call on the tenth day out of the nest, and may have used it earlier.

(c) Other species

Bailly (in Jouard, 1932) states that the young of P. atricapillus are normally fed for the first ten days out of the nest, but young taken from the nest could feed themselves completely after five or six days. The

begging cries of the young disappear after 5 - 6 weeks. Odum (1941) records that in P. a. stricapillus the young can feed independently in about ten days and do not remain with the parents more than three or four weeks. The begging display is closely similar to that described for the other tits.

(d) Other genera

For Psaltiriparus minimus Addicott (1938) gives 8 - 14 days, and for Aegithalos caudatus Naumann (1905) gives about two weeks, for the period for which the fledged young are fed.

(e) General

When the fledged young of Great, Blue or Marsh Tits are particularly hungry they shiver their wings very vigorously and these shivering movements sometimes become sufficient to raise them in the air, so that they fly towards the parent. Adults searching for food are thus sometimes pursued by several of their furiously begging young, who may knock each other off the branches in their efforts to get near the parents. It thus seems that the wing-shivering is to be regarded as a ritualised intention movement, in which the form of movement has remained very similar to that from which it was derived, so that it still serves the same purpose when given at a high intensity. Similarly the crouched position when begging is also probably an about-to-fly intention movement. In all probability the wing-shivering in the pre-copulatory and courtship feeding displays are to be regarded in the same light.

SECTION XV. AGGRESSIVE AND SEXUAL BEHAVIOUR IN LATE

SUMMER AND AUTUMN.

A. Introduction.

B. Parus major.

1. Juveniles

2. Adults.

C. Parus caeruleus

1. Juveniles

2. Adults.

D. Parus ater.

E. Parus palustris.

SECTION XV, AGGRESSIVE AND SEXUAL BEHAVIOUR IN LATE

SUMMER AND AUTUMN.

A. Introduction.

It is well known that many Passerine (and other) species show incipient reproductive behaviour outside the normal breeding season. Such behaviour very rarely proceeds as far as actual nest-building, and it is even rarer for eggs to be laid. The biological function of such behaviour is quite obscure. In temperate latitudes it occurs primarily at two seasons - amongst juveniles which have recently become independent (see Nice, 1943), and again in early autumn (see Morley, 1943). In tits the most conspicuous aspect of such behaviour is the aggressive behaviour amongst the juveniles. The nature of this fighting is not immediately apparent: it is often concerned with food, and yet has much in common with reproductive fighting. The general character of this aggressive behaviour is described in the present section, together with the other aspects of reproductive behaviour which occur at the same time of year. The significance of the fighting is further considered in section XVI.

B. Parus major.

1. Juveniles.

During the first few days out of the nest juveniles did not fight for food, but competed with each other only in the intensity of their begging behaviour towards the parent. Once they had begun to be

independent of their parents, however, aggressive behaviour concerned with food became fairly common. This usually consisted of simple supplanting attacks, which very often developed into actual combats, the two birds falling together to the ground. Sometimes the head-forward posture was used. These supplanting attacks were not always made with reference to food, however. Often one bird supplanted another two or three times in succession, and sometimes a chase followed the supplanting attack: in neither of these cases could food be the immediate object of the aggressive behaviour. Often the supplanting attack seemed to be concerned with food initially, though the subsequent chase was not. On one or two occasions incipient head-up posturing followed the supplanting attack. As has been mentioned previously, such behaviour was seen occasionally in the winter, but it was much more common between June and August than later in the year. (cf. behaviour at pair formation, p. 69).

2. Adults.

There was some recrudescence of sexual behaviour in the adult birds towards the end of the nestling period of their first brood. Wing shivering displays and courtship feeding occurred occasionally at this time. Three males were seen engaged in reproductive fighting of high intensity a few days after the young left the nest. In this year, however, none of the Great Tits in the wood laid second broods, though some pairs did in other years.

During September and October there were again some signs of sexual behaviour in the adult Great Tits. Some birds were seen to be in definite pairs, and the observer was scolded on a number of occasions. Chases were common, and some prolonged skirmishes (reproductive fighting) were seen.

A little song was heard in late September and early October. Some of the birds concerned were certainly in their second year (colour ringed individuals). It is not known for certain if juveniles were also involved.

C. Parus caeruleus.

1. Juveniles.

Aggressive behaviour, very similar to that which has been described for the Great Tit, was common in June, July and August. Supplanting attacks were frequent, and often led to actual combat, to chases, or to slight head-up posturing. The skirmish often included display pecking, and song was common. At least the greater part of the song came from juvenile birds. Although the chases were usually intraspecific, Blue Tits often chased, or were chased by, warblers (Phylloscopus).

2. Adults.

Some indications of ^arecrudescence of sexual behaviour were seen in September and early October. Song was heard occasionally, and there was some reproductive fighting.

D. Parus ater.

Aggressive behaviour amongst juvenile Coal Tits was very marked, especially in June and July. Supplanting attacks often led to skirmishes with marked head-up posturing, and juvenile song was frequent.

E. Parus palustris.

Sexual behaviour in juvenile Marsh Tits during the period immediately after they left the nest was even more marked than in the other Parus species discussed above. The young from two nests were colour ringed (by M. C. Cullen) so that their movements could be followed. The juveniles left their parent's territory when they had been out of the nest about a month, and became scattered all over the wood. Some of these juveniles seemed to establish themselves in a limited area almost immediately, so that they could be found in the same place for several days in succession. At first, however, these "preferred areas" were only temporary, and the bird moved and established itself elsewhere after a few days. Nevertheless it is possible that this should be regarded as an expression of the territorial instinct at a very low intensity, for it was linked with reproductive fighting. Indeed, aggressive ^{behaviour} fighting was common at this time in both first and second year birds, and the reproductive nature of the fighting was clearer than in the other tit species. Head-up posturing, upright flight and display pecking were usual in these skirmishes. The juveniles often used a warbling song which was sometimes, but not always, associated with reproductive fighting. Further, many of the juveniles seemed to be in company with other birds, as though they were paired. Reproductive fighting became rather less common in October, but it occurs occasionally in the Marsh Tit in all months of the year.

At least one of the juveniles remained for most of the winter in the area where it settled a few weeks after leaving the nest. My observations do not show whether such preferred areas become territories in the next year. Morley (1943) states that in winter the Marsh Tit population consists of

territory owners, which associate in flocks with other Marsh Tits inside their own territories; and unpaired flock birds, without territories, which are probably first year birds. It is, however, possible that the differences in the degree of territorial behaviour shown by individuals are of degree only. No doubt, as in other species, flocking is increased and territorial behaviour decreased in cold weather.

In Parus inornatus sexual behaviour of the juveniles is apparently still more marked, for many pair up and occupy permanent territories in late summer, (Dixon, 1949). Aggressive behaviour is also common in late summer flocks of P. a. atricapillus (Odum, 1941).

SECTION xv/ THE RELATIONS BETWEEN THE FORMS
OF AGGRESSIVE BEHAVIOUR.

SECTION XVI THE RELATIONS BETWEEN THE FORMS OF
AGGRESSIVE BEHAVIOUR.

Tinbergen (1942; in litt.) has demonstrated that the causal structure underlying behaviour has a hierarchical nature. He recognises a number of "major moods" or "major drives", to each of which are subordinated a number of "submoods". For example, the (major) reproductive drive of the Three-spined Stickleback (Gasterosteus aculeatus) is activated by a hormonal change accompanied by certain external stimulation. A fish in reproductive mood is brought into the fighting sub-mood by the presence of another male. The fighting mood is expressed by chasing, threatening, biting, etc., according to the opponent's behaviour. A similar scheme has been successfully applied by Baerends (1941) to the behaviour of the wasp Amnophila campestris, and by Råber (1948) to the fighting behaviour of the domestic Turkey (Meleagris sp.).

Such a scheme implies that reproductive fighting, which is activated by the reproductive drive, is fundamentally different from fighting over food, or fighting over roosting sites. The observations made in the present study give considerable support to this view. Reproductive fighting utilizes different displays, is evoked by different situations, and is dependent on a different internal state, from fighting over food. For these reasons, the suggestion made by Conder (1949) that "Individual distance" (which is dependent on food fighting) changes into "mated-female distance" (i.e. an area which includes the female), or into the breeding territory, is not acceptable: the types of fighting concerned in the two situations are quite distinct.

Nevertheless, a closer examination of the facts connected with food and reproductive fighting do seem to indicate certain possible relationships between the two. These are (i) that the activation of one type of fighting lowers the threshold for other types, and (ii) that an animal with a high reproductive fighting drive will also have a high food fighting drive, and vice versa. We shall consider the evidence for these two possible relationships.

(i) During the late winter, when the Great Tits are feeding in flocks, disputes over food are sometimes accompanied by the incipient use of postures appropriate to reproductive fighting. Thus one bird may make a supplanting attack on another, and then show a brief head-up posture. Sometimes postures appropriate to food fighting and reproductive fighting are shown simultaneously, as when a feeding bird adopts a marked wing-raised posture and at the same time makes incipient head-up postures. The most marked head-up postures seen in a food dispute were made by two Great Tits which settled, each in a vertical position, on opposite sides of a piece of fat: it may be significant that the breast of each bird was exposed to the other. Similarly in the Herring Gull (Larus argentatus), Tinbergen (1939b) states that substitute nest-building, common in reproductive fighting, sometimes occurs in food disputes in the reproductive season.

Conversely, the wings-raised and head-forward posture of the tits, which are normally associated with food fighting, occur in reproductive fighting. They are often well marked in intra-specific encounters in the Blue Tit, but rather less so in those of the Great Tit. Further, the head-up posture, unlike the wings-raised posture, is not generally used in

inter-specific reproductive fighting, In inter-specific fighting, as we have seen, both combatants are on their own territory, so that the fighting drive is strong in both. Also, the colour pattern of the opponent is not that which releases the displays appropriate to reproductive fighting. The exact reason for the appearance of the wings-raised posture in reproductive fighting is not yet clear: an exact analysis of the stimulus situation in which this posture appears in both food and reproductive fighting is needed.

In late summer, during the period after the young tits have become independent, head-up postures are often associated with fighting over food. Further, as described on page 223, a skirmish which starts with reference to a food object is often continued into a series of supplanting attacks, or into a chase, which carries the combatants far away from any possible food. Song also often occurs in these skirmishes.

It is difficult to find any hypothesis to cover the above behaviour, other than that the activation of one type of fighting lowers the threshold for other types. Head-up postures were not seen in the food disputes in mid-winter, though these were often intense, so that high intensity of the fighting will not account for their appearance. It is noticeable that behaviour appropriate to reproductive fighting occurs in food fighting only at those seasons when the reproductive drive is active to some extent. This in itself lowers the threshold for reproductive fighting; and we presume that the activation of food fighting lowers the threshold still more, so that certain characteristics of a member of the same species may be sufficient to release activities appropriate to reproductive fighting.

(11) Three separate authorities have now shown for Parus spp. that there is a relation between the order of birds in a "dominance hierarchy" and the distance from the feeding station to their respective territories - Odum (1941) for P. a. atricapillus, Colquhoun (1942) for P. caeruleus, and Brian (1949) for P. major. In each case the top bird in the hierarchy held territory close to the feeding station and the next few birds held territories at successively greater distances from it. Birds without territories were at the bottom of the hierarchy. Colquhoun and Brian appear to have made their observations at seasons when the birds had probably already begun to establish their territories, and infer that the distance to the territories of the different individuals influenced the order of the hierarchy. Odum, on the other hand, began his observations some months before the flocks broke up, and states that "The top three males were the ones that remained on or near the winter feeding range to establish territory and nest". We cannot be sure, therefore, whether in general the dominance hierarchy precedes the establishment of territory, or vice versa. It does seem, however, that there is a relation between the two.

Now the fighting which takes place in the establishment of a hierarchy is food fighting, whereas that in the establishment of territory is reproductive fighting. Here again we see a relation between the two forms of fighting: it seems that those birds with a high reproductive fighting drive have also a high food fighting drive, and vice versa.

Tinbergen (1942) has shown that certain inter-relations may exist between the causal chains underlying behaviour - that is that the activation of one drive may affect activities connected with another. Only two forms of

such inter-relations have so far been studied, namely:-

(a) Suppression. The activation of the fighting drive may suppress courting, and vice versa. Escape may suppress many other activities.

(b) Outlet. Under certain circumstances, as when two mutually incompatible drives are aroused simultaneously, the impulses connected with one activity may find expression in another apparently irrelevant one.

(Displacement activities, see e.g. p. 114).

Here it seems that we have a third type of inter-relation - an activity subordinate to one major drive lowers the threshold for a similar activity connected with another. The evidence available at present does not prove such an inter-relation, but its existence would apparently provide the simplest explanation for the observed facts.

We may inquire into the nature of the similarities between the two activities concerned, i.e. between the different types of fighting. Each is directed (primarily) against other members of the same species, serves to obtain or protect some object or situation important for survival or reproduction, and varies in intensity according to the spatial relationship between the combatants and that object. Further, the basic pattern of attack in each form of fighting is the same - the supplanting attack.

It may be tentatively suggested that the motor patterns of all forms of fighting were primitively the same - i.e. that one group of motor patterns could be evoked by the activation of a number of different drives. Such an hypothesis differs only in degree from the scheme given by Tinbergen (1942, in litt.), for even quite distinct instincts must use the same muscle fibres, groups of muscle fibres, and even groups of muscles: it merely

suggests that the common path along which the impulses travel could exist at one stage higher than had previously been supposed. It is further suggested that, in evolution, fighting techniques then became specialised to suit the situations in which they were evoked, and the different types of fighting thus became differentiated.

A similar hypothesis can probably be applied to fleeing. Råber (1948) has shown that in Meleagris sp. fleeing from males of the same species differs from fleeing from hostile species, for it does not occur in the moulting season, and depends on the activation of the major reproductive drive. Nevertheless, relations, similar to those which it has been suggested exist between the different forms of fighting, may also exist between the different types of fleeing. In this case, however, different motor patterns have probably not been differentiated.

SECTION XV// BEHAVIOUR TOWARDS PREDATORS.

A. General.

B. Behaviour Towards Mammalian Predators.

(a) Grey squirrel.

(b) Man

(i) Winter

(ii) Spring

(iii) Snake display

(iv) Distraction display.

C. Behaviour Towards Avian Predators.

(a) Avian predators in flight.

(b) Avian predators perched.

D. Biological Value of the Responses to Predators.

SECTION XVII BEHAVIOUR TOWARDS PREDATORS

A. General

Although we do not yet know what proportion of the individuals of a passerine species fall victims to predators (but see L. Tinbergen 1946), there can be little doubt that efficient responses to stimuli indicative of possible danger carry a high selective value. Thorpe (1944) has distinguished two types of response given by birds to predators. In some cases there is an innate response to a particular species or kind of predator. For instance, Song Sparrows (Melospiza melodia) recognize owls instinctively. In other cases there is an "instinctive equipment whereby they tend to take avoiding or self protective action to (1) a wide range of stimuli which are likely to be signals for danger, especially any moving object; (2) any stimulus or situation which is strange; (3) any stimulus at an unusually high intensity". It is probable that the response of tits to an avian predator in flight belongs to the first of these two types, and that other responses to predators belong to the second; but of course it is not possible to be certain without evidence from individuals whose past experience is known.

The behaviour of tits towards predators is extremely complex. Both the behaviour patterns and the calls used seem to be very variable, so that exact description is impossible. Therefore,

although it is necessary to divide the behaviour patterns into a number of types for purposes of description, it must not be thought that the categories are very precise ones. The complexity seems to be the result of the activation of three distinct drives; (i) the drive which was controlling the bird's activities before the appearance of the potential predator; (ii) escape; and (iii) attack. One of these drives may suppress the other two, in which case the behaviour is relatively simple. Alternatively the behaviour may be a complex resultant of the activation of two or three of the drives.

B. Behaviour towards Mammalian Predators

Observations were made on the behaviour of the tits towards only two of the mammalian predators present in the wood - the Grey Squirrel and Man. It must be noted that neither of these can be natural predators to the particular population of titmice in question, though the Red Squirrel, which occupied the woods before the arrival of the Grey Squirrel, may have been.

(a) Grey Squirrel (*Scuirus carolinensis*)

The Grey Squirrel occasionally attacks the nests of tits, and eats the eggs and young. With one exception noted below, however, no tit was seen to give any response to the proximity of a Grey Squirrel except a simple avoiding one. Birds which were feeding on the ground or in the trees would merely fly a few feet away when a Grey Squirrel approached too closely.

Occasionally, when squirrels made sudden dashes over the leaves, nearby Great Tits flew up giving the 'chich a chich a' alarm note: this represents a somewhat greater activation of the escape drive than mere flying up, presumably due to the additional ^{stimuli} ~~estimate~~ of noise and movement. Even when a Grey Squirrel walked down the trunk of a tree past a nest box when the young were actually leaving the nest, neither adults nor young gave any response.

On Jan. 14th, 1949, however, a male Great Tit gave a very remarkable display to a Grey Squirrel. The Squirrel had entered a drey 20 feet up in a hazel tree, when the Great Tit flew up and perched about one foot from the drey. It spread its wings to about three-quarters of their full extent in such a manner that their upper surfaces were directed towards the drey. It lowered its head, and slowly swayed it from side to side exposing first one cheek and then the other. The tail was widely spread and usually lowered, though sometimes it was raised. The bird hissed continuously. After about thirty seconds it hopped to a position below the drey and repeated the display, though this time its head was pointing half away from the drey and the upper surfaces of its wings were not directed forward. Then it returned to the first position and displayed again. After a brief break it displayed a fourth time. The whole performance lasted about three minutes. The significance of this very elaborate display, which was not seen at any other time, is quite obscure. It was also witnessed by J.A. Gibb. The only reference in the literature to a similar

display by a member of the Paridae refers to Machlolophus
haplonotus: a female mobbed a Palm Squirrel which approached her
 nest with wings spread and feathers erect (E.A. Butler quoted by
 Hume, 1889). Pettingill (1937, quoted by Bent, 1946) describes
 the mobbing of a Red Squirrel by a pair of P. hudsonicus: the birds
 used actions similar to those used by Great Tits in mobbing a
 Sparrow Hawk, but one of them twice went into what was apparently
 an hypnotic state induced by fear.

(b) Man

(i) In Winter.

When a winter flock of Great Tits is disturbed by man, their
 response occurs in two stages. First one or more birds fly up,
 usually giving the alarm 'chich a chich a chich ich ich ich', and
 the other birds in the flock do likewise. This is an immediate
 and probably an innate response. The further reaction depends on
 the situation. If the reason for alarm is evident, the birds fly
 off, calling 'twinks'. If there is no evident cause for alarm the
 birds continue feeding. A similar two-stage alarm response has
 been described by Tinbergen^{bergen} (1942) in the Herring Gull (Larus
argentatus): he points out that the first alarm evokes a 'mood',
 and that the further response depends on the further stimuli.

In some cases the initial response consists merely of flying
 up, without an alarm call. This appears to represent a lowest
 level of alarm. When an alarm call is given, it may be 'chit',

'twit', 'twit a wit', or 'chich a chich a chich ich ich ich'.

The differences seem to be differences of intensity, and produce correspondingly varied effects on other individuals. Thus the 'chit' call may only cause one or two neighbouring birds to fly up, whereas the full alarm causes the whole flock to fly up.

Occasionally the trilling 'tsee', which is normally given on the approach of an avian predator, was given on the approach of the observer. Why the call appropriate to a flying avian predator should be given on the approach of a man is unknown. In the House Sparrow (Passer domesticus), whose reactions to predators seem to be generally similar to those of tits, Daanje (1941) encountered a similar phenomenon.

A similar two-stage response is given to a wide variety of other stimuli, such as a gunshot, the noise of a tractor, the sudden movement of a squirrel, a pheasant's alarm, and so on. We may thus presume that the response is given to "a wide variety of stimuli which are likely to be signals for danger" (Thorpe, 1944), and not to any particular species or kind of predator.

In Great Tit flocks feeding on the ground such alarms often occur without any apparent initial stimulus. It is, of course, extremely difficult to be certain that there was no initial stimulus, but it is at least possible that these are "Vacuum Activities" or "Leerlaufreaktionen" similar to those which are known in ducks and terns.

We see, therefore, that when a human intruder approaches a

Great Tit flock in winter the escape drive usually suppresses the feeding drive and the birds fly off. Occasionally the activation of the escape drive only causes a momentary cessation of feeding, and the birds fly down again.

(ii) In Spring

In spring, when the Great Tits are feeding in pairs, their behaviour on the approach of a human observer is much more complex. The male flies up and scolds the intruder, while the female remains in the background, or flies^{off}. Females disturbed when alone sometimes also show scolding behaviour. Since they sometimes approach the observer, it seems evident that a fighting drive is activated, though an actual attack is never made. They also show behaviour associated with escape, and with continuing their previous activity. In practice, it never happens that only one of these three drives controls the behaviour. Compound behaviour always appears, and it is for this reason that the behaviour is ~~always~~ so complex.

The principle types of response shown at this time of year are shown below. (It is assumed that the birds are feeding on the ground when first seen, unless otherwise stated).

(i) The bird may simply fly up to a bush, and then fly down again without any audible call. This is the lowest intensity of escape, quickly suppressed by the feeding drive.

(ii) The bird flies up, calling 'chich a chich', and then

flies down again with gentle 'chich ich ich' calls and resumes feeding.

(iii) The bird flies up, calls 'chich a chich', and then flies off giving a series of 'twinks'.

Generally speaking, the possibilities described so far occur later in the day, when the reproductive ^{drive} is low (p.292). They represent, in fact, behaviour identical with that seen in winter. Which of these possibilities actually occurs depends on the extent to which the escape drive is activated. (Another alarm call, 'zur leeeeeeeeeeep leeeeeeeeeeep', seems to be given on the distant approach of danger, and may be followed by the 'chich a chich' if the intruder continues to approach). At other times more complex types of behaviour may appear:-

(iv) The bird flies up, usually calling 'chich a chich', and then remains in a tree, usually facing the intruder, calling 'twink', 'zee twink twink' or 'twink de twink', and flicking its wings. The flicking of the wings seems to be an inhibited intention movement of escape, and it appears that in this case the escape drive is activated but is temporarily inhibited by the attack or feeding drive: invariably, however, the bird flies off after a short while. Sometimes, before it flies right away, the bird flies down to the ground and hops about, still 'twinking' ^{and} flicking its wings, apparently looking for food but in an alert upright posture. Here we see 'feeding' and 'fleeing' mixed, but after a minute or so the bird flies off.

(v) Sometimes the bird flies up, and remains nearby scolding with a wide variety of calls- principally 'pit pit churrrr', 'pit pit chich ich ich', or a very harsh 'chik kik kik kik'. Although it is possible to give approximate verbal descriptions of the calls in this way, intermediates between the verbal types are common. These calls are accompanied by a jerking movement of the body, the bird moving the fore part of the body up and down, and simultaneously swinging it from side to side, so that the head follows an approximately U-shaped course. The tail may move synchronously with (and in the opposite direction to) the body, but in the intense displays the movements become asynchronous. The wings are usually flicked at the same time. The body feathers are sleeked. The movements may be made with all degrees of intensity: sometimes they are limited to incipient jerky movements, while at others the whole body is swayed vigorously to and fro. Usually the bird scolds in this way for a minute or two and then flies off. Sometimes, however, it resumes feeding: this only occurs when the scolding has been comparatively mild.

Since the bird often moves towards the intruder during the scolding, it seems highly probable that an attack component is involved in the behaviour. Indeed similar scolding of a Sparrow Hawk dummy sometimes leads to incipient attack. No doubt the exact nature of the scolding depends on the relative strengths of the three drives concerned. The complexity of the behaviour is illustrated by the fact that such behaviour towards man only occurs

when the birds are in the reproductive mood. So some component of the behaviour must be activated by the reproductive drive. Nevertheless behaviour which is at least superficially very similar is shown to Sparrow Hawks at all times of year. Thus there must be a close connection between the two forms of attack, although they are released by different situations and depend on different internal states. This is, in fact, another instance of one motor pattern being activated by two different drives. We have already seen that this may also be the case with fleeing (p. 236), and that it may have been the case with intra specific fighting (p. 237).

Further, if the bird is engaged in singing when disturbed it rarely scolds. Usually it continues singing, though somewhat erratically, and hops about from perch to perch (conflict between singing and fleeing), and after a while flies right off. Thus the behaviour of a bird disturbed whilst singing differs from that of a bird disturbed whilst feeding.

Not only are the calls highly variable and difficult to place in categories, but they may change one into another through a series of indefinable intermediates. Very often scolding (or twinkling) changes gradually into song.

The occurrence of the 'Twink' and 'Chich ich ich' calls is interesting. We have already seen that 'twinks' are associated with well integrated, long range, flock movements, and 'chich ich ich' calls with the cessation of movement and with short, loosely

integrated movements (p.²⁶). Also the 'chich ich ich' (and 'pit tit churr') is used in reproductive fighting more by the attacker than by the attacked bird: the 'twink', on the other hand, is used more by the attacked bird. Now, in the present case, we find that the 'twink' precedes flying away, and the (gentle) 'chich ich ich' precedes a resumption of the previous activity. In all cases the 'twink' is associated with movement, and the 'chich ich ich' with cessation of movement, or with staying in the same place: yet different drives are concerned in each instance. The real significance and evolutionary origin of these calls remains obscure, and will probably only be revealed by comparative study.

Somewhat similar scolding behaviour is shown by Blue Tits at the same times of year, but has not yet been studied in detail.

(iii) Snake Display.

When disturbed on the nest, members of the genus Parus give an intimidatory display which often gives a human observer the impression that a snake is in the hole. The most conspicuous feature of the display is a hissing sound, comparable to the hissing of a snake. This is sometimes accompanied by blows of the wings against the side of the cavity. Pickens (1928) has given a detailed description of the display in P. carolinensis. He states that the bird first rises slightly on its legs and throws its head back, and then, "as if with a great effort", throws its head forward emitting a hiss, and at the same time the tail is spread and the

wings extended. A display of this type was encountered in Great, Blue and Marsh Tits in the present study. It has also been recorded in P. ater (Jourdain, 1929), P. atricapillus (Jouard, 1932, Burleigh, 1930), P. gambeli (In Bent, 1946), P. rufescens (Bowles, 1909, Burleigh, 1930) and P. inornatus (Allen, 1943; Dixon, 1949). It is not known what predators normally elicit this response, but its survival value is clear. A similar display is known in the Wryneck (Jynx torquilla) - another hole-nesting species (Coward, 1920

(iv) Distraction Display.

When the young are out of the nest, the parents show a very remarkable form of distraction display. This behaviour has so far only been seen clearly in the Blue Tit, though glimpses have been obtained of Great Tits performing a similar display, and J.A. Gibb (personal communication) states that it is regular in that species. In both cases it appears to be released by the cry of pain of the young. At one Blue Tit's nest, from which the young had just flown, the parents at first scolded me with crown feathers raised, flicking wings and straddling walk, and from time to time jerked their bodies in a manner similar to that described for the Great Tit. I managed to catch one of the young, which squeaked as I held it. The parents immediately gave a quite different display, flying towards or past me with slow, moth-like flight, often gliding a foot or two, with slightly raised, not fully spread wings. They gave a continuous hissing quite like that given in the snake

display (v. supra) but less 'breathy'. One of them perched on a branch about three feet away and rolled over on one side and held one wing up, staying like this for two or three seconds. Several times one of the adults showed even more extreme forms of impeded flight, fluttering with moth-like flight, losing height; and sometimes fluttering down thus from branch to branch. During this time the parents often perched within four feet of me. The display lasted about a minute after each/^{time} the young squeaked, and then the ordinary scolding was resumed until the next call from the young.

A similar display in P.a. atricapillus, which was also apparently released by the cries of the young, has been described by Odum (1941).

Such distraction displays may have originated through the conflict of two opposing drives, but they have become highly ritualised and their selective value is clear.

C. Behaviour towards Avian Predators.

Tits show two different responses to avian predators, one being given to a predator in flight and the other to a predator perched in a tree. The behaviour patterns appear to be quite distinct, and are associated with different calls. Often, however, the appearance of a predator in flight evokes some of the calls normally associated with a perched predator, and vice versa.

(a) Avian Predator in Flight

When a hawk approaches a mixed tit flock, one bird gives a high pitched trilling 'tsee ee ee ee ee' and flies into cover, and all the other birds in the flock immediately do likewise. Some writers have called the resultant noise a 'confusion chorus' and believe that the sound makes it difficult for the predator to locate any particular prey. The trilling 'tsees' die away after a few seconds, but the birds remain in cover, usually still and silent, for a minute or longer. As well as the trilling 'tsee', other calls are also given when a hawk passes over a tit flock - especially 'chich a chich a chich' calls, which often precede the trilling 'tsees'. The trilling 'tsee' call was also sometimes given to woodpigeons (Columba palumbus) and Blackbirds (Turdus merula) flying over the wood.

Behaviour of this type has been recorded in Great, Blue and Marsh Tits in the present study: in Psaltiriparus minimus by Grinnell (1903, quoted by Bent, 1946) and Finlay (1905): and in Aegithalos candatus (D. and S. Lack, personal communication).

One brood of Great Tits, which had left the nest an hour previously, were attacked successively by a Sparrow Hawk (Accipiter nisus) and a Jay (Garrulus glandarius). On each occasion the parents called 'chich a chich a chich ich ich ich ich', producing immediate silence in the young, and chased the intruder off. Thus in these cases the parents flew towards the predator and their response to it

was quite different from that given to Sparrow Hawks in winter flocks.

(b) Avian Predator Perched

The 'mobbing' behaviour of tits, which is given to an avian predator perched in a tree, was studied with the aid of a stuffed female Sparrow Hawk, mounted in the typical perched position. The mount was placed on boughs, in positions in which Sparrow Hawks might perch normally, and the behaviour of the tits observed from a distance. In order that the birds in the wood should become conditioned to the mount as little as possible, it was seldom exposed to mobbing for more than five minutes. Forty-five experiments of this nature were made between January and July, 1949. At least one, and often twenty or thirty, tits mobbed the mount on each occasion.

(1) Parus major.

It is not easy to generalise about the behaviour of Great Tits when confronted with the mounted Sparrow Hawk, for there appeared to be much individual variation. This was probably due largely to differences of intensity in the different drives concerned, but little progress has been made so far in its analysis. Most of the movements shown by the Great Tits when mobbing a Sparrow Hawk are very similar to, and probably identical with, those shown by a paired male on the approach of a human intruder, which have been discussed on p. 248.

Typically the birds flew towards the mount, and hopped from twig to twig with raised crest and flicking wings, keeping about ten feet away. Some made diving attacks down towards the dummy and soared up again when about three feet away. Others scolded from nearby twigs with the head down and forward and the tail up, jerking the fore part of the body from side to side, and at the same time flicking the tail from side to side and flicking the wings. The tail was usually moved more rapidly than the fore part of the body, so that the movements were not synchronised. Other birds sat almost motionless, but scolded vigorously. The sound of one bird mobbing caused others to fly towards the mount and join in. Sometimes a bird scolded on hearing others do so, even though it couldn't see the mount itself.

A great variety of calls were used. The commonest was a harsh 'chich ich ich ich', which was often prefaced by 'twinks', 'chich a chich a chich a', 'pit a chich' or 'pit chur'. Often birds gave long series of 'twinks' with no other calls, and sometimes such a series changed gradually into song. Similar scolding behaviour has been described in P. inornatus by Dixon (1949)

Some individuals scolded in this way for only a minute or so and then flew off, but others continued for ten minutes or more if the dummy was left in position. Usually a number of birds collected within a few minutes of the first alarm call, and dispersed over about a quarter of an hour. When a live Sparrow Hawk was being mobbed, it usually flew off after a few minutes,

but the mobbing of Tawny Owls (Strix aluco), which appeared to be similar to the mobbing of Sparrow Hawks, sometimes continued for a quarter of an hour or more. In some experiments, mobbing continued for several minutes after the mount had been removed - the so-called after-reaction (see p²⁹⁷). After-reactions were also noted when tits were mobbing live Tawny Owls.

During the breeding season the behaviour of the tits towards the mounted Sparrow Hawk was similar to that during the winter, except that the males became much more vigorous than the females. On four occasions after the young had left the nest, however, behaviour of a different type was noted:

1. On June 4th a pair of adults, with young only a few days out of the nest, scolded the mount. Their behaviour was typical, except that the female shivered her wings a little while mobbing.

2. On July 8th an adult male shivered his wings in similar circumstances.

3. On May 31st the mounted Sparrow Hawk was placed near a brood of Great Tits which had left the nest a few hours earlier. The female scolded the mount vigorously for about a minute. Then she suddenly stopped scolding and hopped around the tree as though she ^{was} ~~were~~ looking for caterpillars. She pecked repeatedly at leaves - sometimes several times at the same leaf - but apparently picked nothing off them. She continued thus for about ten minutes, keeping between 3 and 10 feet from the mount. During the whole of this time she took no food to her young. All her movements

suggested that she was looking for food (and this was of course the activity on which she had been engaged just previously) and yet apparently she picked up no food at all. It is possible that she was picking up small food particles and eating them herself, but her pecking movements seemed to be incomplete.

4. On June 2nd a female Great Tit, with young nearby, hopped along a branch pecking at the bark in the intervals of scolding. Her movements were reminiscent of the displacement pecking used by males in reproductive fighting.

In all four cases cited above, the Sparrow Hawk mount was presented when the tits were vigorously engaged in feeding their young, and its presence caused that drive to be thwarted. The anomolous behaviour patterns shown are possibly to be regarded as displacement activities. In all cases the behaviour pattern shown was one which was common in its normal context at that time of year. In the case of the female which went on 'searching' for caterpillars, it appeared that the energy appropriate to the thwarted drive found release in the incomplete expression of that drive. It is, however, impossible to assess the significance of such patterns of behaviour until they have been seen more than once.

Juvenile Great Tits in their first few weeks out of the nest gave much less intense reactions to the mount than did the adults. The parent's 'chich a chich a chich ich ich' alarm call caused them to stop begging immediately, but sometimes they did not mob the mount at all, and resumed begging very soon. Those young which

approached the mount often just perched near it looking at it; sometimes they hopped about flicking their wings or jerked their bodies from side to side in a manner similar to, but much less intense than, that of the adults. In any case they seldom remained near the mount for more than a minute or two. Those juveniles which sat looking at the mount appeared to be uneasy: they gave the observer the feeling that "they knew something was wrong, but didn't know what". Sometimes a juvenile sat and looked at the dummy for a minute or more and then squeaked^{also} and flew off in evident alarm. Others slowly approached the dummy, hopping from twig to twig, and then suddenly flew off. One young Great Tit flew over the dummy using the upright flight typical of ^{reproductive} ~~sexual~~ fighting. In general the juveniles called much less than the adults - usually a gentle 'chich ich ich' or begging calls. Juveniles about a month old behaved more like adults, but still their reactions were less intense. This difference between the behaviour of juvenile and adult Great Tits cannot be interpreted without experimental evidence on birds of known history. It seems probable that there is some sort of inborn recognition of a Sparrow Hawk, but that the mobbing behaviour does not mature until the birds are several weeks old. The behaviour of the adults may also be of importance in the forming of conditioned patterns in the young.

(ii) Parus caeruleus, ater and palustris. The patterns of mobbing behaviour in these species were closely similar to those which have been described for the Great Tit. Sitting looking at

D. Biological value of the response to predators

The biological value of the response shown by tits to an avian predator in flight is clear - the action taken is just that which will increase the individual's chance of survival. Similarly the response shown to stimuli indicative of possible danger, the snake display and the distraction display are all of obvious selective value. The cases of the mobbing of perched avian predators, and of the scolding of human intruders by paired males, are more difficult to understand. Although the individual may not be in any immediate danger from a perched Sparrow Hawk (the typical response to a predator in flight is given as soon as the Hawk takes wing), it is impossible to believe that the individual would not be in less danger if it flew off than if it mobbed. The mobbing does, however, make the predator more conspicuous to other tits: perhaps this is a case where it is necessary to postulate a group survival value. The behaviour of the paired male who scolds the human intruder perhaps gives his mate the opportunity to escape - so that we must presume that the danger run by the male is more than offset by the difficulty of finding a new mate.

SECTION XVIII ROOSTING AND AWAKENING.

A. Parus major and caeruleus.

1. General Behaviour

- (a) Late summer and early autumn
- (b) Winter
- (c) Breeding season

2. Times of roosting and emergence

- (a) Late summer and autumn
- (b) Winter
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 - (i) Male
 - (ii) Female

B. Other Parus species.

C. Other genera.

D. Some observations on Great Spotted Woodpeckers and Nuthatches.

E. Winter roosting - general.

F. The study of roosting and awakening behaviour.

SECTION XVIII ROOSTING AND AWAKENING.

A. Parus major and caeruleus.

1. General Behaviour

During the summer the majority of Great and Blue Tits roost in foliage. In winter they roost in holes, cracks in trees or buildings, or in other similar sites. In the study area only a small proportion of the Great Tits, and even fewer of the Blue Tits, roosted in nesting boxes - perhaps because the boxes were too large. Delméc (1940) similarly found that his boxes were used for roosting more by Great Tits than by Blue Tits. The change from summer to winter roosting places takes place between September and November. In spring the males leave the holes again, and start to roost in the foliage a few weeks before the start of nest building: the females roost in the nest-holes until at least a few days before the young fly. Some individuals roost in cavities all the year round. There are a very few records of two birds roosting in the same cavity (Plattner and Sutter 1946, 1947).

(a) Late summer and early autumn.

Although all parts of the wood were used for roosting, there were some areas in which the concentration of individuals was much higher than elsewhere. Such areas were not at all clearly defined. They were several acres in extent and contained plenty of dense elder, hawthorn and hazel cover. Since, however, nearly all parts of the wood contained similar cover, there was no obvious reason why some areas should have

been preferred to others.

The flocks normally moved back towards the roosting area about one hour before sunset. Their return was usually marked by an increase in calling. The flocks then spread out and the individuals settled down to feed quietly. Their movements became extremely difficult to follow, and they seemed just to disappear in the foliage.

In the morning the titmice woke up rather later than most other Passerine species - there was often a lapse of fifteen minutes between the calling of the first Robin (Erithacus rubecula) and that of the first tit. The different tit species started calling at about the same time as each other. There was often a lapse of several minutes between the first call and the time when calling became general. Great Tits gave mostly 'Twinks' and a few 'chich ich ich' calls, and Blue Tits 'Tsip' and 'Drrrrrtttt' and a few 'sip sip sue' calls. The calling usually rose to a crescendo soon after the majority of the birds were awake. Some then started to feed, but many birds continued calling and flying to and fro, apparently at random, for some time. Gradually the individuals gathered into flocks, which moved off in different directions.

(b) *Winter.*

In the study area most of the dead trees had been taken out. Winter roosting sites were available for Great and Blue Tits in nesting boxes, in the few remaining dead trees, and in other natural cavities. The smaller holes and cracks were evidently preferred, and the birds were often seen with tails bent, apparently through roosting in too small cavities. Grinnell (1923) noticed a similar occurrence in P. inornatus.

A medium sized flock of tits roosted in a group of dead elms which contained many woodpecker holes and other cavities. Here observations were made at one particular tree (referred to hereafter as the Roosting Tree), which was used by several Great and Blue Tits as well as by two Great Spotted Woodpeckers and by one or two Nuthatches. Other Tits roosted in neighbouring trees. Even after most of the Great Tits were paired, and had established themselves on more or less definite territories, the tree was often used for roosting by two males. This concentration of birds for roosting should be compared with the situation described by Kluijver (in litt.) in a coniferous wood in Holland. Here all the tits roosted in nest boxes, which were scattered throughout the wood. Most tits established themselves in a "domicile" (see p. 64) ^{by} mid-December, on which they roosted for the rest of their lives. Thus in this area the birds must have scattered to roost.

As in summer, there was usually an increase of calling as the birds returned to the neighbourhood of their roosting sites. Some individuals entered their holes as soon as they arrived at the Roosting Tree, but the majority stayed at the base for some minutes before entering. During this interval the Blue Tits usually fed in the elders at the base of the tree, and only occasionally sat still for any length of time: the Great Tits on the other hand, fed only occasionally, and usually sat in the elders, motionless or preening. Marples (1935) showed that Blue Tits started feeding at a bird table earlier, and finished feeding later, than Great Tits. At this time calling was occasional - Blue Tits calling 'sip sip sue' and 'Drrrrrtttt' and Great Tits soft 'Twinks' and a sleepy, bubbling 'chich ich ich! Often there was a marked silence between the time when

the birds returned to the tree and the time when they entered their holes. The amount of calling was dependent on the weather, being greatest on warm, clear evenings. Sometimes faint 'twinks' were heard from a hole for a few seconds after a Great Tit had entered it.

During early spring, after the flocks had dispersed and most individuals were paired, the calling before roosting was rather more marked. This increased calling came chiefly from the males, the females usually entering their holes silently. Sometimes the males sat 'twinking' and singing for as long as twenty minutes before flying up the tree in stages to enter their holes.

Colquhoun (1942) and Martin (1938) have described a pre-roosting ceremony between members of the pair in the Blue Tit which takes place occasionally in the winter and more frequently as the nesting season approaches. This was seen fairly often, especially in February and March. The two birds flew together from twig to twig, sometimes with raised crest and 'moth-like' flight, calling 'Drrrrrt-t-t', 'Durreeee', or singing. Occasionally the two birds of the pair flew in stages up to the top of the Roosting Tree together, and then spiralled down again to the base. Sometimes they merely sat a foot or two apart before going to roost. Sometimes the male inspected the female's roosting hole after she had entered. Legendre (1928) records finding two birds in one box. Kluijver (in litt.) states that the male also sometimes waits at dawn near the female's roosting site until she emerges. In the Great Tit the members of the pair often associated particularly closely just before roosting, and the male often accompanied the female some way towards her own roosting hole, but nothing comparable to the behaviour of the Blue Tit was seen in this species during the winter in

the present study, though it has been recorded by other writers (see Plattner and Sutter 194⁶₇-194⁷₈).

In the mornings the tits emerged from their holes and spiralled down to the elders at the base, either silently or with thin 'tsee' notes: then there was usually an outburst of calling as in summer. In spring the males usually sang very soon after leaving their roosting places.

In general, each individual occupied the same hole on successive nights, though in many cases tits altered their roosting sites without apparent reason. During the winter only one possible instance was seen of one Great Tit fighting another for a roosting hole at roosting time, but on five occasions one was seen to arrive at its hole to find it occupied by a Great Spotted Woodpecker. Blue Tits were similarly dispossessed on two evenings, once by a Great Spotted Woodpecker and once by a Nuthatch. In all cases the resultant behaviour was similar. The tit first hopped about near the hole, fluttering its wings, or perched with them half open (an aggressive posture, see p.40). It then flew away to the elders nearby, and either hopped around giving harsh 'Drich ich ich' calls or sat preening - perhaps a displacement reaction. After a minute or two it would return to the hole and hop around near it as before. Sometimes the bird tried to enter alternative holes, but in all cases these were already occupied and it showed similar behaviour outside them. One Great Tit which had been dispossessed was seen to threaten two Blue Tits with lowered head and flicking wings. On February 21st, 1949, another Great Tit, finding its hole occupied by a Great Spotted Woodpecker, flew to a branch some distance away and gave a momentary head up aggressive posture although no other tit was near. This bird ^{again} showed behaviour of the same type, outside this hole on the next night, ~~also~~, when the Woodpecker was again in

occupation. One Great Tit who tried to enter a hole occupied by a Great Spotted Woodpecker was pecked vigorously and several feathers floated away.

On two evenings when a Great Tit was seen to enter a hole which it had certainly not occupied previously, it did so directly and apparently confidently, as though the site had been chosen in the day. Once, however, a Blue Tit in similar circumstances inspected the hole several times first, and entered only after much hesitation.

(c) Breeding season.

Some weeks before the start of nest building the male Great Tits started to roost in the foliage, but the females continued to roost in holes. These holes sometimes became their nesting places, but this was not always the case. Gooch (1935) found that one female Great Tit roosted in its nest from the third night after the start of nest building.

A watch was kept on one nest of a Great Tit on a number of mornings and evenings from the beginning of nest building. In the evening, the male accompanied the female to the box, the female usually entering immediately. The male then sat or hopped about a few feet from the box, preening or feeding. After a few minutes he inspected the hole of the box, clinging outside for a few seconds and then hopping up into the tree again. This was repeated several times, the male usually increasing his distance from the box between each inspection, so that he sometimes returned from twenty yards for the final one. Sometimes he merely looked into the hole from a foot or more outside. Whilst outside, the male usually called with 'twinks', 'chich ich ich' or variants of these, and sometimes sang. Only once was the

female seen to re-emerge after she had gone to roost - (the male was singing outside) - but she stayed out of the box for only a few seconds. During the early stages of nest building, the male usually inspected the hole about five times after the female had gone to roost, but this behaviour became less marked during the following fortnight, and he was not seen actually to inspect the hole after the beginning of incubation.

In the early morning, the male normally arrived at the box about half an hour before sunrise. Sometimes he started to sing immediately he arrived, sometimes he sat in silence near the box for a few minutes first. The first few notes of the song were usually thin and breathy, but they quickly gained strength. Different variants of the song were used, the male changing from one to the other without apparent cause. During nest-building and egg-laying the male was very active at this time, singing continuously, hopping around within a foot or two of the nest, and often perching on the roof and peering into the hole. On some mornings the male waited thus for over 40 minutes. When the female emerged, the male usually attempted to copulate immediately, sometimes pouncing on her while she was still within a yard of the box. Usually copulation took place in a hawthorn about ten yards away a few seconds after the female came out. On one morning the male copulated with another female, who had lost her mate, before his own mate emerged.

After the beginning of egg laying the male did not wait quite so near the hole as he had done previously, but sang from points several yards away. Singing was rather more intermittent than it had been previously. Once incubation had started the male became much less interested in the box, but continued to sing in the vicinity until the female came out.

Similar behaviour of the male of P. m. major outside the female's roosting site is mentioned by Zollinger (1930) and described by Kluijver (in litt.). A few observations made at nests of Blue Tits showed that the male of this species exhibited similar behaviour at dawn and sunset to that of the Great Tit. In both species the evening behaviour is clearly similar to that seen in winter, but of a higher intensity.

After the young left the nest the whole brood roosted in a fairly close group in the foliage (see also Bailly, 185³4).

2. Times of roosting and emergence.

(a) Late summer and autumn.

During the period when the majority of the Great and Blue Tits were roosting amongst the foliage, no real attempt to determine roosting and awakening times was made. The time at which the first bird was heard calling, in an area where a number were roosting, was, however, noted on a number of mornings. These records are summarised in Table 2^a by months.

Table 2^a a. Time of first call of Great Tits in relation to sunrise.

<u>Month.</u>	<u>No. of records.</u>	<u>Time in minutes before (-) or after (+) sunrise.</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
June	3	-3	+15	+4
July	1			+3
August	3	-8	-3	-5
Sept.	4	-12½	-0	-6
Oct.	4	-17	-5	-10

Table 2^a b. Time of first call of Blue Tits in relation to sunrise.

<u>Month.</u>	<u>No. of records.</u>	<u>Time in minutes before (-) or after (+) sunrise.</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
June	2	0	+8	+4
July	-	-	-	-
August	2	-4	-4	-4
Sept.	3	-13	-8	-10

These figures do not represent a sufficient number of records to enable any definite conclusions to be drawn, but they suggest that the time of awakening becomes progressively earlier with respect to sunrise in late summer and early autumn. Data for P. m. major in Munich given by Franz (1948) are in approximate agreement with the above figures, but in neither case are the number of observations sufficient to make a detailed comparison worth while. These records may be compared with the data in the next section: the interval between emergence and the first call is not usually more than about two minutes.

No data on roosting times between May and October were obtained in the study area, but a few observations were made between September 14th and 19th, 1949, on tits roosting in the side of a house in Chelsfield, Kent. These are summarised in Table 29.

Table 29. Roosting time in minutes before sunset of Great and Blue Tits.
Observations made between Sept. 14th and 19th, 1949, in Kent.

<u>Species.</u>	<u>No. of records.</u>	<u>Time in minutes before sunset.</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
Great Tit	4	27	11	19
Blue Tit	9	31	6	19

(b) Winter.

(1) Summary of observations.

Observations were made at the roosting tree from November 1948 to March 1949. Up to three Great Tits and two Blue Tits roosted in the tree every night. Although only a few of the tits which used the tree were colour-ringed, these were sufficient to show that the same individuals were not present throughout the winter. It was not possible to recognise the sex of any of the Blue Tits, and of some of the Great Tits, though certainly most of the Great Tit records refer to males.

The records of the times at which the tits were seen to enter their holes in the evenings and leave them in the mornings are summarised by months in Tables 30 and 31. (The times for Great Spotted Woodpeckers and Nuthatches, which were collected at the same time, are given in Section D).

Table 30a. Time of emergence at dawn of Great Tits in minutes before sunrise.

<u>Month.</u>	<u>No. of records.</u>	<u>Time in minutes before sunrise.</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
Dec. '48	3	25	16	21
Jan. '49	7	29	13	22
Feb. '49	8	26	12	19
March '49	15	26	8	19

Table 30b. Time of emergence at dawn of Blue Tits in minutes before sunrise.

<u>Month.</u>	<u>No. of records.</u>	<u>Time in minutes before sunrise.</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
Dec. '48	1	-	-	23
Jan. '49	3	35	21	29
Feb. '49	6	26	19	22
March '49	3	23	9	17

Table 31a. Roosting times of Great Tits in relation to sunset.

<u>Month.</u>	<u>No. of records.</u>	<u>Roosting times in minutes before (-) or after (+) sunset</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
Nov. '48	19	-10	+10	+1
Dec. '48	11	-5	+16	+5
Jan. '49	23	-30	+15	-5
Feb. '49	19	-31	+16	-12
March '49	22	-36	+1½	-16

Table 31b. Roosting times of Blue Tits in relation to sunset.

<u>Month.</u>	<u>No. of records.</u>	<u>Roosting times in minutes before (-) or after (+) sunset</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
Nov. '48	5	+2	+12	+5
Dec. '48	3	+7	+21	+13
Jan. '49	11	-20	+15	+3
Feb. '49	8	-29	+2	-13
March '49	12	-22	0	-13

(ii) General trends Relative to sunrise.

The time of emergence of both Great and Blue Tits changed little between December and March, averaging about twenty minutes before sunrise for the Great Tit and twenty-five minutes before for the Blue Tit. In the Great Tit the few records for females were not appreciably different from those for the males, though Kluijver (in litt.) found that males of P. m. major went to roost in winter about ten minutes later than the females.

Both species went to roost at a higher light intensity than that at which they emerged at dawn. The roosting time in relation to sunset varied markedly with the season. The Great Tits retired slightly later in December (5 minutes after sunset) than in November (1 minute after sunset). After December they retired progressively earlier, averaging 5 minutes before sunset in January, 12 minutes before in February and 16 in March. The time changed most rapidly in late January, during a period of mild weather. The records of Blue Tits were rather few but showed similar trends. They appear to roost a few minutes later than the Great Tits. Martin (1938) found the average roosting time of a Blue Tit in December and January was 4.3 minutes after sunset - a result very similar to that given above, which was at nearly the same latitude. Franz (1948) found that in Munich, Blue Tits awoke at about the same time as Great Tits, but roosted about five minutes later.

Records of the times of roosting and emergence are available for the Great Tit from four other areas. These are compared in Table 32. The figures for Helsinki, Finland, (Lehtonen, 1947), Lapland (Franz, 1943) and Munich, Germany (Franz, 1948) are derived from diagrams in the original papers: actual figures were not given. ^{They are thus only approximate.} The figures for Holland were obtained from the incomplete MS of Kluijver's paper on the Great Tit: his full figures were not available.

Table 32a. Roosting times in relation to sunset of Great Tits in different areas.

<u>Area.</u>	<u>Latitude.</u>	<u>Roosting time in minutes before (-) or after (+) sunset.</u>				
		<u>Nov.</u>	<u>Dec.</u>	<u>Jan.</u>	<u>Feb.</u>	<u>March.</u>
Lapland	67°N		c.+100	c.+70	c.+20	
Finland	60°N	c.+25	c. +25	c.+34	c. +8	-21
Holland	52°N	-5	+5	decreasing to	-10	
England	52°N	+1	+5	-5	-12	-16
Germany	48°N	+10	+15	+5	+5	0

Table 32b. Time of emergence or first call in minutes before sunrise of Great Tits in different areas.

<u>Area.</u>	<u>Latitude.</u>	<u>Awakening time in minutes before sunrise.</u>				
		<u>Nov.</u>	<u>Dec.</u>	<u>Jan.</u>	<u>Feb.</u>	<u>March.</u>
Lapland	67°N		c.110	c.80	c.35	c.15
Finland	60°N	c.35	c. 40	c.44	c.30	c.25
Holland	52°N	26	26	26		
England	52°N		21	22	19	19
Germany	48°N	c.25	c. 25	c.25	c.25	c.20

Although the figures given for the more northerly localities are based on rather fewer records than the others, certain conclusions can be drawn:-

- i). There is fairly close agreement between the records made by Kluijver and his helpers in Holland and those made in England at the same latitude.
- ii). In winter, Great Tits in Munich awaken at about the same time, relative to sunrise, as those in Holland and England. Their roosting times appear to be consistently rather later. The value of this later roosting time is obscure: it may be associated with greater scarcity of food or with climatic differences.
- iii). Whereas in lower latitudes the time of awakening of the Great Tit relative to sunrise remains approximately constant throughout the winter months, in the north the birds awaken considerably

earlier in midwinter than in February. Roughly speaking the time of awakening in the north changes in early spring to a value, which is similar to that obtaining throughout the winter further south.

iv). In midwinter the roosting time in relation to sunset is much later in the north than in Holland or England. The seasonal change in the roosting time in the far north is similar to that in the south, but the actual time of roosting remains later throughout the winter months.

Kluijver (in litt.) shows that the roosting time (but probably not the awakening time) is to some extent dependent on the availability of food. He shows that in spring the males start singing at a lower light intensity (c.1 lux) than that at which they retire in midwinter (c.250 lux). It is reasonable to suppose that a greater light intensity is required for feeding than for singing. In midwinter at 67°N the Great Tits go to roost nearly two hours after sunset, when the sun is 7° below the horizon. Under these conditions Kluijver states that the light intensity would be about 1 lux if no snow were present. However, as Kluijver points out, the light intensity is probably considerably higher than this because of the snow. According to information for which I am indebted to H. M. Nautical Almanac Office, Royal Greenwich Observatory, the illumination to be expected in the absence of snow would be even less than this - perhaps $\frac{1}{2}$ lux. The Nautical Almanac Office had "no precise information regarding the effect of snow on illumination, but as a very rough approximation it is possible to see twice the normal distance over snow-covered ground at low levels of illumination. This infers roughly a five-fold increase in illumination if attributable to that

factor~~s~~ only, but it is probable that the effect of heightened contrast is also involved". It is thus clear that the light intensity at which Great Tits go to roost in the Arctic in midwinter is considerably lower than that at which the Great Tits in more temperate latitudes go to roost. Palmgren (1944) has already shown that, in high latitudes, many species go to roost at relatively lower light intensities in midwinter than at other times of year.

In midwinter, the comparatively late roosting times at all latitudes, and the earlier awakening times at high latitudes, mean that the length of the tits working day is longer, relative to the length of daylight, than in summer. It seems probable that this is connected with the short length of time available for the collection of food in winter. The fact that Great Tits have a shorter working day in September than in March is probably connected with a greater availability of food in September.

(iii) Individual differences.

Individual differences in roosting and awakening times were often considerable. The greatest difference between two individuals on one night was 28 minutes in the case of the Great Tit and 12 minutes in the Blue Tit: in both species intervals of ten minutes were usual. In the morning, individual differences were less marked. Often all the birds came out in the course of a minute or two, and the greatest difference on any one morning between the times of emergence of individual Great Tits was nine minutes.

(iv) Meteorological factors.

Owing to the great individual differences noted above, and to the fact that the same individuals were not watched throughout the winter, it was not possible to make a statistical examination of the effect of the

weather on roosting and awakening times (i.e. on the proximate factors controlling roosting). In general, the birds retired earlier on cloudy evenings than on clear ones. Kluiver (in litt.) gives details of the effects of meteorological conditions in Holland.

(o) Breeding season.

(i) Male.

The times at which males left their boxes were recorded on three mornings in early April. These were 17, 21 and 22 minutes before sunrise - similar in fact to the records which had been made throughout the winter: the last of these was on April 13th. Records of the roosting of one male on April 9th and 10th were respectively 13 and 35 minutes before sunset.

No observations on the time of emergence or roosting of male birds were made during the nesting season. On a number of mornings in April and May, however, the time at which the first Great Tit was heard to sing was noted. These records are shown in Table 33. They give only an approximate indication of the time of emergence, for several minutes may elapse before the bird begins to sing. The actual interval between the time when 207 male arrived at the box and the time at which he began to sing was noted on three mornings - 6, 7 and 2 minutes. He may, of course, have spent some time in getting to the box from his roosting site. In addition, the first notes of the song are usually thin and soft, audible only at short range. The birds concerned had thus probably emerged about five minutes earlier than the figures indicate. On the other hand, these were the first birds heard, and sometimes five minutes elapsed before all birds were singing. They are thus roughly comparable with the figures given for the winter in

the previous section.

In early April singing started at about the same time as in winter - about 20 minutes before sunrise. In mid-April however, i.e. at about the time when nest building began, the males emerged much earlier - averaging about 40 minutes before sunrise. Kluijver's data on P. m. major show even earlier times than this. During late April and early May, when most females were incubating, the time when the first male was heard became later, until it was again about the same as the time at which the birds had emerged in winter. A similar conclusion was reached by Schwann (1921-2, quoted by Kluijver in litt.), but Kluijver could not prove it from his data. There are indications that the Great Tits were rising rather earlier than this at the end of May, just before the young flew.

(ii) Female.

During the period of nesting the roosting and awakening times of the females underwent marked changes. At the start of nest building, or shortly before, the females started to roost earlier and emerge later than during the winter. The length of the female's working day during part of the incubation period was about three hours shorter than it had been before the changes set in. The roosting and awakening times then return^{ed} gradually towards their original values.

Table 33 . Times of roosting and awakening of Great Tits in the breeding season. Times given in minutes before (-) or after (+) sunset or sunrise.
 (E) = 1st egg laid. (I) = Incubation started.. (H) = 1st egg hatched.

April.	First song of male.	Emergence of Female.			Roosting of Female.		
		Box 207.	Box 132.	Box 179.	Box 207.	Box 132.	Box 179.
2nd	-15						
3rd	-19						
4th							
5th	-24						
7th	-20						
9th							
10th	-24						
13th	-23						
14th					-23		
16th	-41	-26					
17th	-40	-20			+ 1		
18th	-42	-20			-21		
19th	-36	-24					
20th					-53		
21st	-33	- 3(E)	+ 6(E)		-53(E)	-19(E)	
22nd	-44	-15			-50	-56	
23rd			+ 3			-69	
24th	-39	- 7	- 1		-70	-87	
25th	-36	- 2	+ 9			-76	
26th			+ 9		-100	-89	
27th	-36	0	+14			-109	
28th		(I)	+ 1		-93(I)	-119	
29th	-35	0	+15(I)		-97	-111(I)	
30th	-30	+ 1	- 5			- 74	

Table 7³. (contd.) Times of roosting and awakening of Great Tits in the breeding season. Times given in minutes before (-) or after (+) sunset or sunrise. (E) = 1st egg laid. (I) = Incubation started. (H) = 1st egg hatched.

May.	<u>First song</u> <u>of male.</u>	<u>Emergence of Female.</u>			<u>Roosting of Female.</u>		
		<u>Box 207.</u>	<u>Box 132.</u>	<u>Box 179.</u>	<u>Box 207.</u>	<u>Box 132.</u>	<u>Box 179.</u>
1st			+15		-100	- 66	
2nd	-34	+18	+ 6		-120		
3rd			+22			-114	
4th		+25	+24		-119	-102	
5th			+36			- 83	
6th			+15			-87	
7th		+29			-113		
8th			+21			-104	
9th			+15			-142	
10th	-24	+20	+30		- 98	-137	
11th			+17			-172	
12th	-21	+13	+ 2(H)		- 80(H)	(H)	-64
13th	-25	+ 4		+13			-66
14th	-29	-17		+14	-48		-77
15th	-17	+ 7					-83
16th							
17th	-13	0					-59
18th				+11(H)	-65		-52(H)
19th				- 9			-61
20th				- 6			-65
21st				-11			-49
22nd				-16			-60
23rd							-73
24th							-46
25th	-13						
26th							
27th							
28th							
29th							
30th	-33						
31st	-29						

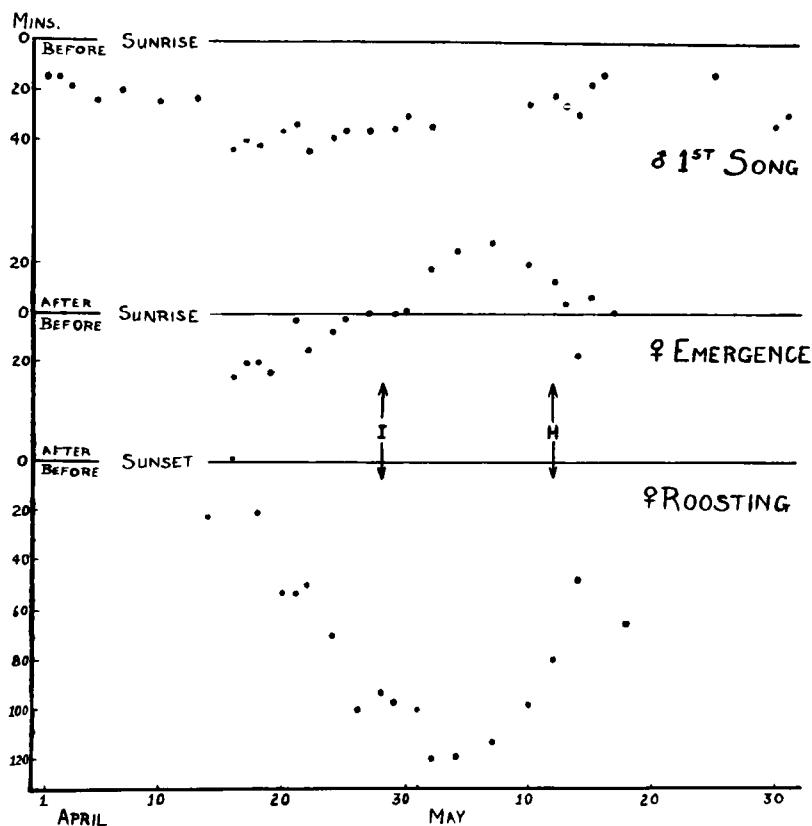


Fig. 4 . Roosting and awakening in the nesting season. Times of 1st song of Males, and times of emergence and roosting of Box 207 Female, relative to sunrise or sunset. Spring, 1950.

I = Incubation started.

H = 1st egg hatched.

In early April, before nest building began, one female went to roost (in Box 159) 25, 16 and 28 minutes before sunset on April 1st, 4th and 7th respectively. These figures represent little change from the roosting times in March. But the same bird emerged 3 and 9 minutes after dawn on April 2nd and 5th respectively - considerably later than most females in March. On April 2nd the bird was heard moving in the box 31 minutes before she emerged; but on April 5th the box was examined 6 minutes before she emerged, and she was apparently still sleeping.

During the breeding season fairly complete records of the times of roosting and emergence of female 207 were obtained: some records were also made at two other nests (132 and 179). These are shown in Table³³.

During the early part of nest-building the female of box 207 continued to emerge at about the same time as she had done in winter, but she rose later during egg laying. It would thus seem that her change to a later waking time came at a later point in the season than that of ^{the} female of box 159 cited above. At the start of incubation female 207 emerged at about sunrise, and became later still until on the tenth day of incubation she did not emerge until 29 minutes after sunrise. After this she emerged progressively earlier, until the time when she stopped roosting on the nest.

During nest-building the roosting time of female 207 varied from 23 minutes before sunset to one minute after sunset. Just before the laying of the first egg she started to become earlier, until in the middle of incubation she was roosting two hours before sunset. The times then became gradually later, but on the second and sixth days after the young hatched she was still going to roost 48 - 65 minutes before sunset.

The female of Box 132 had already started to emerge after sunrise by the day on which the first egg was laid. The changes in her times of

emergence were similar to those described for 207 female: her latest time was 36 minutes after sunrise on the seventh day of incubation. Her roosting times also followed a similar pattern to that of 207 female, though the times were rather more irregular and the maximum of 172 minutes was not reached until the day before the eggs hatched. Unfortunately this bird then deserted.

The few data available for the female of Box 179 during the last part of incubation and the first few days after the young hatched show trends similar to those of 207 female.

No data were obtained on the changes in roosting and awakening times during the rearing of second broods, since ^{none} some of the Great Tits in the study area attempted second broods in the year in which these observations were made. Kluijver (in litt.) has shown that the changes are similar to those which occur during the rearing of the first brood.

B. Other Parus Species.

In other Parus species, as in P. major, holes are in general preferred as roosting sites in winter, and foliage in summer. There are, however, some species which roost in foliage throughout the winter (e.g. P. a. atricapillus; Odum, 1941), and others in which there is great variation in the sites chosen, so that some individuals roost in holes in summer and others roost in foliage in winter (e.g. P. ater hibernicus, Ruttledge, 1946; see also Dunsheath and Doncaster, 1941). Odum (1941) found that in winter, members of a flock of P. a. atricapillus tended to roost near each other in the same part of the wood.

In all species the female roosts in the nest cavity during nesting, but

the actual stage at which she begins to do so seems to vary, even within one species. The cavity may have been her winter roosting site, or she may start to use it only a few weeks before nesting, (e.g. P. inornatus, Dixon, 1949), or only a few days before the first egg is laid (e.g. P. rufescens, Williams, 1941). No doubt these variations partly depend on whether the winter and nesting areas are the same, and on the availability of other roosting and nesting sites. Usually the female stops roosting in the nest before the young leave (e.g. P. atricapillus, Odum, 1941; Verheyen, 1947; P. palustris, Steinfatt, 1938). At this stage the old nest is perhaps unsuitable owing to the presence of parasites. The male roosts near the nesting hole.

An evening ceremony, similar to that described above for Blue and Great Tits, has been recorded by Dixon (1949) for P. inornatus, and also by Williams (1941) for P. rufescens.

There are few data on roosting and awakening times for other species, but the information available seems to indicate that tits in general roost earlier and rise later than other woodland species, at any rate in temperate latitudes. Williams (1941) found that P. rufescens roosted very much earlier than Thryomanes bewickii, and Odum (1941) found that P. a. atricapillus was early to roost and late to rise compared to other small birds. In both these species the females usually roosted before the males.

In the present study Marsh tits were often heard calling several minutes after the Great and Blue Tits had gone to roost, but there was little difference in the time at which these three species emerged at dawn. Thus these three species have, in the same area, progressively longer days with decreasing body size. (Marsh Tits are on average lighter than Blue Tits). The difference between the roosting and awakening times of Great Tit and

and Willow Tits found by Franz (1948) appear to have been small.

Odum (1941) found that P. a. atricapillus went to roost relatively later in October than in the winter months, and a few figures given by Rutledge (1946) for P. ater hibernicus point to a similar trend in this species. This is the opposite to what is suggested by the figures for Great and Blue Tits in the present paper. At other seasons Odum's data indicate trends similar to those found in the present paper.

C. Other Genera.

The male roosts with the female in the nest in Psaltriparus (Skutch, 1935; Addicott, 1938; Bent, 1946), Auriparus (Bailey, 1923; Whitaker, 1943), Aegithalos (Loos, 1913; Owen, 1945^b; personal observations) and probably in Remiz (Kozlova, 1933). At some nests of Aegithalos the male roosts outside the nest during the latter part of the feeding of the young. In Auriparus, nests are also used for roosting in winter (e.g. Bent, 1946). Winter flocks of Aegithalos species often roost in very close groups in bushes. Paschnatz (1936) has given a good description of this behaviour: he also gives some data on roosting times. Naumann (1905) states that Aegithalos caudatus sometimes roosts in holes.

D. Some Observations on Great Spotted Woodpeckers (Dryobates major) and Nuthatches (Sitta europea).

During the winter Great Spotted Woodpeckers and Nuthatches as well as tits roosted in the Roosting Tree. Their roosting and awakening

times may be compared with those of the tits.

(1) Great Spotted Woodpecker (Dryobates major).

Two male Great Spotted Woodpeckers used the tree for roosting. They did not use the same holes every night, and on some nights only one roosted in the tree. The two birds often fought near the tree at roosting time.

Table 34a. Roosting times of Great Spotted Woodpeckers relative to sunset.

<u>Month.</u>	<u>No. of records.</u>	<u>Roosting time in minutes before (-) or after (+) sunset.</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
Nov.	8	-13	+12	- 2
Dec.	7	-14	+ 6	- 6
Jan.	15	-54	+11	-12
Feb.	16	-63	- 5	-35
March.	14	-86	-26	-47

Table 34b. Times of emergence of Great Spotted Woodpeckers in relation to sunrise.

<u>Month.</u>	<u>No. of records.</u>	<u>Times of emergence in minutes before (-) or after (+) sunrise.</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
Dec.	2	-16	- 2	- 9
Jan.	6	-17	+ 7	- 1
Feb.	12	-12	+30	+ 9
March.	15	-10	+23	+ 8

The roosting and awakening times are summarised in Table 34. The records for both individuals have been shown together. The awakening times refer to the time when the bird actually left the hole: on some mornings they could be seen peering out of their holes at intervals for as much as twenty minutes before they finally emerged.

It will be seen that the Great Spotted Woodpeckers usually went to roost before sunset, even in midwinter, and that the roosting times became progressively earlier after midwinter; until, late in March, they were going to roost well over an hour before sunset.

The times of dawn emergence were considerably later than those of the tits in all months. In midwinter the woodpeckers emerged shortly before sunrise. In January and February they became later, until, in March, they emerged on average 8 minutes after sunrise.

A few observations made by Pynnönen (1939) on this species at $62\frac{1}{2}^{\circ}\text{N}$ in Finland gave the following roosting times:- Dec. 6th, c.60 minutes after sunset; Jan. 22nd, 20 minutes after sunset; Feb. 25th, c.46 minutes after sunset; March 11th, 48 minutes after sunset. Thus, at this latitude, the birds roost considerably later in midwinter than in England. Franz (1943), at 67°N , found roosting times of about 50 minutes after sunset in February.

The greatest recorded difference on any one day between the roosting times of the two individuals was 34 minutes: that of the awakening times was 22 minutes.

(ii) Nuthatches (Sitta europea).

A single male nuthatch roosted in the tree in December. It was joined by a female in late January, and from then on both birds roosted in neighbouring branches. The female was usually, but not invariably, a minute or two earlier in going to roost, and later in emerging, than the male. The records for both birds are shown together in Table 35.

Table 35a. Roosting times of Nuthatches relative to sunset.

<u>Month.</u>	<u>No. of records.</u>	<u>Roosting time in minutes before (-) or after (+) sunset.</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
Nov.	3	-11	- 4	- 7
Dec.	3	- 7	+ 5	- 2
Jan.	5	-31	+ 6	-10
Feb.	15	-52	-11	-33
March	14	-55	- 6	-27

Table 35b. Awakening times of Nuthatches relative to sunrise.

<u>Month.</u>	<u>No. of records.</u>	<u>Awakening times in minutes before (-) or after (+) sunrise.</u>		
		<u>Earliest.</u>	<u>Latest.</u>	<u>Average.</u>
Jan.	2	+ 2	+12	+ 7
Feb.	10	-10	+13	0
March	16	- 7	+14	+ 2

The times are in general intermediate between those of the Great Spotted Woodpeckers and the Great Tits. In midwinter the Nuthatches roosted within a few minutes of sunset: the time became relatively earlier in January, so that in February and March they usually went to roost about half an hour before sunset. They usually emerged within a few minutes of sunrise. There are not enough records to show whether or not there is a seasonal variation in the time of dawn emergence.

E. Winter Roosting - General.

The roosting and awakening behaviour of four hole nesting species has been studied. The following comparisons may be made between them.

(i) The length of the day's activity in midwinter in these species increased with decreasing body size - Great Spotted Woodpecker, Nuthatch, Great Tit, Blue Tit. This difference probably tends to disappear at high latitudes.

(ii) All these hole-roosting species had shorter days than at least the majority of the species in the same area which did not roost in holes.

(iii) In all four cases the roosting times in midwinter were rather later in relation to sunset than those in late January - March, and probably later than those in November. In the Great Spotted Woodpecker and Great Tit the seasonal changes in the roosting times is even greater in high latitudes than in England.

(iv) The dawn emergence times of Great and Blue Tits remained constant from late November to March in the area of the present study. Great Tits in the sub-arctic, and Great Spotted Woodpeckers both in sub-arctic and mid-temperate latitudes, emerge earlier relative to sunrise in midwinter than in spring.

(v) All species emerged at dawn at a lower light intensity than that at which they went to roost in the evening. Franz' (1948) records show that in midwinter in high latitudes this difference disappears - presumably because it is essential for the birds to utilize all the available light.

(vi) In all species, roosting times were considerably more variable - both from day to day and between different individuals on the same day - than awakening times.

F. The Study of Roosting and Awakening Behaviour.

It is possible that no entirely satisfactory account of the variation of roosting and awakening times can be given until sufficient data are

available for the behaviour of the species to be compared (i) with that of the same species at different latitudes, and perhaps in different habitats, (ii) with closely related species and (iii) with species with similar ecology. Data of this nature are not yet available for any species.

When such an analysis is attempted, a clear separation must be made between the ultimate and the proximate factors influencing the bird's behaviour. In the first place there is presumably an optimum length of the active day, which is determined in part by the time needed to discharge the various activities of life (feeding, courting, sleeping, etc.). The susceptibility of the bird to predators under different conditions of light may also influence the value of this optimum. In general, it is true to say that birds which roost in holes are better protected from cold and from predators than other similar birds which do not roost in holes. The optimum length changes with the season. In winter, when the length of the day available for feeding is relatively short and the night is long and cold, it is evidently necessary to utilize the hours of twilight for feeding, even though feeding may be less efficient then. In the breeding season early rising may be of importance for the projection of the territory. The optimum length (both the absolute length and the length relative ^{to the} solar day) also changes with latitude. All factors which affect the optimum length of the active day may be considered as ultimate factors.

Each bird has an internal diurnal rhythm of activity which causes it to be active for a period near to the optimum. (See e.g. Palmgren, 1949). This internal rhythm is modified by environmental stimuli so that the bird's active day is kept in the correct relation to the solar day. These environmental factors, in their relation to the internal motivation, are

probably similar to the sign-stimuli (Tinbergen 1948) associated with other instinctive activities. If this is the case, the difficulty which has been experienced in evaluating them in the past is due to (i) The complex nature of the adequate sign-stimulus: contributions are made by stimuli acting through different sense organs, (ii) The differential relation between the internal state and the adequate sign-stimulus. If the motivational factors are high, only a small influence from external stimuli is needed before the drive reaches the threshold value. (iii) The fact that other environmental factors may, through their influence on other drives, influence the effectiveness of the 'roosting drive': thus Kluijver (in litt.) shows that the availability of food may effect roosting times. The nature of the effect which incubation has on the roosting times of the female is obscure. Light is probably the most important of the proximate factors. Kluijver (in litt.) has given an analysis of some of the proximate factors in the case of P. m. major.

This discussion is, of course, largely hypothesis, but is intended to suggest how the study of roosting and awakening behaviour should be attempted.

A recent discussion of roosting behaviour in P. m. major, from a rather different point of view, is given by Franz (1948). This author does not always make a clear distinction between ultimate and proximate factors.

SECTION XIX PERIODIC VARIATIONS IN THE FREQUENCY OF
INSTINCTIVE ACTIVITIES.

SECTION XIX PERIODIC VARIATIONS IN THE FREQUENCY OF
INSTINCTIVE ACTIVITIES.

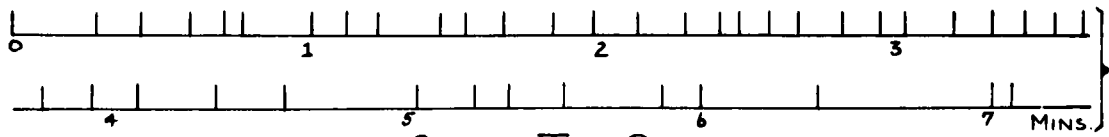
In the preceding sections a number of examples of the daily variation in the frequencies of various activities have been given.

These may be grouped under four heads as follows:-

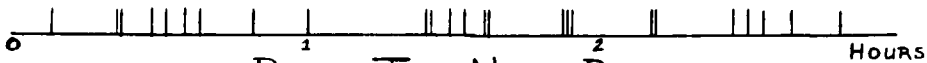
A. Rate of movement of flocks.	p. 18 .
Twink calls from flocks.	p. 22 .
Degree of integration of flocks.	p. 28 .
Reproductive fighting.	p. 132 .
Song.	p. 106 .
Hole inspections.	p. 169 .
Nest building.	p. 180 .
Feeding of female by male.	p. 194 .

All these activities show a peak in the early part of the day, either at dawn or in the first hour or two afterwards. They are at a minimum in the afternoon, and sometimes have a second peak in the evening. Some similar records have been obtained by Lehtonen (1947). Although it has not yet been proved, it seems highly likely that these diurnal variations are dependent on changes in internal factors, and not merely on fluctuations in the environment.

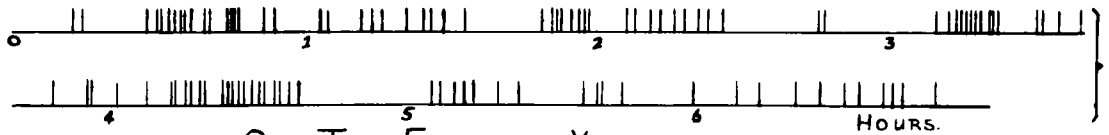
B. Incubation. The diurnal variation in incubation is small. The periods-off the nest tend to be longer in the afternoon, but the periods-on are shorter at some nests and longer at others. Since Kluijver (in lit.) has shown that there is a greater coefficient of correlation between temperature and the lengths of the periods-off than with the periods-on, this variation may be largely due to external factors, (pp. 197-204).



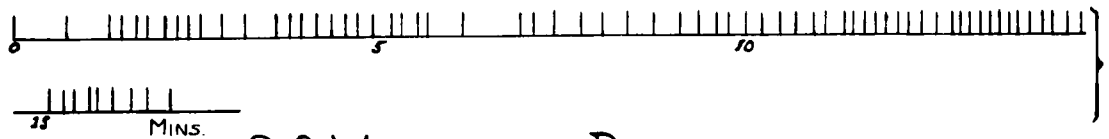
GREAT TIT SONG



BLUE TIT NEST BUILDING.



GT. TIT FEEDING YOUNG



G.S. WOODPECKER DRUMMING



G.S. WOODPECKER YIKING

Fig. 5 . Frequency of occurrence of various activities.
 Each vertical stroke indicates one song
 (i.e. a series of phrases), one visit to the
 nest, one 'roll' of drumming, or one 'yik'.

Activity
performed

293a

Threshold

Level of
energy

Level after
Activity performed
once.

Rate of
building
up energy.

Constant Drive

Zero

Activity
performed

(a)

Threshold

Level of
energy

Level after
Activity performed
once.

Rate of
building
up energy.

Zero

Activity
performed

(b)

Threshold

Level of
energy

Level after
Activity performed
once.

Rate of
building
up energy.

Zero.

(c)

Fig. 6 . Idealised representation of three possible types of fluctuation of the internal drive governing an instinctive activity.

C. Feeding the young. No regular variation, though some tendency for a peak in the early part of the day or in the evening. (p.213).

D. Roosting. The actual records of roosting times are given in Section XVIII. The rhythm of roosting and wakening is the most obvious case of the diurnal variation of an activity. The work of Palmgren (reviewed 1949) seems to show that it depends on an internal rhythm, modifiable by certain internal factors (e.g. the onset of incubation) and also guided by a complex of external factors, which may be different in different cases (e.g. predominately daylight in temperate latitudes, and humidity in the Arctic).

Casual observations indicated similar diurnal rhythms in other activities, though no definite data were obtained. Thus the displays in the pre-nesting season (p.76), territorial behaviour (p.83), scolding human intruders (p.248) and courtship feeding (p.146), seemed to be similar to other reproductive activities (type A). Preening seemed to have a peak just after dawn, another near mid-day and a third just before roosting time. It is possible that Incubation (type B) and Feeding the young (type ^CD) are really only modifications of type A.

The literature on the diurnal variation of activities in birds has been reviewed recently by Calhoun (1944) and Palmgren (1949), and such 24-hour periodicities will not be discussed further here.

Although all the activities associated with the reproductive drive seem to have a similar diurnal rhythm, they are not, of course, all shown simultaneously. Rather each activity is to be seen at somewhat irregular intervals. These intervals are determined by the fluctuations of the

internal drive, by the inter-actions between the drives (see Tinbergen, 1942; in litt.; also p.²³⁶), and by the changing stimulus situation.

Activities such as nest-building, feeding of the female by the male, and feeding of the young, show indications of a rhythm. Each activity tends to occur in bursts, in each of which the activity is repeated several times, with intervals in which it occurs only occasionally. Similarly song occurs in outbursts, which occur with decreasing frequency throughout the day. Even within each outburst fluctuations in the intensity and rapidity with which the notes are delivered can be detected: these presumably correspond to internal fluctuations in the rate of accumulation of "reaction specific energy", which are of an even shorter periodicity than those discussed above. (See e.g. the diagram for the drumming of the Great Spotted Woodpecker, Fig.5).

If we assume that each activity is associated with the expenditure of energy which is (more or less) specific to it, in the manner pictured by Lorenz (in litt.) we may imagine three idealised possibilities. If the rate of building up energy were constant, we should expect that the energy would reach threshold level at regular intervals and so the activity would occur regularly, (Fig 6). If, on the other hand, the rate of building up energy showed sudden marked fluctuations to a high level, with long periods at or near zero level in between, we should expect the activity to be performed in short bursts with intervals between. The third possibility is that the rate of building up energy should fluctuate more slowly. In this case the intervals between the performances would decrease as the building up became more rapid until, when the rate was at its maximum, a burst of activity occurred: then, as the rate decreased,

the intervals would become longer. Of course, if the rate is low "bursts" may not occur, and the activity will be repeated at more or less regular intervals.

The feeding visits of the male Great Tit, and some other activities, correspond most closely to the third of these possibilities. A close inspection of Fig. 5, will show that the feeding visits tend to occur in bursts, after each of which the intervals between visits increase and then decrease again until there is another burst of activity. In practice, of course, there may be numerous complications which make the rhythm far less regular than is shown in the idealised Figure 6. Among such complications may be mentioned:-

1. Each visit to the nest involves a chain of activities, and the energy expended in carrying through this chain of activities may not be the same on each visit. Thus food may be more difficult to find on one visit than another, more time may be spent in nest-building on one occasion than on another, and so on.

2. When an action, or chain of actions, is performed once, the threshold level for it to be performed again seems to be lowered by that performance for a short time interval. Thus during the intervals between the bursts of activity, when the bird is only visiting the nest occasionally, one of these occasional visits may be followed by another. After such a double visit the level of energy may be lowered abnormally, so that a longer interval than would be expected may elapse before the next visit.

3. External stimulation may complicate the situation in several ways. In feeding the young such stimulation may come either from the young

or from the food. It is known that broods of many young receive more visits than broods of few young (e.g. Gibb, in litt.), but the exact way in which this effects the rhythm of feeding the young is not yet known. Also the discovery of a plentiful supply of food may stimulate the parents to feed very rapidly (Pullen, 1946): here again the mechanism is unknown, but it may be compared with the situation when food is difficult to find and more energy is used up on each trip.

4. External stimulation may also act by influencing other drives which may interact with or inhibit the drive in question.

Considerations of space forbid the presentation of numerous examples of these fluctuations, but a few are shown in Fig. 5. One point requires emphasis. Each burst of activity usually starts gradually, and dies away gradually. In most cases the growth of activity at the beginning is ^{more} rapid than the dying away at the end. The fact that ^{the rate of building up energy} a ~~drive~~, once aroused, takes some time to ^{decrease} ~~die away~~ is responsible for the "after-reaction", (~~see p.~~) Thus on several occasions when the Sparrow Hawk dummy was removed whilst the tits were scolding it, the birds continued for several minutes. In reproductive fighting the after impulses are usually dissipated as song. The after-reaction usually consists of a number of short bursts of activity, occurring, as we should expect it, at increasingly long intervals. In each successive burst the activity usually appears at a lower intensity than it did in the previous one: the reason for this is not clear.

The actual roles of internal and external factors in the causation of these rhythms are, of course, open to experimental investigation.

SECTION XX THE GENUS PARUS.

In the preceding pages the annual cycle of the Great Tit has been outlined, and some aspects of its behaviour analysed. Wherever information was available, comparisons have been made between the Great Tit and the other species of the genus Parus. In general, the different Parus species show remarkably similar behaviour: the differences which do occur may be grouped as follows:

(i) General outline of the annual cycle. The only differences which occur between the species lie in the degree of migration or dispersal shown (Section V), the occurrence of second broods (p.226), and the extent to which individuals flock or hold territories in winter (p.48). These differences are probably all directly related to local ecological conditions. Indeed differences of this type may even exist between different populations of the same species.

(ii) Nest sites. We have seen that the different Parus species occupy slightly different nest sites: also, some species excavate their own holes and others occupy natural holes (Section XI). Such differences are also clearly related to local ecological conditions. This is illustrated most clearly by the ~~fact that~~ those species which nest in coniferous woods, where natural holes are scarce; P. cristatus usually excavates its own hole and P. ater often nests in holes in the ground.

(iii) Roosting times. Even the same species may show different diurnal rhythms of roosting and awakening in different areas. Similar differences exist between different species in the same area. These also are clearly related to local ecological conditions, for those species with the larger body-size have the shorter active day (Section XVI)!

(iv) Displays. Such differences as do exist between the displays and the details of the behaviour patterns are for the most part of degree only. Thus all the Parus species which have been studied exhibit the head-up posture in reproductive fighting, but in the Great Tit this has been elaborated much more than in the other species. Similarly, all species use gliding or moth flight in the early courtship displays, but they are much more common and elaborate in the Blue Tit than in the others.

(v) Calls and songs. The most obvious differences between the species lie in the call notes and songs. Such differences may have^{or have} had selective value in the prevention of inter-breeding. However, there are often marked individual and geographic differences even within one sub-species, and little is yet known of the degree to which songs are inherited or learnt.

(vi) Feeding behaviour. Only brief references to feeding behaviour have been made in the preceding sections, but it is here that the most noticeable differences between the Parus species are to be found. Ecological differences must exist between the various species, and these must ultimately depend on differences in behaviour as well as on structural adaptations. It is generally true to say that the various species deal with their food in much the same way once they have found it, so that the differences must lie in the food-searching or appetitive behaviour, and in the innate releasing mechanisms of feeding. Thus although it is often said that the appetitive behaviour is the least stereotyped part of an instinctive chain of behaviour, yet the appetitive behaviour associated with feeding ^{is} was probably sufficiently rigid to have provided a basis for speciation .

We thus see that the major differences between the Parus species are related to ecological factors, while the displays and other similar behaviour is much more conservative.

Unfortunately sufficient data are not yet available for comparison to be made between the different genera of the Paridae, except in the matter of nest-building. Here we have seen that members of the different genera build very different nests, the only obvious similarities being between Psaltriparus and Aegithalos (Section XII).

POSTSCRIPT. AGGRESSIVE BEHAVIOUR TOWARDS STUFFED BIRDS.

- A. Introduction.
- B. Techniques.
- C. Behaviour towards the Dummies.
- D. Preliminary Summary of Results.

POSTSCRIPT. AGGRESSIVE BEHAVIOUR TOWARDS STUFFED BIRDS.

A. Introduction.

In the springs of 1949 and 1950 a further study of reproductive fighting was made with the aid of stuffed specimens. These were placed near the nests of Great and Blue Tits during incubation and the feeding of the young.

The objects of the experiments were: (i) To obtain more information concerning the mechanisms involved in reproductive fighting. A stuffed bird outside the nest presents a constant stimulus situation, and thus a much simpler one than any occurring in natural skirmishes. Since the external stimulus situation is constant, changes in behaviour must be due to internal changes in the bird. (ii) To obtain information on the relative effectiveness of the different parts of the plumage colour patterns in releasing reproductive fighting. For this purpose experiments were carried out with stuffed birds whose colour patterns had been altered in various ways. A large number of tests will be necessary before final conclusions can be drawn, and it is planned to continue this work over several seasons.

Because of the late breeding season the 1950 programme is not yet complete. The present section is therefore confined to brief discussions of the techniques used, and of the behaviour of the birds towards the dummies. It includes also a short summary of the results obtained so far.

B. Techniques.

Male Great and Blue Tits, stuffed and mounted in a normal perched posture, were used. In order to investigate the releasing values of the various parts of their colour patterns, dummies with parts of the normal pattern occluded were used. Attempts to dye the feathers failed, so poster paints were employed. These had a slight tendency to matt the feathers; but the effect was at most a small one. The following dummies were employed.

GA. Normal male Great Tit.	BA. Normal male Blue Tit.
GB. Male Great Tit with the white cheeks painted black.	BB. Male Blue Tit with head all blue.
GC. Male Great Tit with underparts completely black.	BC. Male Blue Tit with underparts all blue.
GD. Male Great Tit with underparts (including throat) completely yellow.	BD. Male Blue Tit with black ventral stripe similar to that of a Great Tit.

W. Wood Warbler (Phylloscopus sibilatrix).

The dummies were attached to the top of a vertical stick which also bore two horizontal sticks at right angles to each other slightly below the dummy. This stick was placed at standard distances from the nest boxes.

In order to compare the effectiveness of dummies with different colour patterns in releasing fighting behaviour, it is, of course, necessary to eliminate or keep constant all other factors which might influence the response, so far as is possible in the field. These factors, and the steps taken to deal with them, are listed below:-

(i) Posture of dummy. All dummies used were mounted as nearly as possible in the same posture, and were placed facing towards the nest-box.

(ii) Distance from the nest-box. Standard distances were used.

(iii) Seasonal variations. The strengths of the fighting and fleeing drives show marked seasonal changes (p. 32). The extent of these changes during incubation and the feeding of the young is being tested experimentally, but they appear to be small in the Great Tit. In the meantime only experiments carried out at approximately the same stage in the breeding cycle have been compared.

(iv) Diurnal variations. The strengths of the fighting and fleeing drives show marked diurnal changes, (p. 32). It is, of course, impracticable to carry out all experiments at exactly the same time of day, but work was confined to the period 0700 - 1100 hours G.M.T.

(v) Weather. Weather conditions have a marked effect on the occurrence of many of the activities associated with the reproductive drive. This factor cannot be eliminated, but no observations were made on rainy or very dull days.

(vi) Inter-actions between drives. The response of a bird to the dummy may depend to some extent on the strengths of the other drives influencing its behaviour. Examples of this will be seen in the next section. (cf. also Tinbergen, 1948). It is not possible to control this factor in the field, but it must be considered in assessing the results.

(vii) Conditioning. If the responses towards different dummies are to be compared, it is necessary to ensure that the birds used have not

become negatively conditioned (see p.¹³³) to dummies, or that the effects of conditioning are ^{eliminated} stimulated. In the first series of experiments which were carried out (series A), an attempt was made to eliminate the effects of conditioning as follows. Twelve nests were used to compare the relative effectiveness of six different dummies. At nest 1, dummy A was presented first, followed by B, C, D, E and F. At nest 2, dummy B was used first, followed by the remainder C, D, E, F and A - and so on at the nests 3 - 6. At nests 7 - 12 the order of presentation of the dummies was the reverse of the above - i.e. F, E, D, C, B, A. By following this scheme the effects of conditioning should have been on the average the same for all dummies. In order to reduce them still further, however, no dummy was exposed for longer than 3 minutes on any one occasion, and no nest was used more often than once every other day. This meant that the above scheme was not always followed strictly for every individual, for it sometimes happened that one bird of the pair scolded the dummy for three minutes before the other appeared on the scene: the dummy then had to be removed although it had only been seen by one of them.

In spite of these precautions, the effects of conditioning were still considerable. Nearly all the actual attacks were made on the first two or three occasions when a dummy was presented at any one nest. It was therefore clear that this technique did not give the best results possible, for the differences between the responses to the different dummies were smaller after some conditioning had taken place than before. The results of experiments made later in the series at any one nest thus

tended to obscure those of earlier ones.

In order to get the best results, therefore, comparisons were made between the responses of birds which were seeing a dummy for the first time. Dummies were thus presented at as many different nests as possible (Series B).

C. Behaviour Towards the Dummies.

The responses shown by both Great and Blue Tits to the dummies were always of an aggressive, and never of a sexual, nature. They varied from immediate attack to a mere hesitation in the bird's breeding activities.

In vigorous attacks the bird flew onto the dummy's back and pecked at its head. Occasionally, in less intense attacks, the bird merely sidled along the horizontal stick and pecked at the dummy from an inch or two away: on such occasions the attack drive was presumably only slightly greater than the fleeing drive. Head-up postures usually preceded and sometimes followed attacks. In the Great Tit these were never so marked or sustained as those occurring in natural skirmishes, but female Blue Tits sometimes gave quite well-marked head-up postures. Sometimes the bird gave slight head-up postures although no actual attack was made.

Between attacks the bird hopped about near the dummy with feathers sleeked, wings very slightly open, tail slightly spread and the body in a crouched, horizontal, position.

When the dummy was scolded, but not attacked, the bird hopped around in a similar fashion. Great Tits usually called "chich ich ich ich", but "twinks" were also used and were usually associated with wing-flicking. Blue Tits called "derr tt tt tt". Blue Tits usually raised their crest feathers (this was much less evident in Great Tits) and often also their cheek feathers. Blue Tits, and to a lesser extent Great Tits, often jerked the body from side to side with a pendulum-like movement. Similar behaviour towards predators seems to be due to a conflict between attack and escape.

The wings were usually opened rather more in Blue Tits than in Great Tits. They often flicked or shivered their wings while scolding or attacking the dummy. Flicking the wings seemed to indicate inhibited fleeing, as it does in other contexts, (see p. 247). Wing-shivering also sometimes seemed to be associated with inhibited fleeing. At other times it seemed to be connected, not with flying away, but with flying to the nest with food. Since wing-shivering forms part of the begging display of the female in courtship feeding, it may also sometimes have been connected with this. On only one occasion was a Great Tit seen to shiver its wings while scolding a dummy.

Male Blue Tits often used the 'straddling walk', half spread wings and spread depressed tail which are often seen in the early courtship displays (p. 258). The significance of this is obscure.

In some experiments the presence of the dummy merely caused the bird to hesitate slightly in the course of its previous activity. Birds would hop about near the dummy without scolding, or sit and look at it from a few feet away.

It was often evident that the behaviour towards the dummy was influenced by the strength of other drives. Thus females returning to incubate would often hesitate, look at the dummy, and then enter the box. Sometimes females made vigorous attacks, and then entered the box almost immediately. Male Blue Tits often offered the female food while she was attacking the dummy, and sometimes the female would snatch the food between attacks. Sometimes the male would move hesitatingly backwards and forwards between the dummy and the female, suggesting that the attack and feeding-the-female drives were alternately governing his actions, though neither was strong enough to produce a complete chain of behaviour.

Although the dummy was sometimes attacked immediately, on other occasions the bird gave a response of gradually increasing intensity - slowly working up through scolding to attack. Conversely, the response invariably waned after a while. Such changes clearly depend on the relative rates at which the attack drive builds up and is dissipated.

D. Preliminary Summary of Results.

For the reasons explained above, the Series A experiments were inadequate to provide proof of differences in response to differently coloured dummies of the same species, though they were suggestive. They did, however, show that dummies of a different species produced a much smaller response than those of the same. The results are summarised in Tables 36 and 37, and show the following tendencies:-

(i) Responses of Great Tits.

(a) In general, males showed a rather stronger response to the dummies than females.

(b) Blue Tit dummies evoked a much weaker response than the normal Great Tit dummy. Even the addition of a black ventral stripe to the Blue Tit dummy made no apparent difference to the response.

(c) A Great Tit dummy with all black underparts evoked approximately the same response as the normal, but a dummy with all yellow underparts evoked a smaller response.

(d) A Great Tit dummy with an all black head appeared to be rather less effective towards males but rather more effective towards females.

(ii) Responses of Blue Tits.

(a) In general, females showed a rather greater response to the dummies than males. This was particularly the case early in incubation, when males often disregarded the dummy in attempting to feed the female.

(b) A Great Tit dummy evoked a smaller response, and a Wood Warbler dummy a much smaller response, than Blue Tit dummies.

(c) A Blue Tit with all blue underparts was about as effective as a normal Blue Tit.

(d) A Blue Tit with a black ventral stripe seemed to be slightly more effective than a normal Blue Tit. This may be a case of a 'super-normal' stimulus.

Of course, many more experiments are needed to confirm these results. A little further evidence is available from the Series B

experiments: the records of the responses of Great Tits and Blue Tits on the first occasions on which dummies were presented are shown in Tables

and 36 .39 These illustrate even more clearly some of the tendencies shown by the series A experiments.

The work is being continued.

Table 36 . Series A experiments. Frequency distribution of responses of Great Tits to dummies. The series was begun at each nest within a few days of the start of incubation. Dummies at 8 ft. from nest.

	<u>Response of Male.</u>				<u>Response of Female.</u>			
	<u>Attack.</u>	<u>Scold- ing.</u>	<u>Hesita- tion.</u>	<u>No re- sponse.</u>	<u>Attack.</u>	<u>Scold- ing.</u>	<u>Hesita- tion.</u>	<u>No re- sponse.</u>
Normal Great Tit.	2	5	3	0	0	5	3	0
Great Tit with Black Head.	1	5	2	0	3	1	4	0
Great Tit with all Black Under-parts.	2	5	3	0	1	6	2	0
Great Tit with all Yellow Under-parts.	0	9	2	1	0	2	5	0
Blue Tit.	0	6	1	2	1	1	3	0
Blue Tit with Black Ventral stripe as in Great Tit.	0	4	7	1	0	4	2	0

Table 37 . Series A experiments. Frequency distribution of responses of Blue Tits to dummies. The series was begun at each nest within a few days of the start of incubation.
Dummies at 8 ft. from nest.

	<u>Response of Male.</u>				<u>Response of Female.</u>			
	<u>Attack.</u>	<u>Scold- ing.</u>	<u>Hesita- tion.</u>	<u>No re- sponse.</u>	<u>Attack.</u>	<u>Scold- ing.</u>	<u>Hesita- tion.</u>	<u>No re- sponse.</u>
Normal Blue Tit.	2	6	1	0	5	2	1	0
Blue Tit with Blue Head.	1	7	2	0	3	1	4	0
Blue Tit with Blue Under-parts.	1	8	1	0	4	1	1	0
Blue Tit with Black Ventral Stripe as in Great Tit.	4	5	0	0	5	4	2	0
Normal Great Tit.	0	6	3	0	1	3	4	2
Wood Warbler.	0	2	1	4	0	0	1	4

Table 36 . Series B experiments. Frequency distribution of responses of Great Tits to dummies. Dummies presented during incubation at 3 ft. from nest.

	<u>Responses of Male.</u>				<u>Response of Female.</u>			
	<u>Attack.</u>	<u>Scold- ing.</u>	<u>Hesita- tion.</u>	<u>No re- sponse.</u>	<u>Attack.</u>	<u>Scold- ing.</u>	<u>Hesita- tion.</u>	<u>No re- sponse.</u>
Normal Great Tit.	7	3	0	0	1	4	1	0
Great Tit with Black Head.	1	5	0	0	2	2	2	0
Great Tit with Black Underparts.	3	1	0	0	1	3	1	0
Great Tit with Yellow Underparts.	2	2	0	2	1	3	4	0

Table 39 . Series B experiments. Frequency distribution of responses of Blue Tits to dummies. Dummies presented during incubation or the first 2 days after hatching at 3 ft. from the nest.

	<u>Response of Male.</u>				<u>Response of Female.</u>			
	<u>Attack.</u>	<u>Scold- ing.</u>	<u>Hesita- tion.</u>	<u>No re- sponse.</u>	<u>Attack.</u>	<u>Scold- ing.</u>	<u>Hesita- tion.</u>	<u>No re- sponse.</u>
Normal Blue Tit.	2	6	0	0	2	4	2	0
Blue Tit with Blue Head.	0	3	1	0	0	5	1	0

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