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TERRITORY AND BREEDING DENSITY IN THE GREAT TIT, *PARUS MAJOR* L.¹

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Abstract. This paper describes an investigation into whether or not spring territorial behavior was limiting the breeding density of a population of Great Tits on Wytham Estate, near Oxford. The analysis of distances between neighboring nests showed that nest sites were more spaced out than would be expected from a random distribution; this indicated that interactions between the birds produced at least a local density-limiting effect. In 2 successive years, established territorial pairs were removed from a stable spring population in mixed woodland. The removed birds were rapidly replaced by new pairs. These newcomers were largely first-year birds; they came from territories in the hedgerows that surrounded the wood; the vacated hedgerow territories were not refilled. The hedgerows were found to be suboptimal in terms of reproductive success. Thus territory limited the breeding density in the optimal habitat.

Song advertisement is probably important in maintaining territorial boundaries, hedgerow birds being able to detect the presence of individual woodland territory holders by recognizing their songs.

The effect of winter food supply on the population was investigated by supplying excess food throughout one winter. This artificial food supplement appeared to have no effect on the number of Great Tits breeding in the wood, but did produce an increase in the case of a related species, the Blue Tit.

The results show that territorial behavior influences density; this is not considered to be a function of territory in the evolutionary sense, but rather a consequence of spacing out that has been selected for in some other context. A possible advantage of spacing out in the Great Tit is as a defense against predators. Territory size varies considerably from year to year. These variations are the result of interactions between the birds themselves, rather than direct adjustments of territory size to fluctuations in some environmental resource.

Even though territory has an effect on the number of birds breeding in the wood, it is not an important density-dependent factor acting to regulate the population.

This paper describes an attempt to investigate experimentally whether or not spring territorial behavior was limiting the breeding density of a population of Great Tits on Wytham Estate, near Oxford. Apart from exemplifying the general problem of territorial behavior and population dynamics, which has attracted much attention in recent years (e.g. Wynne-Edwards 1962; Brereton 1966; Crook 1965, 1968; Lack 1966; Chitty 1967a, b; Rowan 1966; Brown 1969a, b; Fretwell and Lucas 1969, Fretwell 1969, Fretwell and Calver 1969), the Great Tit was particularly interesting in this respect since the background information concerning its population ecology is extremely well documented. Long-term studies have been carried out in Holland since 1912 (Kluijver 1951, 1966, 1967) and in Oxford since 1947 (Lack 1966, Perrins 1965). In addition there have been several shorter term studies, for example in Belgium (Dhondt and Hublé 1968), Germany (Creutz 1962), Sweden (Ulfstrand 1962) and Latvia (Vilks 1966). In spite of this wealth of data, the factors determining numbers of Great Tits are not well understood.

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Before describing the present findings, the relevant conclusions from the long-term study carried out by various workers at the Edward Grey Institute in Wytham Woods will be briefly summarized. The Great Tit in Wytham breeds almost exclusively in nest boxes (which are supplied in excess); thus the basic data of the Oxford study consist of a census of all breeding pairs, eggs laid, young hatching and young leaving the nest. The Great Tit in England is nonmigratory, and in some years of the study an estimate of the winter population has been made between November and January (see Lack 1966, p. 59 and p. 67 for method).

The average clutch size is around nine eggs, and each pair produces, on average, about six fledged young. Both clutch size and hatching success are density dependent, and appear to have a major influence in regulating the population (Krebs 1970a) (the term regulate is used in the restricted sense of referring only to the action of density-dependent factors on the population).

The disappearance of Great Tits in Wytham outside the breeding season can be divided into "autumn disappearance" (between July and November-January, when the winter population estimate is made) and "winter disappearance" (be-

tween the winter population estimate and April, when the breeding census is taken). The autumn disappearance is mainly of juveniles (in most years the ratio of juveniles to adults has fallen from 3:1 at fledging to 1:1 in winter). This disappearance is large and is mainly responsible for annual fluctuations in breeding numbers (Lack 1966, Fig. 15). Perrins (1965) has suggested that juvenile disappearance in fact occurs in the first few weeks after fledging and is due directly to starvation. Food is known to be short at the end of the breeding season (nestlings of late broods frequently die of starvation) and observations of a sample of color-ringed fledglings indicated that a greater proportion of lighter than heavier birds (the former presumably have less food reserves) had already disappeared within a month of leaving the nest. Kluijver (1967), however, has suggested that in Holland autumn disappearance is due to emigration caused by territorial behavior (see also Watson 1967a, Tompa 1964, Pinowski 1965 and Gibb 1960 for autumn territorial dispersion in various species). In Holland, unlike England, Great Tits usually raise two broods. Thus at the time when Oxford Great Tits are thought to be short of food, the Dutch birds are successfully raising a second brood, suggesting that in Holland food is not scarce. Ringing recoveries show that in Holland (Kluijver 1967) and Belgium (Dhondt and Hublé 1968) second-brood young are dispersed further than the first brood by October. Kluijver attributes this to the superiority of first brood young in competition for territories in early September. Although Wytham Great Tits do show some autumn territorial behavior (pers. obs., but see Hinde 1952), it is possible that the mechanism of autumn disappearance is different in the English and Dutch populations.

In discussing the causes of winter disappearance, Lack (1966) considers four possibilities: predation, disease, starvation and territorial behavior. The first two are dismissed as being unlikely causes. No estimate of winter food availability has been made in Wytham, but the fact that tits spend most of the day in winter feeding (Gibb 1954), suggests that food might be scarce. The fourth possibility, that winter disappearance in the Great Tit is caused by territorial behavior in the spring, was originally suggested by Kluijver and Tinbergen (1953) in Holland. These authors found that in narrow strips of broadleaved woodland, the breeding density was higher and more stable from year to year than in surrounding areas of pine wood. This was taken to indicate that the optimal areas (broadleaved wood) were filled up first, until the territorial behavior of residents re-

sulted in later settlers breeding in suboptimal (pine) habitat ("the buffer effect"). Thus territory limited breeding density in optimal habitats. The results, however, are not unequivocal. Kluijver and Tinbergen divided their data into three groups: one for 10 years' observations at Hulshorst and two sets of 12 and 9 years' data from a larger area at Wageningen. Only one of these areas (Hulshorst) showed a strongly significant buffer effect in mixed woodland. Further, in this area the Coal Tit showed a similar buffer effect, although it is primarily a pine wood species and should therefore have shown a reverse buffer effect. Lack has argued that the main objection to territorial control of breeding density in the population in Marley Wood is that the density has been rather variable from year to year, especially in 1961, when the breeding density was 70% higher than in any other year. These year-to-year variations have not been related to changes in availability of food for the young. The possibility that territorial behavior played a role in this winter disappearance was investigated in the present study.

SPACING OUT OF NEST SITES

One indirect method of testing whether or not territoriality limits breeding density is to test whether it results in spacing out of nests (Patterson 1965). As Gibb (1956) has pointed out, the difference between "spacing out pairs present" and "limiting breeding density" is only one of degree. If pairs are spaced out over a large area, the density in a locality within the area is automatically limited.

Methods

The spacing pattern of Great Tit nests was investigated as follows. An accurate map of all nest boxes in Marley Wood (described in Perrins 1965) was made. This was based on a large-scale aerial photograph (1:1,600) and triangulation of nest box positions using a prismatic compass. The coordinates of each box were measured and the distance to the nearest neighboring nest of each occupied box was calculated by computer.³ Each of 10 years' data were analyzed in this fashion to provide an observed distribution of nearest neighbor distances. The 10 years (1958-67) were arbitrarily divided into "high density" (50 or more pairs, mean = 63) and "low density" years (mean = 38 pairs), in order to detect any possible density-related differences in spacing. The null hypothesis was that boxes were being occupied at random. The random distribution was obtained by programming the computer to "occupy" a number

³ Programs written by J. M. Cullen.

of boxes at random. Only boxes which had been used at some time during the 10 years were offered as available for "occupation" by the computer. The random occupation process was repeated 30 times with 38 boxes being occupied (corresponding to low-density years) and 30 times with 63 boxes occupied. The average random distributions were taken for each of these densities and compared with the observed distributions.

Results

Figure 1 shows that both in high- and low-density years boxes close together were occupied less often than would be expected on a random basis; i.e. nests were spaced out. A measure of the degree of spacing was obtained by expressing the difference between observed and expected distributions as a percentage of the expected (Fig. 2). This suggests (although not very convincingly) that the "spacing pressure" was stronger

near a nest and decreased with increasing distance. This would be expected if, as has been previously suggested (Hinde 1952 p. 53, Dhondt 1966), the aggressive tendency of the Great Tit is highest near the center of the territory and decreases towards the boundaries. In "high density" years there was a spacing effect which was noticeable up to 40 m from the nest; in low density years up to 50 m from the nest.

Some authors (e.g. Brown 1969b p. 294) have argued that spacing out which results from "avoidance" of neighbors should be distinguished from spacing out as a result of actual territorial repulsion. However, these two are not alternative mechanisms; rather avoidance is the effect of repulsion. In some cases it may be possible to make a subjective distinction between situations in which an individual "shows aggression" to an intruder and this leads to withdrawal of the latter, and situations in which the resident "does nothing" and the intruder withdraws. This division becomes less easy to make in cases where "territorial aggression" involves cues that we cannot normally perceive (e.g. ultra-sound [Sewell 1968], scent [Schenkel 1966]). This distinction also becomes difficult in dealing with spacing out in some invertebrates (e.g. Crisp 1961, Connell 1963). Since avoidance and repulsion cannot be considered as separate phenomena, it seems reasonable to include all cases of spacing out of individual's home areas as examples of territory.

Although results described above show that, locally at least, interactions between birds were limiting density, further investigation was required to show what influence this had on the total number of birds breeding in the population.

THE REMOVAL EXPERIMENTS

The hypothesis that the presence of territory holders limits numbers in a given area can be tested experimentally. If, when territorial residents are removed from a stable population, they are replaced by new individuals (which are not merely neighboring residents expanding their territories), it can be deduced that prior to removal, potential settlers had been prevented from occupying territories by the presence of residents. If, as is the case in most territorial species, holding a territory is a prerequisite for breeding, the removal experiment tests whether territorial presence limits breeding density. If replacement occurs, further observations would be necessary to establish the origin and fate of nonresidents (e.g. Watson 1967a) and to test exactly what aspects of the territory holder's presence (e.g. visual stimuli, vocalizations, chasing off intruders) are required

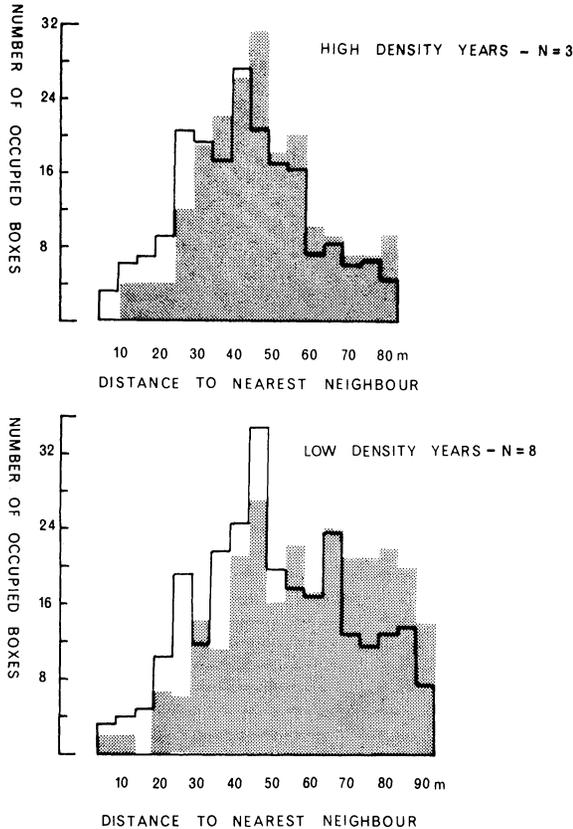


FIG. 1. Histogram of observed and expected distributions of nest box occupancy in "high" and "low" density years. The numbers of boxes actually occupied at different distances from the nearest neighbor are shown by the shaded histograms, the expected distribution, obtained by random occupation of boxes, is shown by the open histograms. The difference between observed and expected distributions is significant ($P < 0.05$ for high density, $P < 0.001$ for low density years).

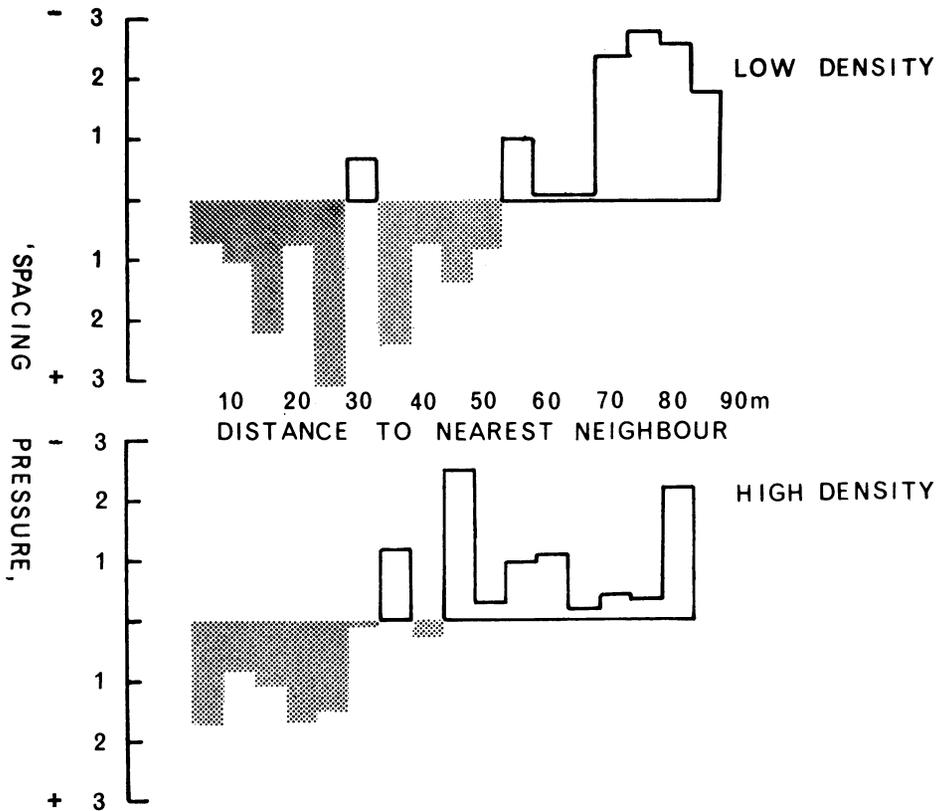


FIG. 2. The "spacing pressure" at different distances to nearest neighbor. "Spacing pressure" = $-(\text{Observed} - \text{expected})/(\text{expected}) \pm$ positive values are shaded.

to prevent immigrants from settling (Patterson 1965).

The first documented removal experiment on wild birds was performed 20 years ago (Stewart and Aldrich 1951, Hensley and Cope 1951). These authors censused the territorial males of some 50 species of birds in a 16-ha woodland. After nesting had started, they shot as many birds as possible in a 3-week period. The total number of territorial birds shot was three times the original estimate of birds present. There must have been considerable immigration during the experiment. It was not established conclusively, however, that the newcomers were not merely returning migrants that would have settled in any case. In addition, in some of the species removed, only males were replaced. Subsequently removal experiments have been performed on populations of several species of birds (Bendell and Elliot 1967, Coulson 1968, Dorney 1960, Harris 1970, Holmes 1966, Orians 1961, Patterson 1965, Watson 1967a, 1965, Mewaldt 1964, Young 1964); mammals (Andrzejewski and Wroclawek 1962, Healey 1967, Smyth 1968); insects (Jacobs 1955, Moore 1964) and fish (Gerking 1953, Clarke 1970). The most

detailed and complete of these studies is that of Watson on the Red Grouse (*Lagopus lagopus*) (Watson 1967a; Watson and Jenkins 1968; Jenkins, Watson, and Miller 1967). In this species, the late summer (August) population contains about 50% territorial pairs, which have a high survival rate and breed the following spring, and 50% nonterritorial birds. The nonterritorial surplus do not breed or show sexual behavior; during the winter they are driven off the heather moors by territorial birds and virtually all die of predation, disease or starvation before the following spring. One hundred and nineteen territorial birds were shot at various times of year, of which almost all were replaced, most rapidly in autumn and least rapidly or not at all in the spring (when most surplus birds have died). In a related species, the Ptarmigan (*Lagopus mutus*), Watson (1965) also found replacement of removed territory holders. In this species territories are set up in the spring. Again, surplus birds are thought to have suffered high mortality and did not breed. Two North American tetraonids, the Ruffed and Blue Grouse (*Bonasa umbellus* Band and *Dendragapus obscurus*) (Dor-

ney 1960, Bendell and Elliot 1967), however, showed virtually no replacement in the spring (autumn territories were not studied in these two species). In all the other removal experiments mentioned above, removed individuals were replaced, although in some cases the origin of the newcomers was not clear. They may have been returning migrants that would have settled anyway (Holmes 1966), or, in one case, simply the removed individuals returning to their territory from the place to which they had been transported (Gerking 1953). The only experimental removal of breeding passerines (Mewaldt removed sparrows [*Zonotrichia*] from a winter population) is that performed by Orians (1961) on Red-Winged Blackbirds (*Agelaius phoeniceus*). Orians found rapid and complete replacement of territorial males; most of the newcomers were first-year birds that probably would not otherwise have bred. Various descriptive studies of passerines have presented good evidence of a nonterritorial surplus or sudden emigration from an area at the time of establishment of territories (e.g. Delius 1965, Carrick 1963, Snow 1958, Smith 1967, Tompa 1964).

The study area

The removal experiments were carried out in Bean Wood, a 15.5-ha mixed woodland on Wytham Estate near Oxford. The area is relatively isolated from the rest of Wytham Woods (Fig. 3), being surrounded on three sides by farmland and on the fourth side by parkland. It is joined to the nearest woodland area by a narrow strip of open scrub area approximately 200 m long. The area is similar in vegetation to, and about 1.6 km from Marley Wood, the site of the long-term study. The dominant canopy tree is oak (*Quercus robur*), with a dense understorey of mainly noncoppiced⁴ hazel (*Corylus avellana*), with varying amounts of elder (*Sambucus niger*), black-thorn (*Prunus spinosa*), ash (*Fraxinus excelsior*) and birch (*Betula* spp.). Some areas are more open, with some large oaks, little understorey and a ground layer of bracken (*Pteridium aquilinum*) and bramble (*Rubus* spp.). Nest boxes were put up in the area in 1961 (Perrins 1965) and the number increased in 1964 to provide a considerable excess. During the study there were 120 boxes in the area, of which never more than 65% were occupied at a time. Apart from Great Tits (14, 14 and 16 pairs bred in the study years), the boxes were used by Blue Tits (*Parus caeruleus*), occasional Coal and Marsh Tits (*P. ater*, *P. palustris*), and up to 10 Tree Sparrows (*Passer montanus*).

⁴ Editor's footnote: Coppiced trees are those that have been cut and later stump-sprouted.

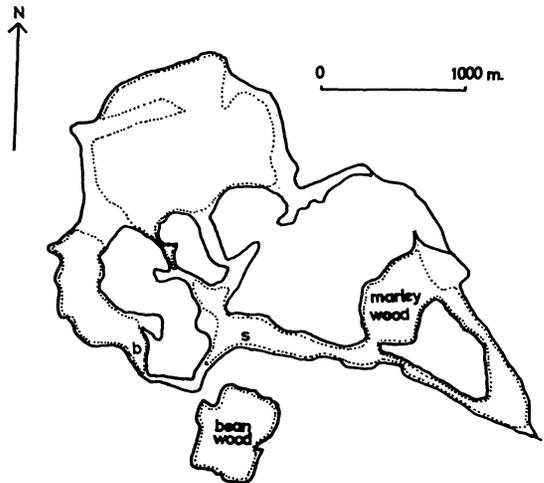


FIG. 3. Wytham Woods, showing the study area and Marley Wood (after Perrins 1965). The areas enclosed by the dotted lines are the areas containing nest boxes. *b* and *s* mark the areas from which most ringed immigrants to the Bean Wood came (see discussion). The solid lines enclose large open areas of grassland or plough.

Methods

Throughout the study, virtually all territorial males and a large proportion of females were individually color-ringed. Birds were caught for ringing by baited mist nets in winter, using funnel traps (baited with sheep's fat) and chardonneret traps (with a stuffed bird as a lure) to catch individual territory owners, or by trapping at the nest.

A detailed description of setting up of territories has been given by Hinde (1952); my observations agree largely with his. During late January and early February, pairs which have been feeding in flocks gradually settle in a restricted area (flocks normally range over about 8 ha and rarely move more than 1 km, even to an exceptionally good food supply [Kluijver 1951, Vilks 1966, pers. obs.]). At first, the home range of a pair is not defended against other birds, which may still be moving in flocks. There is a smooth and gradual transition from home range to territory as defense of the area increases. Not all birds settle at the same time; adults which have bred in the previous season may remain on their territory throughout the winter, never joining the flocks.

Settling and establishment of territories were observed during the winter of 1967, 1968 and 1969, mainly from mid-January onwards. Three techniques were used to measure territories. (i) An individual or pair was followed for as long as possible (usually less than 15 minutes) and its movements plotted directly on a 1:2,500 scale map. Many such observations were then superimposed onto one map and a perimeter was drawn

around the home range of each pair. (ii) All observations of flights or singing posts were recorded on a map in a similar fashion to that described above. (iii) The area over which a pair would respond to playback of song on a tape recorder (Fi-Cord 202a or Uher 4000L) was measured (Dhondt 1966). This method gave the most precise and rapid measure of territory size, but not all birds would respond to the tape recorder.

Replacement of removed pairs

Before performing the removal experiment it was necessary to establish, by means of a control year, the "normal" temporal pattern of settling, so that the removal experiment could be performed at the appropriate time of year (after normal settling in the wood was complete, and yet not too late in the season, when any surplus birds might have died or "given up" trying to settle). In the control year, 1967, the wood was completely occupied by early March; from then until egg laying in late April, the territories remained stable. The longest interval between pairs settling was 9 days. Thus it was decided to carry out the removal in subsequent years only when an interval of more than 15 days had elapsed with no new birds settling.

During the period March 12–15, 1968, half the pairs in the wood were shot (seven males, seven females). Replacement started within a few hours, three new males settling in the area during the shooting period (these were shot in addition to the seven pairs). Within 6 days of completing the removal, 5 new pairs had settled; thus a total of 13 birds (8 males, 5 females) had replaced the 14 removed.

The experiment was repeated on March 19–24, 1969. This time six pairs were removed and four replacement pairs settled in the wood within 3 days. A further natural experiment took place on April 8, 1969, when one resident pair disappeared (cause unknown) and never reappeared; as a result three new pairs settled in the wood, the last one arriving on April 21 when egg-laying in the area had just started. Thus resettlement is rapid and complete (27 out of 28 birds replaced). One observation (the pair that settled on April 21, 1969) suggests that newcomers will take up territories even after breeding has started. All the newcomers subsequently bred in the area. There was no difference between newcomers and residents in mean clutch size or fledging success (Table 1).

After resettling, territories again formed a complete mosaic over the wood (Fig. 4). The spaces not filled by newcomers were filled by expansion of the territories of resident birds during the re-

TABLE 1. Mean clutch size and fledging success of resident birds versus newcomers

	Clutch size	Fledging success
Residents	8.4	90%
Newcomers*	8.5	90%

*Newcomers are new birds invading an area, replacing those that were shot by the experimenter.

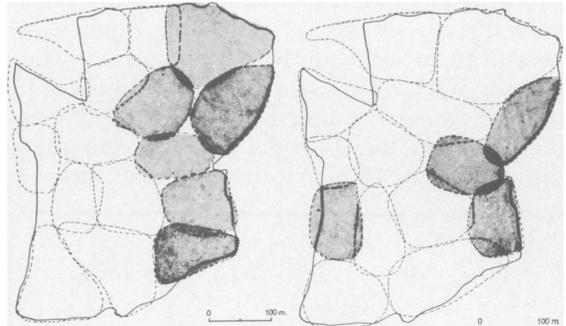


FIG. 4. An example of the replacement of removed birds. Six pairs were shot between March 19 and 24, 1969. (left, stippled area). Within 3 days, four new pairs had taken up territories in the wood (right, stippled area). There was some expansion of residents' territories during the removal so that after replacement territories again formed a complete mosaic over the wood.

TABLE 2. Territory sizes of resident birds before and after their neighbors were shot

	Before (ha)	After (ha)
1968	1.18	1.38
1969	1.34 ^a	1.90 ^a

^aSignificantly different; $P < 0.02$

moval period (Table 2), suggesting that prior to removal there was pressure preventing expansion Watson (1967a).

In some cases, residents not merely expanded their boundaries during the removal period, but completely left their original territory to occupy one in the removal area. This type of movement suggests that the birds moved to more preferred areas of the wood from less preferred areas. In cases where birds completely altered the position of their territory, they moved from open areas to those with a dense understorey of hazel. In one case where the owners of a territory in an open area were shot, no newcomers settled in the area; it was filled only by expansion of neighboring residents' territories. These observations suggest that Great Tits prefer woodland with a dense understorey to those with little understorey (assuming that both have a similar number of can-

opy trees, as was the case in the Bean Wood). The nature of different habitats within the wood is further discussed in Krebs (1970a).

Observations made during the period of rapid resettlement after the removal experiments suggest that there were more birds attempting to settle than finally succeeded in taking up territories. Males (sometimes with mate) were seen to fly into the wood, start to sing quietly and then more loudly. Almost immediately the resident male would approach and either chase off the intruder directly, or sing very loudly near him, which would lead to his immediate withdrawal. These incidents were relatively rare before the removal, but much commoner after (4 incidents in 42 hours' observation in the 2 weeks prior to removal in 1969, and 11 in 18 hours during 6 days after the

removal). Confirmation that such incidents really were attempted settlings came when one pair disappeared on April 8, 1969 (see above). A male who had repeatedly made unsuccessful settling attempts acquired a permanent territory within a few hours of the space being created (see Fig. 5 for details).

The replacement birds

Having demonstrated the existence of a surplus of potential breeders who were prevented from settling by some aspects of the residents' presence, the question remained "Where do the replacement birds come from?" As mentioned earlier, in some species there is an obvious floating surplus population (for example in the Skylark *Alauda arvensis* [Delius 1965] and Red Grouse [Watson 1967a]); this is not the case in the Bean Wood Great Tits. After the first removal experiment, it was suspected, on the basis of recognizing individual songs, that the newcomers were paired birds occupying territories in the hedgerows of the farmland surrounding the wood. In 1969 virtually all hedgerow Great Tits within 800 m of the wood were color-ringed. Of the seven replacement pairs subsequently appearing in the wood, five came from known hedgerow territories (all within 400 m of the wood), the birds making unsuccessful attempts to settle were also identified as hedgerow birds. This confirmed the idea that the "surplus" birds coming into the wood after the removal were already established on territories in hedgerows, rather than being non-territorial individuals as, for example, in the Red Grouse and Red-winged Blackbird. Most of the hedgerow birds had been trapped in the wood during the winter; thus they had formed part of the woodland winter population and, as the results of the removal experiment suggest, had been forced to move out when territories were set up in February.

The newcomers were largely first-year birds (Table 3). Hedgerows as a whole contained a higher proportion of first-year birds than woodland (but not significantly so), but the newcomers contained more yearlings than the total hedgerow sample (Table 3). In other words, yearling hedgerow males are more likely to move into woodland than are hedgerow adults. This is illustrated more directly by the fact that in 1969 three adult males with hedgerow territories adjacent to the wood did not move in after the removal, whilst first-year birds from further afield "hopped over" these territories to settle in the wood (Fig. 6). The hedgerow territories vacated by movement of birds into the wood were not reoccupied, suggesting that there was no further surplus population.

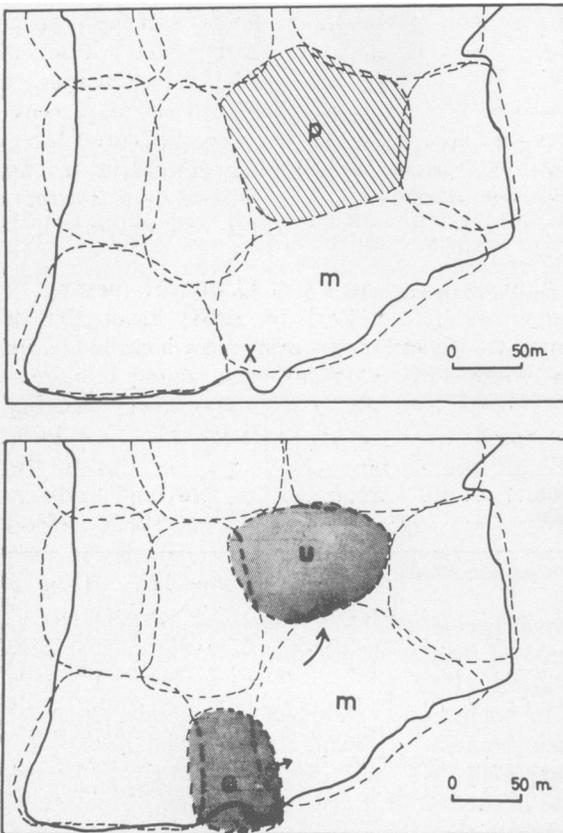


FIG. 5. An illustration of the degree of competition for woodland territories. A paired hedgerow male (O) had been observed over a period of 2 weeks repeatedly trying to establish a territory at point X. Male (M) always rapidly chased off male (O). On April 8, 1969 male (P) and his female disappeared (presumed dead). Male (M) moved his territory slightly towards the empty territory of (P) (shown by arrows), leaving a small gap at X. Within a few hours the hedgerow male (O) had established a territory at X, he abandoned his hedgerow territory and subsequently bred in the wood. Later another hedgerow male (U) established a territory within the site formerly occupied by (P).

TABLE 3. Ages of males in different habitats before the removal experiments

	Adult	First year	% first years
Hedgerow.....	8	8	50% ^a
Newcomers.....	1	12	92.5% ^a
Woodland.....	23	6	21%

^aStatistical significance, hedgerow vs. newcomers: $P < 0.02$, hedgerow vs. woodland: $P < 0.1 > 0.5$ ($\chi^2=2.87$)

TABLE 4. Success rate of hedgerow nests^a versus woodland nests

	Successful ^b	Unsuccessful	% successful nests
Hedgerow.....	2	7	22%***
Woodland.....	54	5	92%***

^aData for Great Tits and Blue Tits combined.
^bSuccessful here means not evicted by Tree Sparrows.
 ***Significantly different, $P < 0.001$.

one Great Tit); of these seven were evicted by Tree Sparrows before or during egg laying (since Tree Sparrows are dominant to both tit species in nest site competition, the two can be treated as one in this respect). Thus the success rate of hedgerow nests was significantly lower than that of woodland nests (Table 4), the main cause of failure being the relative shortage of nest holes and/or the abundance of tree sparrows. Eviction by Tree Sparrows seems (on the small sample of nests) to be an important factor in nesting success in the locality studied here. Tree Sparrows have, however, become exceptionally abundant in the area only since 1961 (A. S. Cheke pers. comm.), and may therefore be a factor of temporary importance.

A much wider survey of Great Tits nesting in hedgerows (from 1951 to 1968) from British Trust for Ornithology nest record cards shows that those birds which do raise young in hedgerows have a smaller clutch and lower fledging success than woodland birds (Table 5). Part, but not all, of these effects may be due to the slightly higher proportion of yearling birds in hedgerows (Table 3). Yearlings in Marley Wood raise on average 0.9 young per pair fewer than older birds (Perrins 1965 Table 12). Thus if there were on average twice the proportion of yearlings in hedgerows as in woodland,⁵ the largest difference in number of young produced per pair due to the age factor would be 0.5 young (this would occur if hedgerows contained 100% yearlings, and woodland 50%). Even allowing for the maximum age effect, the difference between woodland and hedgerows in terms of young raised per pair is still significant. If all rural habitats other than woodland are pooled (this includes hedgerows, orchards, rural gardens and some unspecified areas), there is also a marked reduction in the number of young raised per pair as compared with woodland. Thus hedgerow, and all other man-made rural habitats, can be regarded as suboptimal in terms of reproductive success, both

⁵ This is a liberal estimate since in many years the Marley breeding population has contained more than 50% yearlings, in these years there cannot have been twice the proportion of young birds in hedgerows.

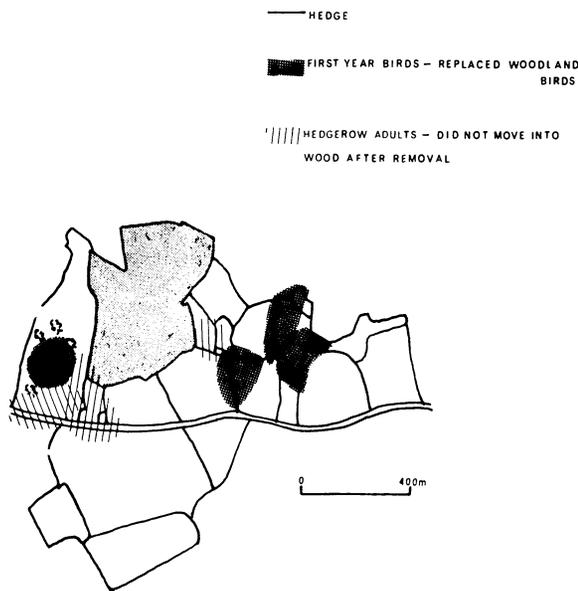


FIG. 6. Map of Bean Wood (stippled area) and some of the surrounding hedgerows to show the origin of known replacement birds. Area to left of wood is parkland with a few tall oaks.

Success in woodland and hedgerow

The fact that birds moved from hedgerow to woodland territories when given the opportunity showed that hedgerows are less preferred, which in turn, assuming birds tend to select the best habitat (Hildén 1965), might suggest that they are suboptimal in terms of reproductive success. Three possible types of disadvantage of hedgerows can be suggested. (i) Hedgerow birds form a doomed surplus which die without breeding (as in the Red Grouse); this is apparently not the case since some birds remained on hedgerow territories throughout the breeding season. (ii) They survive but do not breed. (iii) They breed but with a lower success or at lower density than equivalent woodland birds; this corresponds to the situation suggested by Kluijver and Tinbergen (1953) for mixed and coniferous woods at Hulshorst (see below). The problem was investigated further by putting up nest boxes in hedgerows. Nine tits started nesting in hedgerow boxes (eight Blue and

TABLE 5. Reproductive success of hedgerow birds, from B.T.O. cards^a

	Clutch	Young raised	% nesting mortality
Marley ^b	9.8	9.3	5%
Mixed Wood (BTO)	8.8	8.3	6%
Hedgerow (BTO)	7.9	6.85	13%
Rural (BTO)	8.3	6.7	21%

^aBritish Trust for Ornithology nest survey record cards. From unpublished data analyzed by H. Mayer-Gross.

^bThe Marley Wood data (Lack 1966, Table 10) are included for comparison, the apparently higher clutch size in Marley than in the B.T.O. woodland sample is possibly due to observer bias, the boxes in Marley being inspected more frequently and thoroughly. The 'rural' group includes all rural habitats other than woodland (hedgerows, orchards, gardens, etc.). All figures based on samples of more than 50 nests. The differences in number of young raised in mixed wood and rural habitats are highly significant. ($P < 0.001$).

because many nests are evicted by Tree Sparrows (a recent and possibly temporary effect) and because birds that do breed successfully raise fewer young than woodland birds.

The present situation is somewhat different from that at Wageningen described by Kluijver and Tinbergen, since they failed to show any significant difference in reproductive success per pair between the optimal and suboptimal areas (Kluijver 1951) (although the density was lower in the poor areas). Brown (1969a) and Fretwell and Lucas (1969) have recently reconsidered Kluijver and Tinbergen's data. Brown has pointed out that, since in the Great Tit, as density increases fecundity decreases, the reproductive rate of the population may be maximized by the fact that some birds settle in the suboptimal areas when the density in good areas is high. If all the birds settled in the optimal areas, the reproductive success of each individual would be lower than if some individuals settled in the poor areas. The fact that at Wageningen individuals in the poor areas had as high a reproductive success as those in good areas is evidence in support of Brown's idea of optimum mix between habitats.

Fretwell and Lucas have argued along similar lines and suggested that it is useful to distinguish between two types of density-limiting effect of territory: (i) the Wageningen type of situation, in which the birds settling in poor areas do not suffer a reduced breeding success and (ii) the situation in which the birds in poor areas do suffer a reduced success (e.g. present work). The first effect, Fretwell and Lucas argue, can be explained in terms of all individuals selecting the habitat in which they will do best, the role of territory here is simply to provide a gauge by which later settlers can judge how crowded the good areas are, and whether or not they should be avoided (Lack 1952, Gibb 1961). In the second case, the failure of later birds to settle in optimal areas is not merely due to habitat selection which includes avoidance

of crowded areas, but to more active territorial repulsion which results in some individuals breeding less successfully.

It is possible that two different mechanisms are operating as Fretwell and Lucas suggest, but it may be that in both cases birds are always trying to settle in the optimal areas (i.e. habitat selection does not involve avoidance of crowded areas), and that if the second-choice habitat happens to be nearly as good as the first, birds at a lower density in suboptimal areas will not suffer a lower reproductive success. In this respect it is worth noting that the mixed wood at Wageningen was young and of poor quality (and only in narrow strips the width of one territory); in subsequent studies, considerable differences between mixed and pine wood in terms of reproductive success have been found (Lack 1966 pp. 54-57). In addition, both the reproductive success and breeding density in more mature mixed woods have been found to be higher than in Wageningen mixed woods. Thus the Wageningen data are probably not especially satisfactory for drawing general conclusions about the relative quality of mixed and pine wood and factors (such as habitat selection) associated with this.

The density of Great Tits in hedgerow habitats was much lower than that in woodland, which might be expected since the habitat is suboptimal (e.g. Kluijver and Tinbergen 1953, Smith 1966). The total surface area (= map area) of hedgerow territories was on average three times as large as that of woodland territories (Table 6). However, since hedgerow territories contained many large open spaces, a more direct comparison of hedgerow and woodland territories, to see if they were equivalent in "quality," was made by comparing the volume of canopy (assuming that canopy volume gives an indication of the availability of food, cover, roosting sites, etc.). The canopy volume of 12 hedgerow territories was measured by estimating the canopy area from aerial photographs, and multiplying this by an estimate of average hedgerow canopy height obtained from profile photographs. The canopy volume of woodland territories was estimated in a similar fashion. These approximate calculations show that although the *total surface area* of hedgerow territories was much greater than that of woodland, the *canopy volume*, a more directly comparable measure of territory size, was significantly smaller (Table 6).

One puzzling feature of the results described so far is that adult males did not leave hedgerow territories when given the chance. It is possible that, having once bred or attempted to breed in hedgerows, the birds became more familiar with the habitat and could exploit it more effectively than

TABLE 6. Sizes of territories in different habitats, 1969

	Surface area (ha)	"Canopy volume" (see text) (m ³)	N
Hedgerow	3.72	8.5×104**	12
Woodland	1.34	11.4×104**	16

**P < 0.01

TABLE 7. Testis size in three male Great Tits from woodland and three from hedgerow

	Woodland (mg)	Hedgerow (mg)
Individual measurements.....	78,132,140	23,32,70
Averages.....	117	42

unfamiliar woodland. This is unlikely in view of the fledging success data in Table 5, which, as pointed out, seems to apply to adults as well as first-year birds. Further, adults would be just as susceptible to eviction by Tree Sparrows. A second possibility is that hedgerow birds are qualitatively different from those in woodland. A small sample of hedgerow adults suggests that they have smaller testes than woodland adults taken at the same time of year (Table 7). This could reflect some more general physiological differences rendering hedgerow adults less efficient in territorial disputes. The differences in testis size could, on the other hand, equally well be an effect and not a cause of the birds being in a suboptimal habitat. In the Kittiwake, Coulson (1968) has provided suggestive, but circumstantial, evidence that males settling at the edge of the colony (which have a lower breeding success) are physiologically inferior to those at the center, although here also the cause-effect relationship is not clear. A third suggestion, perhaps the most straightforward, is that the attachment of adult males to hedgerow territories is due to site tenacity. The Great Tit, in common with most bird species, normally stays on the same territory once it has bred there (Hinde 1952 p. 34, Kluijver 1951 Table 8, Wynne-Edwards 1962 p. 460-62 and Hildén 1965 for reviews, Coulson and White 1958). Thus if a pair is forced to breed in suboptimal habitat in its first season it may, by what would normally presumably be an adaptive mechanism in optimal areas, become attached to this area and breed there subsequently even if the possibility of moving to better areas arises.

Behavior involved in maintaining territories

As was mentioned earlier, the removal experiments per se do not show exactly what sort of behavior on the part of woodland birds is involved

in actually preventing hedgerow birds from settling in the wood, but do show that something to do with territoriality is involved. The observations of attempted settlings suggest that direct conflicts (both chasing and singing) are important types of behavior for repelling intruders that are actually in the territory. However, intrusions by hedgerow birds did not occur at a very high frequency before the removal experiments, when territories were stable. Therefore it seems likely that a mechanism other than direct conflicts between individuals helps to prevent hedgerow birds from settling, or trying to settle, in the wood. In addition, it has to be explained how some hedgerow birds, whose territories did not immediately adjoin the wood, detected the disappearance of woodland territorial birds within a few hours. These two facts, the infrequency of direct conflicts, and the rapid detection of a territory holder's absence, suggest that territorial spacing is maintained by frequent advertisement which carries some distance; the most likely method of achieving this is by song. The hypothesis that hedgerow birds are kept out of the wood by the song of residents requires that each male can recognize the individuals from territories within earshot on the basis of song. Each male has several song variants, most of which can certainly be used for individual recognition by human observers (Gompertz 1961, pers. obs.); an experiment was therefore carried out to test if males can distinguish between songs of different individuals. Six territorial males were presented with a 3-minute tape record of a neighbor's song and a similar tape of the song of a bird from 2 km away. The time between starting the song presentation and noting the first response was recorded. On each of 8 mornings both songs were presented to all the males in the centers of their territories, the presentations were separated by 2 hours, and the order of presentation was alternated on successive days. The results (Table 8) showed that males responded differently to neighbors' and strangers' songs (see also Falls 1969, Bremond 1968, Lemon 1967), they responded more rapidly to the song of a strange bird than that of a neighbor (similar results reported in Falls 1969 have been obtained in Ovenbirds *Seiurus aurocapillus* and White-throated Sparrows *Zonotrichia albicollis*). Thus territorial males can recognize other individuals on the basis of song alone, and it is possible that hedgerow males assess whether or not particular territories in woodland are occupied simply by listening to songs. There are two ways in which this hypothesis could be tested directly. The most elegant, but not the most practicable, experiment would be

to remove woodland males, replace them immediately with tape records of their own song and observe whether or not this prevented or delayed the immigration of hedgerow birds. A less refined, but technically more feasible, experiment would be to increase the rate of singing of particular males by hormone treatment, and note if there are any consequent changes in size of territory, rate of intrusions, etc. Watson (1969), using this technique successfully on Red Grouse, implanted testosterone into territorial males and observed that they became more "aggressive" and increased their territory size as a consequence. Two attempts were made to use this technique to change the behavior of territorial males, one using testosterone (which has been shown to influence song in a number of birds [Andrew 1969]) and one using luteinizing hormone (which also seems to influence territoriality or aggression in some birds [Crook and Butterfield 1968, Matthewson 1961]). The experiments were carried out in winter 1969 and 1970 in an isolated copse of 7 ha, containing six territorial males. Both experiments were preceded by 1 week of control observations during which rates of singing, rates of territorial interactions, rates of intrusions, amount of overlap between the territories, and size of territories were measured. Three males were injected with hormone, and three with placebo: in the 1969 experiments 10 mg testosterone from an aerosol spray (Krebs 1970b) and in the 1970 experiments 7 mg N.I.H. L.H. in a beeswax-arachis oil mixture (Zarrow and Gallo 1966). No significant changes in any of the parameters measured resulted from hormone treatment. It is not clear why the hormones failed to produce any effect: the experiments were deliberately carried out in late January through early February, when territories are just being established, and presumably endogenous hormone levels are fairly low. It is possible that any effects the hormones did have were masked by greater fluctuations resulting from daily changes in temperature and other environmental features.

In summary, it is suggested that two types of

TABLE 8. Response of territorial males to playback of songs of territorial neighbors and strangers

	Responded ^a	Did not respond
Neighbor song.....	19	29
Stranger song.....	37	11

$$\chi^2=12.36 \quad P < 0.001$$

^aRespond includes: approach tape recorder/sing or call near tape recorder during the three minutes of playback of song.

behavior are involved in preventing hedgerow birds from settling in woodland: (i) chasing off actual intruders (this is relatively rare, especially when territorial boundaries are stable) and (ii) song advertisement, which allows recognition of individual territory holders and maintains territorial spacing from a distance, without direct conflict.

AVAILABILITY OF WINTER FOOD AND BREEDING DENSITY

The data presented so far suggest that behavioral interaction, rather than food acting directly (as Lack suggested for the Great Tit) was the proximate mechanism determining numbers of birds breeding in the wood. It was still possible, however, that both food and territoriality were influencing breeding density. In some species of bird there is good evidence that availability of food in winter influences subsequent numbers (e.g. Newton 1964, Murton et al. 1966). In the Red Grouse, although the number of birds breeding in an area is limited by territorial behavior, the breeding density in different areas is correlated with food quality (Moss 1969). Artificially improving the food supply resulted in an increase in breeding density (Watson 1967b). The decrease in territory size after improving the food supply was not immediate but lagged 1 year (after the birds had bred in the experimental area) (Watson 1969). It seems therefore that food did not influence territory size directly, but through some intermediate mechanism such as increased tolerance of chicks raised on good quality food (Watson 1969), or increased pressure on territories as a result of high chick survival. Stenger (1958) and Smith (1968), without discussing further whether the link was direct or indirect, found a relationship between territory size and food supply.

Methods

The influence of winter food supply on the breeding density of Great Tits was investigated by providing excess food to the Bean Wood population during the winter 1968-69. (This was undertaken in conjunction with P. J. Jones, who has reported elsewhere the effect of feeding on the laying date of the birds [Jones 1970]). Since Blue Tits are regularly censused in the breeding season, the effect on this species was also observed. The control area for this experiment was Marley Wood (see Fig. 3). Sunflower seeds were chosen for feeding, since they are readily eaten by all tit species (Gibb 1957, pers. obs.), and contain protein of a high nutritive value, at least for domestic chicks (*Gallus domesticus*). Grau and Almquist (1945) have shown that sunflower seeds are as

effective as fish meal as a protein source for growing chicks and that other seeds, such as peanuts and cottonseed, are not so effective (Grau 1946). The seeds were provided at 16 hoppers wired on to trees (at a height of 1.5 m) and spaced out over the wood on a roughly rectangular grid. Feeding lasted from October 1, 1968 until April 21, 1969 (when egg laying had started); during this period the hoppers were inspected at least once, and in cold weather twice, daily. In total 1,000 kg of seeds were consumed. Birds were mist-netted at all the hoppers irregularly through the winter (nets were never left up for more than 2 hours at a time). The numbers of various species trapped at the hoppers were as follows: 103 Great Tits, 179 Blue Tits, 11 Coal Tits, 12 Marsh Tits, 6 Willow Tits. In addition to the tits, about 400 (maximum) finches (*Chloris chloris*, *Fringilla montifringilla*) visited the hoppers.

By the end of the winter virtually all Great, Coal, Marsh and Willow Tits visiting the hoppers were ringed. Thus a liberal estimate of the number of Great Tits visiting the hoppers is 120. In the subsequent breeding population of Blue Tits, 57% had been ringed in the winter; thus, if 179 Blue Tits comprised 57% of the winter population, the total winter Blue Tit population must have

been over 300. Coal, Marsh and Willow Tits store food; no attempt was made to estimate either the amount stored or the proportion of stored seeds that were subsequently eaten. Besides the various bird species visiting the hoppers, some seed was taken by woodmice (*Apodemus sylvaticus*), but judging by the fact that droppings were only rarely found on or near the hoppers, this was not a major factor. Squirrels (*Sciurus carolinensis*) take seeds by opening the hoppers, Gibb (1957) has determined the weight of sunflower seeds required to keep various tit species alive in winter in outdoor aviaries. Calculating from Gibb's figures, and allowing for the maximum winter tit population, and for the fact that a considerable portion of seeds may have been stored and not eaten, the various tit species would have needed about 250 kg to maintain themselves continuously for 28 weeks. Thus if tits only ate one-quarter of the total seed consumption and relied entirely on sunflower seeds, there would still have been enough to maintain them.

Results

The breeding densities in Marley and Bean Woods have been recorded for some years and the two areas usually fluctuate in parallel. Thus,

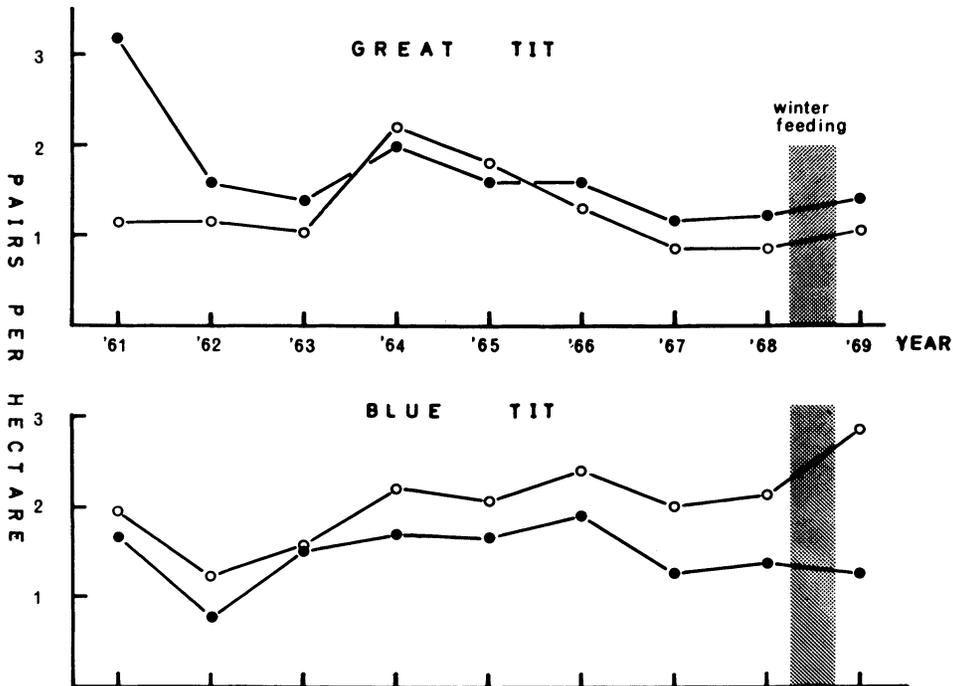


FIG. 7. The effect of winter feeding on breeding density. Breeding density was measured by counting the number of birds breeding in boxes, except in the case of the Bean Wood Great Tits where, since the population was disturbed by shooting some birds before the breeding season, the breeding population was taken as the number of territorial pairs before shooting. Open circles: Bean Wood, where excess food was provided during the shaded period. Solid circles: Marley Wood, which received no excess food.

if winter feeding had a measurable effect, the breeding density in the experimental area should have showed a larger increase relative to the control area than had previously been recorded. The results are shown in Fig. 7. The Great Tit showed no increase relative to the control area. The Blue Tit, however, increased in the experimental area and decreased in density in the control. This was the first time in 9 years that the two populations had fluctuated in opposite directions; the Bean Wood population was significantly higher than in the previous 8 years ($P < 0.05$).

A large proportion of the breeding birds of both species were trapped in both areas and, of the birds caught, only one had moved from one area to the other: a Blue Tit that had been in the experimental area in winter and subsequently bred in the control area. The breeding population of Blue Tits in both areas contained a similar proportion of first-year birds (1.3:1 in Bean Wood, 1.4:1 in Marley), thus winter feeding did not selectively influence the survival of one age class.

The results suggest that the territorial limitation of breeding density in the Great Tit, demonstrated by the removal experiments, is not influenced directly by winter food supply, or at least not by an artificial supplement. The fact (Table 9) that winter survival in the Great Tit is not closely related to the size of the beech mast crop (beech mast is an important winter food of the Great Tit in some years), also suggests that breeding density is not influenced by winter food. A recent study, in which a population of Coal Tits were supplied with excess food throughout the autumn and winter also failed to produce any notable increase in subsequent breeding density (Crooke and Deadman pers. comm.).

The increase in density of the Blue Tit after feeding could be explained in several possible ways. (i) It may be that territory limits breeding density in the Blue Tit as in the Great Tit, but that in the former species food directly influences territory size, by, for example, altering the birds' "level of aggression." (ii) The breeding density of the Blue Tit may be directly determined by availability of food in winter (as Lack has suggested for the Great Tit) and the provision of food in winter simply increased the survival rate of birds in the wood. (iii) The increase in density may have resulted from an increase in the amount of immigration from surrounding areas. In winter Blue Tits (and Great Tits) wander over a relatively large area and the location in which individuals finally settle and breed may be influenced by the food supply in different places (although Hildén [1965] has suggested that in most species habitat selection is not influenced prox-

TABLE 9. Winter survival in years with and without a beech mast crop^a

	% survival ^b	number of years
With beech crop.....	55%	8
Without beech crop.....	50%	5

$$t=1.6 \quad P > 0.10$$

^aThese data must be treated with caution, since the figures supplied by the Forestry Commission on beech mast years are not based on the Wytham Wood area, and the size of the crop may show considerable local variation (R. B. Collins, pers. comm.).
^b% survival = (breeding population/winter population), measured in Marley Wood.

imately by food). There is some evidence to support the last idea: a higher proportion of known ringed adults immigrated into the Bean Wood breeding population in the food supplement year than in previous years (3 out of 18 known adults in the experimental year, 1 out of 24 in the previous 4 years).

If, as suggested, the effect of winter feeding on the Blue Tit was to influence the birds' choice of where to settle, the different results obtained for the Blue and Great Tits might have been because the two species differ in importance of the proximate stimulus of food in habitat selection. Von Haartman (1954 p. 15) has also suggested a difference between the two species in factors influencing habitat selection, namely that Great Tits are more influenced by the presence of nest sites than are Blue Tits. He found that Great Tits could be induced to colonize a variety of woodlands simply by supplying nest sites, whilst Blue Tits could not.

The different effects of winter feeding on the two species could have been due, not to differences in the mechanisms of habitat selection and/or determination of breeding density, but simply to the fact that Blue Tits eat sunflower seeds more readily than Great Tits. This seems unlikely, since both species eat the seeds in captivity, both were caught regularly at the feeding stations, and normally Great Tits eat more seeds (of various species) in winter than do Blue Tits (Betts 1955). Another possible reason for the negative result in the case of the Great Tit is that so few Great Tits were surviving at the beginning of the experiment (October 1), that even with increased survival as a result of feeding, not enough birds were present to produce a marked increase in the breeding population. This also seems unlikely, in view of the fact that there were over 100 Great Tits in the wood during the winter and yet only 16 pairs established territories there. It is possible that many of the winter birds were adults with established territories elsewhere and not potential set-

ters, but the results of the removal experiment show that there were some potential settlers being excluded from the wood in the spring.

In summary, although the results from 1 year's feeding must be treated cautiously, they suggest that whilst the availability of food in winter does have an influence on breeding density in the Blue Tit, it has no influence on the Great Tit. The difference between the two species may lie in the effect of food as a proximate stimulus in the choice of settling locality.

DISCUSSION

Effect of territory on total numbers in the population

Both the demonstration of spacing out of nest sites and the replacement of removed territory holders show that something to do with territorial presence limits the number of pairs of Great Tits breeding in the wood. The availability of food in winter apparently has no influence on breeding numbers in the Great Tit, although it does in the Blue Tit. Can we interpret these data as meaning that some aspect of territoriality limits the numbers of Great Tits breeding in the total population? The answer, of course, depends on what is meant by a population (Kuenen 1958). Some ecologists mean by a population any group of animals of the same species living in a more or less defined area (presumably one that is convenient to study) (e.g. Milne 1957, Solomon 1957, Reddingius 1968). Others (e.g. Bakker 1964) adopt a more rigorous view and argue that a population must be more or less isolated from other groups of the same species (it is not, however, usually practicable to deal with a *completely* isolated unit). While the Bean Wood was chosen for the study because it is a more or less isolated habitat unit (i.e. it is a population in the sense of, for example, Reddingius [1968]), it is not so isolated in respect of the Great Tit population. The degree of isolation from neighboring woodland can be measured, since nearly all nestlings and adults from nearby woods are ringed. In the period 1964–68, only 7.5% of the birds that bred in the Bean Wood were ringed immigrants from other woods (Table 10). Most (77%) of these immigrants came from within 600 m of the Bean Wood. The remaining immigration into the Bean Wood breeding population was of unringed birds and amounted to 33% of the breeding birds in 1964–68. The origin of these unringed birds is, of course, not certain, but it is very likely that most of them came from nearby hedgerows (some could have been woodland birds that escaped being ringed as adults or nestlings). These figures suggest, then, that if the view is

adopted that an ecological population should be a "reasonably" isolated group, the breeding birds in the Bean Wood can be regarded as comprising a population separate from nearby woodland but not separate from hedgerows in the vicinity. The removal experiments show, therefore, that the breeding *density* in optimal habitats is determined by territoriality. What determines the total *numbers* breeding in the population has not yet been established, although in the present study, since quite a large proportion of hedgerow birds apparently did not succeed in raising young, territoriality did have some effect in determining the total numbers breeding in the population.

The function of territory in the Great Tit

It has now been established by removal experiments that the numbers (at least in local areas) of several animal populations are limited by territorial behavior in some sense. This does not necessarily mean that the total production of the

TABLE 10. Percentage of breeding birds that were immigrants into the Bean Wood population, 1964–68

Immigrant from ^a	Males	Females	Total in population
Other woodlands	2%	13%	7.5%
Other areas, same woodland	25%	41%	33%

^aKnown immigrants: 77% came from areas b and s in Figure 3, less than 600 m away; 23% came from Marley Wood (Fig. 3), less than 1,600 m away.

population is reduced as a result of territorial regulation (Brown 1969b), nor does it necessarily mean that territoriality evolved primarily as a population regulation mechanism (as suggested by Wynne-Edwards 1962). In an ecological sense, territoriality is a form of (interference) competition (Miller 1967) (the demand of two or more individuals of the same or different species for the same resources of the environment in excess of the immediate supply). To state simply that territorial behavior evolved as a population regulation mechanism makes no reference to limited environmental resources. However, if an area is defended because it contains, for example, a nest site (a limited resource), this will automatically lead to density limitation as a secondary *consequence* rather than a *function*, in the evolutionary sense, of territory (Crook 1968, Schoener 1968, van den Assem 1968). Hinde (1956) pointed out that the defense of a territory will have other consequences (which may appear to be functions) as well as its true function(s) and that the latter may be difficult to establish, for a particular species, apart from these cases in which territoriality is asso-

ciated only with one particular activity (e.g. mating in lek species [Buechner 1963, Hogan-Warburg 1966; Kruijt and Hogan 1967]).

In the Great Tit, pair formation normally takes place before territories are set up; this cannot, therefore, be a function of territory. It might be expected that nest site defense would be an important function of territory in a hole-nesting species (Tinbergen 1964), however this cannot be the only function of territory in the Great Tit since it does not account for the large area defended. (Another hole nester, the Pied Flycatcher [*Ficedula hypoleuca*] defends only the area immediately around the nest [von Haartman 1956].) Further, potential interspecific nest competitors are not excluded from the territory (Hinde 1952 p. 63). Territorial defense stops at the time the young hatch out (Hinde 1952, pers. obs.); thus it would appear unlikely that preserving a food supply near the nest for feeding the nestlings (Howard 1920) is an important function. Hinde (1952 p. 53) pointed out that the parents appeared to collect food for the young largely within the territory. Others, however (Kluijver 1951, Royama pers. comm.) have observed the parents collecting food outside their territory. (Kluijver's observations may be misleading in that the birds were lured out of the territory with an artificial food source.) In order to investigate this further, parent birds were marked with radioactive tags to enable continuous recording of their movements for 1 or 2 hours at a time (Krebs 1970b). The results indicated that most of the food for the young is collected within the territory. It seems that, although overt defense of the territory has virtually ceased, the boundaries are so well remembered from the previous 2 months of display and fighting, that they are not violated. Thus territory in the Great Tit could function to preserve a food supply for the young near the nest, even though it is not defended at the time the young hatch out. This mechanism could only work in a species like the Great Tit in which breeding is highly synchronized. Establishing the territorial boundaries before the food is required is adaptive in that, during the period when the parents are busiest (feeding the young), they do not spend time defending a food supply, and yet have an undisturbed supply near the nest. The fact that territory size in different years has not been correlated with subsequent availability of food for the young (Lack 1966) does not invalidate the nestling food supply hypothesis, since other proximate factors could well be important in determining territory size.

Tinbergen, Impekenov, and Franck (1967) and Croze (1970) have shown that spaced-out pop-

TABLE 11. Predation on nests at different distances from nearest neighbor [data from Marley Wood 1958-68]^a

Distance from nearest neighbor	Predated	Not predated	% predation
Less than 45 m	43	147	23%
More than 45 m	34	273	11%

$$\chi^2=11.1 \quad P < 0.01$$

^aFor the purposes of this analysis only first brood nests and only nests with eggs or very small young were included. In nests with older young, the amount of noise the young make may be important in attracting predators; thus the hunger state of the young will influence the likelihood of predation.

ulations of artificial prey objects suffered a lower predation rate than similar, but less spaced-out populations. Thus territory could have a selective advantage in spacing out nest sites as a defense against predators. Lack (1968 ch. 13) has recently emphasized this selection pressure as possibly accounting for the nesting dispersion of many solitary bird species. This possible function of territory was examined by comparing the predation rate (largely by *Mustela nivalis*) on nests closer together than 45 m, with predation on more spaced-out nests (Table 11). This showed that nests close together stand a higher chance of being predated.

The data shown in Table 11 result from two effects:

(1) *Differences in overall predation rate between years of different density.*—In years of high density predation is proportionately more severe (Krebs 1970a). This effect alone does not necessarily indicate that predator selection leads to spacing out of nests, weasels might "switch on" to eating tit eggs above a certain threshold overall density and then find nests independently of nearest neighbor distance; since in high density years the average internest distance is relatively low, this would produce an effect similar to that shown in Table 11.

(2) *Differences within a year between spaced and less spaced nests.*—This was examined for the years in which most nests were predated by plotting per cent predation against nearest neighbor distance. Two of the 3 years treated separately showed a negative correlation between per cent predation and nearest neighbor distance (Fig. 8) and the average within-year effect was significant ($P < 0.01$). Thus selection pressure resulting from predation leads to spacing out of nests.

It is possible that the birds, by nesting in boxes, may be abnormally conspicuous and accessible to predators. Unfortunately no comparable data for tits in natural holes are available. However, it may be tentatively concluded that the evolutionary function of territory in the Great Tit is spacing

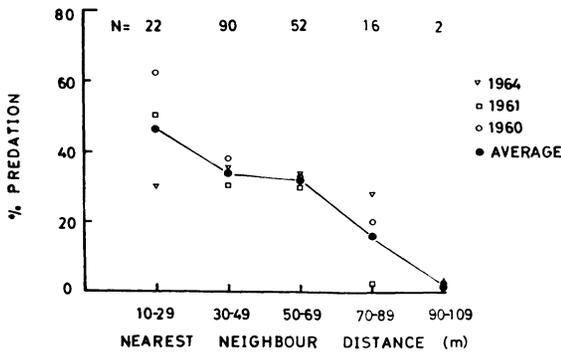


FIG. 8. Per cent predation at different distances from nearest neighboring nest, in the 3 "high density" years. $P < 0.01$ for average of 3 years. N = total number of nests on which each average point is based.

out as a defense against predators, with an alternative or complementary selective advantage in preserving a food supply for feeding the young.

Factors determining territory size

Having shown that territoriality determines breeding density, it remains to explain why the breeding density (and therefore territory size) has been rather variable from year to year, especially in 1961 in Marley Wood, when the density was 70% higher than in any other year. Several theoretically possible ways in which territory could influence breeding density (i.e. ways in which territory size could be determined) are shown in Figure 9. (a) The situation suggested by Lack is that territory has no limiting effect on breeding density; all the birds that survive the winter take up territories and breed (Fig. 9, upper left). (b) A second possibility is that territories are noncompressible and have a sharply defined size. This might be constant for the species (Fig. 9, upper center, solid line) or might be adjusted proximately to prevailing food (or other environmental resource) conditions (solid versus broken line). (c) A third possibility is that territory size is not proximately adjusted to the environment, but is determined by pressure from intruders (Fig. 9, upper right). Lack, following Huxley (1934), suggested that if territory determined breeding density in this fashion, territories will be compressed as pressure from potential settlers increases, but only up to a fixed limit (as this limit is approached, resistance to further compression increases). The lower three diagrams in Figure 9 show three examples of situations which could yield considerable variations in territory size and yet territory size is not related directly to the environment. (d) Territories might have a restraining, rather than limiting influence on density (Fig. 9, lower left). (e) Territories might be compressible to a certain

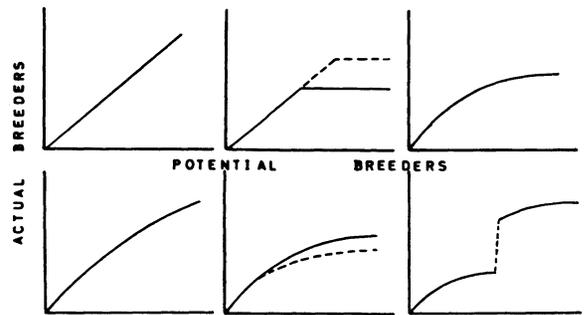


FIG. 9. Some theoretically possible ways in which territory could influence breeding density (see text).

minimum size (Fig. 9, lower center), but the minimum size varies according to the pattern of settling on territories. (f) Another possible situation in which territories have more than one limit of compression is shown in Figure 9, lower right. In this case the limit of compression is determined by the number of potential settlers. The first compression limit holds only until a certain level of pressure is reached; beyond this point the demands on the bird to defend its territory are so great that the limit of compression is "set" to a new, lower level.

It should be emphasized that these possible methods of territory size determination refer to proximate mechanisms. It is quite possible that territory size is proximately determined by, for example, pressure from intruders, and yet ultimately related to food supply.

Having presented some theoretically possible ways in which territory might influence breeding density (i.e. ways in which territory size might be determined proximately), the extent to which predictions of the various hypotheses are fulfilled will be considered. The removal experiment shows that territory (in some sense) determines breeding density; thus Figure 9, upper left can be rejected. As Lack (1966) has pointed out, the year-to-year fluctuations in territory size in the Great Tit have not been related to subsequent availability of food for the young, nor was territory size related to winter food supply (from the results of the feeding experiment). Thus territory size has not been related to fluctuations in the most obvious environmental variable, food supply.

Some available data are at least consistent with the idea that territory size is determined in a proximate sense by pressure from intruders (Fig. 9, upper right and lower three diagrams). (i) During the removal experiments, residents expanded their territories into the vacated area, suggesting that prior to the removal, territories were being compressed. (ii) Birds with territories at the edge of the wood, which have fewer neighbors,

TABLE 12. Mean size of territories (in hectares) at edge versus in center of wood^a

Edge	Center	Number
1.36	1.12	28

^aThe difference is statistically significant ($P < 0.05$.)

have larger territories than central birds (Table 12), suggesting that having more neighbors leads to greater compression of territories (see also Kruijt and Hogan 1967, Armstrong 1965). (iii) The nest spacing analysis shows that the spacing system operates at low and high densities, but is compressible. Although these data suggest that territories are compressible, they do not establish whether territories have one limit of compression or several. It seems unlikely, however, that territories have only one limit of compression since, as Lack points out, this would suggest that territory has limited the breeding density at the most only once in Marley Wood (in 1961 when territories were compressed to a much greater extent than in any other year).

Van den Assem (1967) has shown that in the three-spined stickleback (*Gasterosteus aculeatus*) territories are compressible to a certain minimum size, but that the minimum size varies considerably according to the pattern of settling. If territorial males are introduced into a tank simultaneously, nearly twice the density that can be attained with successive introductions is tolerated. A. Zahavi (pers. comm.) has observed a similar phenomenon in White Wagtails (*Motacilla alba*) in aviaries. Similarly, Bernstein (1969) has observed that when Pigtail Macaques (*Macaca nemestrina*) are introduced into an enclosure simultaneously, there is much less fighting than with successive introductions. Simms (1965) has presented suggestive evidence that in a population of blackbirds (*Turdus merula*) the size of territories was influenced by the pattern of settling. Territories were smaller when the area was resettled after the residents had been killed in an exceptionally hard winter. This may have been because settling was more synchronous after the heavy mortality of residents. This kind of mechanism might account for the exceptionally high density in Marley Wood in 1961 and is graphically represented in Figure 9, lower center.

Settling on territories in the Great Tit takes place in February, adults from the previous breeding season tending to settle before first-year birds. Since the extent to which birds show territorial behavior at this time of year is strongly influenced by weather (Hinde 1952 pp. 67, 45), it might be expected that the temperature in February would

influence the pattern of settling and (if synchrony of settling influences the compressibility of territories) subsequent breeding density. Birds are more likely to show territorial behavior if the weather is warm, thus if the weather in February is consistently warm it could be expected that the settling of first-year birds (normally "late settlers") would be brought forward, and settling would be more synchronous. Figure 10 shows that there is a positive correlation between mean February temperature and subsequent breeding density ($P < 0.01$). (Note that the regression line is calculated from a partial regression, taking into account the winter juvenile: adult ratio, which, as pointed out earlier, has a strong influence on subsequent breeding density). The mean February temperatures for the years plotted on the graph cover a range of 5.6°C which, according to the regression equation, would account for a difference of about 20 pairs between the coldest and warmest years. Thus, if synchrony of settling really is influenced by the temperature in February as suggested above, the observed relationship between February temperature and breeding density is consistent with (but of course does not prove) the hypothesis that the settling pattern influences the compressibility of territories (Fig. 9, lower center).

There is no evidence that specifically supports these suggestions represented in Figure 9, lower left and right, although some evidence is at least consistent with them. The nest spacing analysis is consistent with the hypothesis that territory has a restraining, rather than limiting effect on the density (Fig. 9, lower left). The final suggestion (Fig. 9, lower right), that territory size is in some way related to the pressure from potential settlers at the time when territories are established, is supported by two lines of evidence. (i) In the year (1961) in which territories were exceptionally small, there was an exceptionally large number of "potential settlers" (i.e. a large winter population:

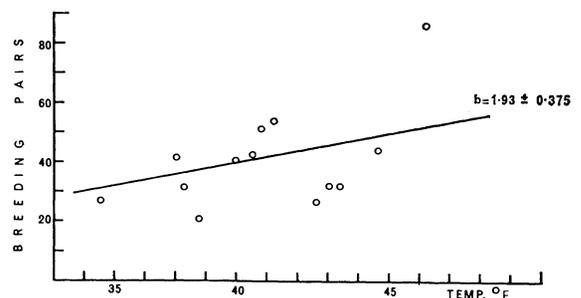


FIG. 10. Partial regression of breeding numbers on mean February temperature. The third variable, held constant in the partial regression, was juvenile to adult ratio in winter. This is known to have a strong effect on subsequent breeding density (Lack 1966).

Figure 11). (ii) Figure 12 shows that birds with more neighbors spend a greater proportion of time defending their territories (irrespective of territory size). If number of neighbors is considered as an index of pressure from rivals, one could envisage a point at which the pressure became so great that individuals could not effectively defend their territories in the time available each day. At this point the birds might suddenly shrink their territories (assuming that small territories require less time to defend).

Summarizing, although territory influences den-

sity, it does not limit the breeding density to a constant level each year. The year-to-year variations in territory size can be explained without postulating that territory size is directly adjusted to annual fluctuations in some environmental commodity. A further point arising from this argument is that the factor(s) determining territory size may be separate from those determining why the particular species should defend territories in the first place.

The observed relationship between winter numbers and breeding numbers in Marley Wood is shown in Figure 11. The data are not really adequate to say which of the various possibilities in Figure 9 most closely resembles the real situation, other than saying that some mechanisms involving variable limits of compression would explain the abnormally high density in 1961.

Territory and population regulation

Although the results have shown that territory determines the numbers of birds breeding in the wood, its influence as a density-dependent (regulatory) factor has not yet been discussed. It is often considered that territory, if it influences numbers, is likely to do so in a strongly density-dependent fashion; this view follows from the hypothesis that territories have a fixed limit of compression. However in the Great Tit, territory has at the most only a weak density-dependent effect (Krebs 1970a); this results from the fact that territory size is so variable from year to year. Thus, at least for the Great Tit, territory should not be regarded as a powerful regulating factor. A. Watson (pers. comm.) has independently reached a similar conclusion for the Red Grouse, although territorial behavior is an important factor determining survival in the population in this species, it apparently does not have a powerful regulatory effect.

In summary, the breeding density of the Great Tit in optimal habitats (mixed woodland) is determined by some aspect of spring territory. Birds which are excluded from optimal areas breed in marginal habitats (e.g. hedgerows); some do not succeed in raising any young and those that do raise young raise fewer than woodland birds. Although behavioral interactions limit the breeding density in certain areas, it is not yet certain to what extent they limit the total number of birds breeding in the population. There are considerable year-to-year variations in breeding density (and therefore territory size), which are not related to food supply, either during the winter or during the time the young are in the nest. It is possible that these differences in territory size are

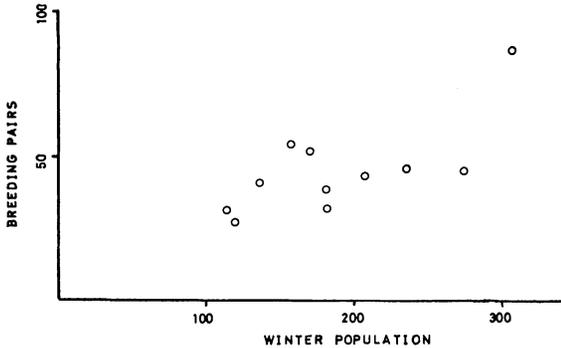


FIG. 11. Relationship between winter population and subsequent breeding population in Marley Wood.

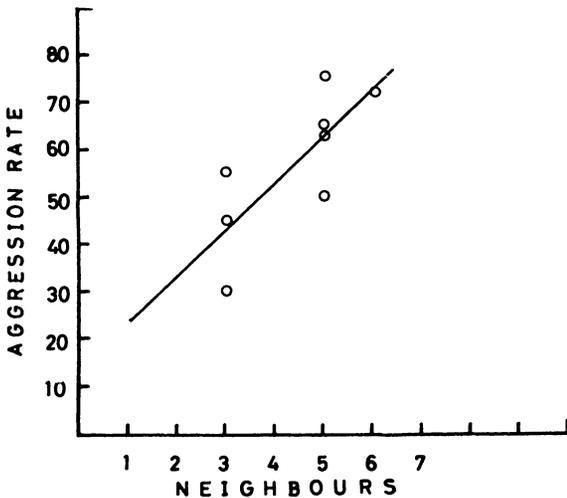


FIG. 12. The relationship between number of neighbors and "aggression rate." Aggression rate was measured by calculating the percentage of all occasions on which a male was seen (in late February), in which the male was engaged in territorial defense when first sighted. Each point is based on more than 20 sightings. The fitted regression ($b = 9.9 \pm 3.6 [P < 0.05]$) is a partial regression holding territory size constant. (A partial regression of aggression rate on territory size [holding neighbors constant] produced no significant relationship, although a negative relationship would be predicted from Table 12. There are several possible explanations for the absence of this predicted correlation, the most likely is that different individuals differ in their "spontaneous" aggressiveness).

due to proximate factors associated with settling on territories.

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