THE IMPORTANCE OF NESTBOXES FOR TERRITORY SETTLEMENT, SURVIVAL AND DENSITY OF THE GREAT TIT

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CONTENTS

1. INTRODUCTION

A number of recent studies have demonstrated that territorial behaviour in some species can depend on the short-term value of the resources within the territory, however, not all studies reveal these relationships (Davies 1980, Patterson 1980 and Wittenberger 1981 for reviews). In the first case the size and time of existence of the territory appears to be inversely related to the abundance of resources (e.g. Cody & Cody 1972, Lyon 1976, Wolf 1978, Gass 1979, Pyke 1979, Davies 1980). Work by Gill & Wolf (1975), Kodric-Brown & Brown (1978), Montgomerie & Gass (1981) and Ewald (1985) suggests that in these species territory settlement and its size may actually be a balance between the benefits and the costs of its defence. Short-term changes in the resources are taken into account and the territory-size is adjusted frequently. This strategy is common in species with short-term territories which are frequently set up anew.

In the second category, it has been suggested, the birds settle and defend an area that is so large as to contain sufficient resources at all times, even though at many times the territory may contain far more resources than required.

It is assumed that the size of the territory claimed is based on the prospective value of its resources. This value is the immediate and the prospective value of its resources during the entire period that the resident bird can expect to use the territory. These resources can be needed either continuously or only for restricted periods, such as nesting holes and special food required during the breeding period. This strategy has been found in species with a long-term territorial system where stability in territory size prevails even though there are considerable annual variations in the abundance of resources (e.g. Harris 1970, Southern 1970, Charles 1972, Spray 1978, Patterson 1980).

The Great Tit uses features of both tactics in relation to food abundance, a resource that shows large temporal and spatial variability. Drent (1983) showed that regardless of the strategy territorial males have to cope with the resistance of the neighbours. Attempts to adjust the size of the territory can only be successfully undertaken when neighbouring males have disappeared. Territorial males that have not been successful in adjusting the size of their territory, do not give up their ownership, when there is a local food shortage, but change tactics, namely by at times foraging with flocks in and around the territory. As territorial status enhances dominance outside the territory, the birds are reluctant to give up their territories completely.

In September of the year of fledging young males usually start to claim a territory on vacant ground between the territories of adult males or in less defended boundary areas (Dhondt 1970, Drent 1983). The number of territories of juveniles, and consequently their average size, could be accurately predicted on the basis of the density of resident (old) territory owners and the density of nonterritorial (juvenile) males, while the patchiness of the habitat was only of secondary importance (Drent 1983). In September densities depend on reproduction, survival and

migration in the preceding winter, spring and summer, which in turn strongly depend on foraging conditions in the study area and its surroundings (Drent 1984).

If foraging conditions in and around the territory allow it, the settled males tend to stay in the area the whole year and successfully defend their territories against nonterritorial males. In areas with an excess of cavities (nestboxes) and a rich seed-food supply (beechmast crop and/or artificial supply) in winter, the density of territories in September is crucial for the territory density at the start of the next breeding season (Drent 1983).

The Great Tit is a secondary hole-nesting bird. The holes are used for roosting from October till the breeding season. In summer and early autumn the birds normally roost in the open, pressed close against trunks or in dense foliage of trees and shrubs (Hinde 1972, own obs.). Virtually all pairs breed in nestboxes if these are present in excess. In winter most territorial males and their females roost in these boxes (Kluyver 1957, Dhondt 1970, own obs.). An earlier study showed that roosting in cavities during winter gives protection from predation by owls and bad weather. All the Great Tit rings found in owl pellets belonged to individuals that roosted not or infrequently in cavities. Mist-net captures directly after awakening showed that the plumage of birds that had not roosted in nestboxes often was very wet after rainy nights, with all the possible negative consequences for survival.

Great Tits frequently compete with each other and with other species for cavities from mid-October until and including the breeding season. Most intraspecific skirmishes for cavities occurred between territory owners and newcomers. These skirmishes were all won by the local territory owners.

A number of authors (e.g. Haapanen 1963, Von Haartman 1971, Van Balen et al. 1982) have shown that in areas with a low hole density (young and managed woods) the density of singing males and breeding pairs is relatively low. Territory and breeding densities usually increased when nestboxes were placed in these woods. The situation was reversed when the boxes were removed (Enemar et al. 1972, Dorn-
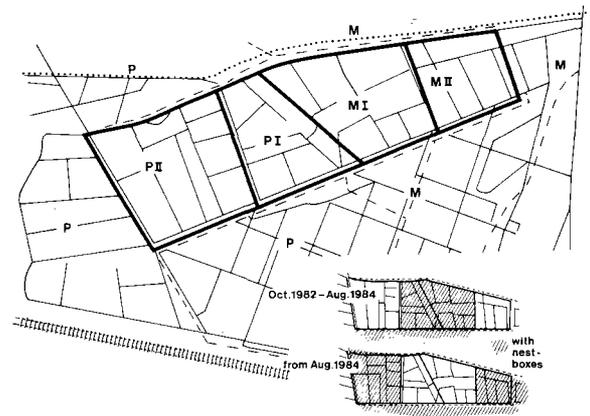

Fig. 1. Study area Buunderkamp. M = mixed forest, P = pine forest. The distribution of nestboxes before 1-9-1984 and after 1-9-1984 is shown at the bottom.

busch 1973, Dhondt & Eyckerman 1980, Currie & Bamford 1982). In mature, neglected mixed forest these manipulations had little or no effect on breeding density. Introduction of nestboxes only changed nest-site choice in favour of nestboxes (Drent 1984).

The above data clearly show that cavities in the territory appear to be an important resource for the owners with respect to survival and reproduction and that a shortage of cavities could limit territory and breeding densities. The first aim of the research presented in this paper is to analyze the role of cavities in territory settlement and in the determination of size or location. The second aim is to analyze how nestboxes affect survival and reproduction after settling and thus the density of territories and breeding pairs over a longer period of time. To achieve this we manipulated nest-box densities and measured territory settlement as well as the survival rate and the reproduction of the owners.

2. AREA OF STUDY AND METHODS

The study was conducted from February 1983 onwards in a 47 ha section of the estate the Buunderkamp near Arnhem, The Netherlands. In the study area as a result of intensive management there were very few tree holes, the number was well below the nest-site requirements of populations in comparable areas with nestboxes. There were some tree-holes available outside the study area. The study area (Fig. 1) consisted of two subareas: one (P) a mosaic of plots of poor coniferous forest with a small number of Birches (*Betula* spec.) along the paths, and the other (M) a mosaic of

plots of fairly rich mixed forest, with coniferous and deciduous trees (Beech *Fagus silvatica* and Birch), and scattered small Oaks (*Quercus* spec.). Both areas were surrounded by the same type of forest. Each subarea was divided into two parts (I and II) of about equal size. At the start of the study nestboxes were placed at 50 m intervals in PI and MI. In September 1984 the nestboxes were moved to PII and MII. In both situations the greatest distance between sites in subareas without nestboxes and the boundary of an area with nestboxes or some tree holes was 300 m. In order to avoid the influence of differences in supply of seed food between habitats and between years, caused by differences in the beechmast crop (Perrins 1966, Drent 1979, Van Balen 1980), sunflower seeds were provided in excess from September to April at feeding sites 300 m apart, both within and around the experimental areas. Twice a week captures were made with mistnets at the feeding sites. The age and sex were recorded and body weight, tarsus length and (in winter 1984/1985) the surface of the black breast-stripe were measured, the latter by means of photographs taken in a standard way. Each bird was marked individually with a special code of a numbered aluminium and several coloured rings, to facilitate observations and analysis of data on an individual basis.

From October to March the nestboxes were inspected for roosting birds twice monthly. In winter 1984/1985 tree holes were also inspected for roosting birds. Between April and July nestboxes and treeholes were inspected once a week to measure the reproductive parameters. Field observations on the presence and the behaviour of individual birds were carried out several times a week during routine walks that covered the whole study area and its direct surroundings. Consequently there is accurate knowledge of the presence of individual birds in the areas of study. During these walks territories were mapped by plotting the observed border disputes. Information on the fate of individuals, that had disappeared was obtained by frequent capture-recapture sessions and observations outside the experimental plots (Drent 1984) and searches for remains of Great Tits such as feathers left by predators, raptor pellets and fox droppings.

3. RESULTS

3.1. TERRITORY SETTLEMENT BY JUVENILES

Confirming previous results (Drent 1983) juvenile males settled in September in territories that were empty because the previous owner had either died or moved. This was the case in both areas. The pattern of settlement and the characteristics of the new owners did not differ between areas with (n = 20) and without nestboxes (n = 12). Settlements occurred simultaneously. The new owners were all first-brood juveniles, that had usually been present locally from within a month after fledging (80% *v.* 83%). Moreover there were no significant differences in body weight (18.42 g, s.e. 0.15 *v.* 18.54 g, s.e. 0.18), in tarsus length (20.08 mm, s.e. 0.16 *v.* 19.91 mm, s.e. 0.16) and the surface

of the breast-stripe (12.30 units, s.e. 0.56 *v.* 12.21 units, s.e. 0.63). Also in areas without nestboxes these features did not change for different distances between the territory and the nearest nestbox. Almost all new owners were paired.

The density of successful juvenile males in September (Y) could be predicted from the density of adult territorial males (X_1) and juvenile nonterritorial ones (X_2) on basis of the equation $Y = 6.52 - 0.77 X_1 + 0.21 X_2$ (Drent 1983). The data on the densities obtained in this study are presented in Table 1. As the daily activity range of all juvenile males was much larger than one subarea, the same parameters were used for the density of nonterritorial males in both subareas.

When the equation is applied to these data, the densities of settled juvenile males in both years and subareas were very close to the expected values, while the small deviations were not in the same direction. These results imply that the same equation holds for both situations, in other words that the presence of nestboxes is not essential for settlement of juvenile males in autumn.

Some territories became vacant during autumn, winter and spring. As long as nonterritorial juvenile males were present, the vacant ground was usually claimed by one of them regardless of the presence of nestboxes. In the absence of nonterritorial males, the vacant area was divided among territorial neighbours, re-

Table 1. Density (number per 10 ha) of adult territories and juvenile non-territorial males (candidates) in September 1983 and 1984 in subareas with (+) and without (−) nestboxes, and the density of juvenile males which had occupied a territory before 1 October. Bottom line: expected density of juvenile territorial males (see text). Number of territories in parentheses.

Density	1983		1984	
	+	−	+	−
Adult territories (X_1)	7.1	5.1	4.8	7.5
Juvenile non-territorial males (X_2)	6.7	6.7	10.0	10.0
Juvenile territories	2.5 (6.0)	3.7 (8.8)	4.6 (11.0)	2.9 (7.0)
Expected juvenile territories (Y)	2.4 (5.8)	4.0 (9.4)	4.9 (11.6)	2.8 (6.7)

Table 2. Proportion of males with a territory in subareas with (+) and without (−) nestboxes which shifted the position of the territory by at least 75 per cent within two weeks. Data for summers (1 April–30 September) and winters (1 October–31 March) added for 1983–1985. X^2 contingency table with Yates correction: * P < 0.05; ** P < 0.005.

	Summer		Winter	
	+	−	+	−
Number of males	36	36	48	46
Per cent shifted	3 **	36	8 *	26

sulting in a decrease of territory density (see 3.6). A similar phenomenon occurred when the mate of a territorial male disappeared. Territorial males remained unmated only after all unpaired females and females paired with nonterritorial males had become mated with a territory owner.

3.2. SITE FIDELITY

The defence of the territory against intruding nonterritorial males did not differ between males in territories with and without nestboxes. However, there was a marked difference in the tendency to shift the position of the territory. When a territory owner without a nestbox had used a cavity in a nearby area, either for roosting or breeding, he more frequently initiated boundary conflicts on the side nearest this cavity (see also Drent 1983). These attempts to shift the position of the territory were only successful if one of the neighbouring territory owners disappeared or changed the position of his territory. When nonterritorial males started to compete with territory owners for vacant ground the latter were always victorious. The analyses of all shifts, in which the position of the territory shifted more than 75 per cent of its area within two weeks, revealed a marked difference between males from subareas with or without nestboxes (Table 2). Both in summer and winter more males of subareas without nestboxes shifted than males of subareas with nestboxes. Most of these shifts occurred into areas with an excess of nestboxes or natural holes (Fig. 2). The shifts by territorial males in subareas without nestboxes were for 92% (n = 24) towards areas that included cavities, which had been used earlier. In contrast, territorial males in subareas with nestboxes made such shifts in only 20% (n = 5, χ^2 with Yates correction = 9.375, p < 0.005). In September, most adult territory owners, that occupied areas without nestboxes, had previously used nestboxes elsewhere (see 3.3 and 3.4). Hence, it could be expected that in winter in areas without nestboxes adult males shift their territories more frequently than juvenile males. This was indeed the case, but not significantly so, 31% (n = 32) v. 14% (n = 14; χ = 1.4536, p > 0.10), probably because during winter a number of juvenile males had gained experience of roosting cavities outside the territory. This contradicts an earlier finding that in areas with a surplus of cavities adult territory owners had a higher site fidelity than juvenile ones (Krebs 1971, Drent 1983).

3.3. ROOSTING SITES

Territorial males and their mates had a strong preference for roosting sites within their own territory. If undisturbed at night, they roosted for long periods (often more than 2–3 months) at the same site. The birds showed no interest in cavities until October when there was a sudden increase in nestbox inspections and skirmishes over cavities, both by territorial and nonterritorial birds. Particularly territorial tits shifted more and more from roosting in open sites to cavities, preferably nestboxes. From mid-November all territorial males and their mates (n = 95) in subareas with an excess of nestboxes roosted inside their own territory, 83 per cent in nestboxes, about 8 per cent in other cavities and the remainder in the open (see Fig. 3). In the
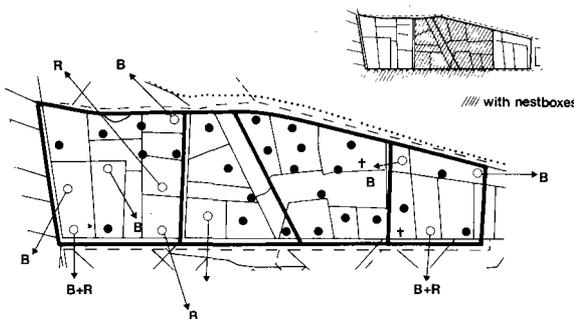

Fig. 2. Changes in the position of the territory between 1-7-1984 and 1-9-1984 in subareas with and without nestboxes. Black dots: stable. Open dots: shift of more than 75 per cent in the direction of the arrow towards former breeding site (B) or roosting area (R). Cross: territory owner dead.
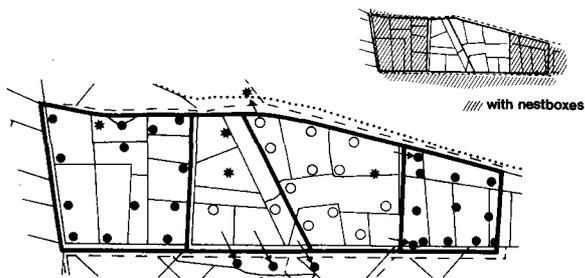
Fig. 3. Roosting sites of males with a territory in the subareas with and without nestboxes in October 1984. Black dots: inside territory in nestbox. Stars: inside territory in natural cavity. Open dots: inside territory in the open. Arrow: outside territory in nestbox (black dot) or in natural cavity (star).

subareas without nestboxes less than 75 per cent of the territorial birds (n = 91) roosted within their territory, a small number of them in the few natural cavities, but most of them in the open. At least 25 per cent of the territory owners irregulary used nestboxes outside their territory and subarea. They all had a territory directly adjacent to an area with nestboxes (Fig. 3). These birds used these boxes about twice as frequently as nonterritorial birds in subareas with nestboxes.

Birds that did not roost in nestboxes had a much higher chance of being the victim of Long-eared and Tawny Owls. Unfortunately only a few owl pellets were found in the study area. The eight rings of territory owners that were found belonged to birds that did not roost regularly in nestboxes: six had territories in subareas without nestboxes, the two others in subareas with nestboxes.

Using nestboxes outside their own territory increases the chance of becoming involved in skirmishes with the local territorial male. During nestbox inspections in winter several damaged bodies were found, suggesting that skirmishes had more than once been fatal, mostly for the intruder (9 intruders compared to 2 local territorial birds).

The need for cavities for roosting within the territory was shown by offering nestboxes in midwinter (1984/85) for only 7 days in the subareas without nestboxes. During the first night 51 per cent of the territorial birds (n = 49) roosted

in these nestboxes. In contrast, extra boxes placed in subareas which already had an excess of nestboxes were not occupied.

3.4. BREEDING SITES

In subareas with nestboxes virtually all territorial pairs (n = 61) nested in boxes in their own territory (Fig. 4). A breeding attempt in a natural hole was exceptional. In the subareas without nestboxes only 18% of the pairs (n = 45) attempted to breed in natural holes in these areas; 14% in and 4% outside their territory. All other pairs (82%) were found breeding outside these subareas. They left the territory temporarily and started breeding as guest pairs in territories of other males where there was an excess of cavities (see also Eyckerman 1974, Drent 1978, 1984, Van Balen et al. 1978, Dhondt & Schillemans 1983). These attempts were mostly (75%) made in nestboxes and mainly in the nearest territory in which there was an opportunity (Fig. 4). At the end of the breeding attempt all guest pairs returned to their territories. After the nestbox distribution was reversed in 1984, in the following spring the former guest pairs nested within their own territory in a nestbox.

As a consequence the breeding density in areas with nestboxes was nearly twice as high as was expected when only territory density was taken into account (Table 3). In the areas without nestboxes the situation was reversed. Here, the density of breeding attempts was only about 25 per cent of the expected value.
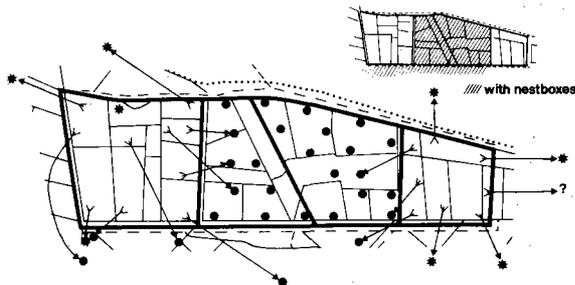

Fig. 4. Breeding sites of pairs with a territory in the subareas with and without nestboxes in 1984. Black dot: inside territory in nestbox. Star: inside territory in natural cavity. Arrow: outside territory in nestbox (black dot) or in natural cavity (star).
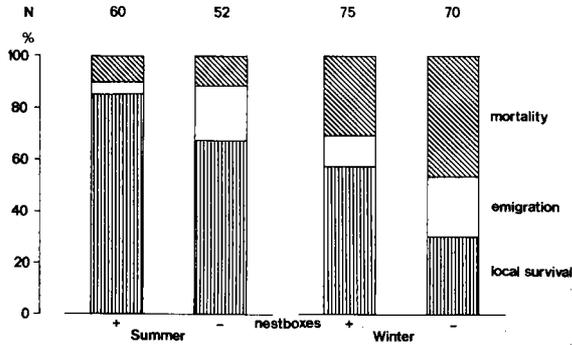
Table 3. Territory density (T.D.) in April and the breeding density (B.D.) in 1983 to 1986 in two habitats with and without nestboxes. Figures denote density of males per 10 ha.

Habitat	Nestboxes	T.D. April 1983	B.D. May 1983	T.D. April 1984	B.D. May 1984	Nestboxes	T.D. April 1985	B.D. May 1985	T.D. April 1986
Pine II	−	5.4	1.8	6.0	0.6	+	7.0	11.0	7.1
Pine I	+	5.8	8.7	5.8	7.7	−	5.2	1.9	2.9
Mixed I	+	7.8	16.3	9.3	16.3	−	6.3	1.5	3.7
Mixed II	−	7.9	2.6	9.2	0.0	+	11.2	17.2	10.6

3.5. SURVIVAL AND EMIGRATION OF TERRITORIAL BIRDS

For an analysis of the effect of the presence of nestboxes on the survival and emigration of territorial males and their partners, several variables have to be taken into account. These variables are:
1. sex (male, female),
2. age (juvenile, adult),
3. habitat (poor, mixed),
4. winter severity (above, below normal),
5. season (summer: 1/4–30/9, winter: 1/10–31/3),
6. presence of nestboxes (with, without).
Winter severity is included because of its well-known effect on survival, and season is included as the effect of the presence of nestboxes on the survival rate is expected to be greater in winter, when the boxes are used for roosting.

The main questions are if the presence of nestboxes (6) is related to survival (7a) and to the emigration of the birds that survived (7b). In order to correct for variation in the other variables, two log-linear analyses of the 2^7 contingency tables were carried out, one for survival and one for emigration. It appeared that age, habitat and winter severity were not significantly related to survival and emigration, a result that is in accordance with results obtained earlier (Drent 1979, 1983, 1984).

Similar analyses were done with the remaining four variables: sex (1), season (5), presence of nestboxes (6), survival (7a), and emigration (7b), respectively. Table 4 shows that, when the data for both seasons are combined, survival is positively related to the presence of nestboxes, sex and season, namely survival is highest when nestboxes are present, is higher for males than for females, and is greater in summer than in winter. For emigration, the relationships are reversed, but only those for nestbox presence and season are significant.

Separate analyses for the summer and winter seasons gave in the summer a significant positive correlation between survival rate and sex, and a negative one between presence of nestboxes and emigration, while in the winter season survival appeared to be positively related to both variables and emigration only negatively to the presence of nestboxes.

Therefore the data of both age classes, the two habitats and the years were combined, but presented separately for the seasons, the subareas with and without nestboxes and the sexes (Fig. 5 and 6).

Confirming earlier results (Drent 1979, 1983, 1984), in the subareas with nestboxes the local survival rate of males and females was high and the emigration and mortality rate low, the latter being significantly lower in summer than in win-

Table 4. Values of the likelihood-ratio-test of a loglinear analysis of the relation of survival/emigration and presence of nestboxes, sex and season (data from 1983–1986). In all tests, d.f. = 1.

	Seasons combined				Summer				Winter			
	survival		emigration		survival		emigration		survival		emigration	
	G	P	G	P	G	P	G	P	G	P	G	P
Presence of nestboxes	4.26	< 0.05	31.02	< 0.0005	0.11	> 0.50	15.81	< 0.0005	7.27	< 0.01	19.20	< 0.0005
Sex	9.82	< 0.005	1.79	> 0.10	4.77	< 0.05	0.51	> 0.25	6.13	< 0.025	1.73	> 0.10
Season	52.13	< 0.0005	13.09	< 0.0005	—	—	—	—	—	—	—	—

Fig. 5. Local survival, emigration and mortality rate (per cent of number at start, = N) of males with territories in subareas with (+) and without (−) nestboxes in summer (1 April–30 September) and in winter (1 October–31 March), totaled for the period 1983–1986.
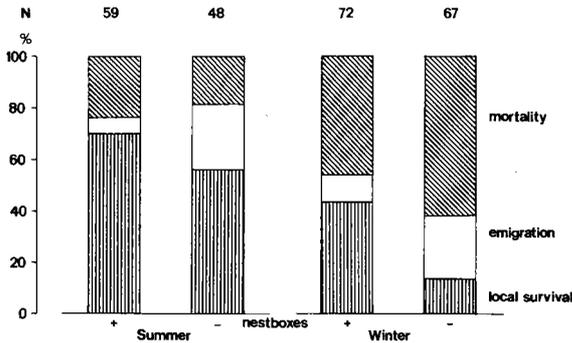
Fig. 6. Local survival, emigration and mortality rate (per cent of number at start, = N) of females mated with territorial males in subareas with (+) and without (−) nestboxes in summer (1 April–30 September) and in winter (1 October–31 March) totaled for the period 1983–1986.

ter. The difference in mortality rate between the seasons and the sexes was mainly a result of a difference in the predation rate by Sparrowhawks. A similar but more marked difference between the seasons and the sexes was found for the subareas without nestboxes.

When the data between subareas with and without nestboxes are compared, marked differences in survival and emigration rate were found. In summer only the emigration rate made a difference in the local survival rate. The mortality rate in summer for both sexes was the same in the two subareas. However, in winter differences in mortality and emigration rate (emigrated birds among the survivors: 35 *v.* 16%) contributed to the lower local survival rate in subareas without nestboxes. The differ-

ence in mortality in winter was mainly due to three factors: 1. a higher chance of being caught by owls at night (see 3.3), 2. a greater chance of fatal accidents during skirmishes for roosting holes, and 3. a higher mortality rate during periods of unfavourable weather, especially rain and snow at night. Females were more vulnerable to these factors than males, resulting in a sex-related difference in mortality rate.

3.6. TERRITORY DENSITY IN THE COURSE OF THE YEAR

The territory density in the course of the experiments is plotted in Fig. 7. In agreement with the literature (*e.g.* Dhondt 1970, Drent 1984) the territory density in the two habitats with nestboxes was always higher in mixed than in pinewood. In both habitats the density was highest in September and decreased by about 15 per cent towards the breeding season. The density decreased again by about 15 per cent between the breeding season and September. The peak density in September and the differences between the habitats and the years could be predicted from relationships with the density of already settled (adult) males and that of present nonterritorial (juvenile) males (see 3.1 and Drent 1983).

The presence or absence of a surplus of nonterritorial males throughout winter and spring should be taken into account when comparing subareas with and without nestboxes. When nonterritorial juveniles were present, as was the
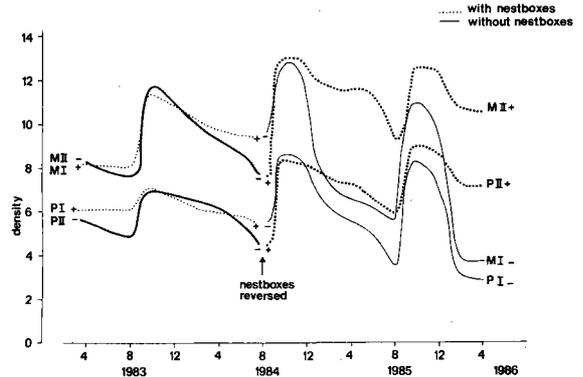
Fig. 7. Changes in territory density during 1983–1986 in two habitats. Solid line: with; Dotted line: without nestboxes; M = mixed; P = pine forest. Lines drawn on the basis of half-monthly counts.

case in winter 1983/1984, the lower local survival rate of territory owners in the subareas without nestboxes was almost completely compensated for by new settlements. Therefore the territory densities only changed slightly upto the breeding season and showed a rather similar trend, irrespective of the presence of nestboxes. As, however, adult males were replaced by juveniles, the age composition changed more in subareas without nestboxes (highest mortality and emigration) than in subareas with nestboxes. At the beginning of autumn there was no significant difference between the subareas in the proportion of adult males among the territory owners (74% (n = 23) v. 67% (n = 21), n.s.), whereas at the start of the breeding season there were more adults among territory owners in subareas with, than in areas without nestboxes (both n = 19, 63% v. 37%; Fisher test one-sided, T_L = 1.9466, p < 0.03).

During the winters of 1984/1985 and 1985/1986 the number of potential candidates had dropped from mid-January onwards to almost zero as a result of a high mortality and emigration rate, due to the severe winter weather, while immigration was almost non-existent. Consequently, replacement of lost territorial males was incomplete. This meant that there were many fewer territorial males and that there was a great decrease in the territory density in the subareas without nestboxes compared to those with nestboxes. In spring the territory density in the mixed woods with nestboxes had dropped to below that of pinewoods with nestboxes and was only slightly higher than that in pinewoods without nestboxes.

In competition for vacant ground, males who arrived earlier were more successful than those that arrived later (Drent 1983). Hence, during winter, as a result of occupation of vacant areas by juveniles that had been unsuccessful earlier or arrived later, a change was expected in the composition of the juvenile territorial population in relation to the duration of presence. In autumn most juvenile territorial males were already present from within a month after fledging (summated over two winters: 77% (n = 22) v. 75% (n = 16) in the two subareas; n.s.). As territories more often became vacant in subareas without nestboxes than in those with nestboxes, the proportion of juvenile males, that arrived earlier, among juvenile territory owners decreased less markedly in subareas with nestboxes than in those without nestboxes (to 72% (n = 18) and to 37% (n = 16), respectively), resulting in a significant difference in composition between the subareas (Fisher test, one-sided, T_L = 2.3813, P < 0.01).

The same phenomena applied to females mated with territory owners. In the winter of 1983/1984, with a surplus of unmated juvenile females, all the lost mates of territory owners were replaced. Therefore all the territorial males in areas with and without nestboxes were mated. However, the difference in the disappearance rate between subareas with and without nestboxes caused differences in the composition of the female population in these areas, with regard to age and duration of presence. In the winter of 1984/1985 there was a shortage of unmated females due to the very high emigration and mortality rate of the females and the lack of immigration. Consequently, some males remained unmated. All these males had a territory in the subareas without nestboxes (see Table 5), the areas with the highest mortality rate

Table 5. Reproductive success of pairs with a territory in the subareas with (+) and without (−) nestboxes and of guest pairs, originating from outside the subareas, attempting to breed inside the subarea with nestboxes. The data are summed up for the breeding seasons 1983, 1984 and 1985. * χ^2 contingency table with Yates correction, P < 0.05; ** Wilcoxon test, P < 0.01.

	Territory-owners		Guest pairs
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	−	+	
Number of males	50	61	
Per cent unmated	10.0	0	
Number of pairs	45	61	37
Per cent with at least one fledgling	44.4 *	65.6	* 37.8
Per cent with second brood	20.0 *	55.9	* 27.2
Number of fledglings per pair	2.9 **	4.3	** 2.6
Number of fledglings per successful pair	6.0	6.5	7.0

and the lowest chance of reproduction within the territory.

3.7. REPRODUCTIVE SUCCESS

In all three breeding seasons and in both habitats, identical differences were found in the reproductive success of pairs with territories in subareas with and without nestboxes and pairs that came from elsewhere but attempted to breed there as guest pairs. Therefore the data are presented totalled for all years and habitats (Table 5). Pairs with territories in the subareas with nestboxes were more successful in producing fledglings and second broods than pairs of the other two categories, between which there were no differences. This advantage disappeared completely when calculated for pairs which produced at least one fledgling.

Consequently the differences were caused by a difference in the loss of total clutches or broods. This loss was related to breeding in natural holes or as a guest pair in a territory of another male. Only 28 per cent of the breeding attempts in natural holes (n = 25) resulted in one or more fledglings compared to about 70 per cent of the attempts in nestboxes. As 40 per cent of the pairs, whose territory was in a subarea without nestboxes (N = 45), bred in natural holes, compared to only 2 per cent of the pairs with a territory in a subarea with nestboxes (n = 61), this difference in fledgling success between holes and nestboxes affected the former more than the latter category. Guest pairs breeding in nestboxes more often deserted their nests than local territorial pairs. This was sometimes due to actions of the local territory owner. Moreover guest pairs started a repeat clutch or a second brood less often than local territorial breeding pairs. Since most pairs with territories in subareas without nestboxes breed as guest pairs elsewhere (see 3.4), this explains the difference in reproductive success between the two categories of territorial pairs.

Assuming that all pairs stayed in or returned with their broods to the territory, reproductive success will cause a big difference in the density of juveniles in the two subareas. In the area without nestboxes the number of fledglings will amount to only 68 per cent (1983: 73%, 1984: 60% and 1985: 63%) of the number expected

from the reproductive success in the nestbox area.

However, there was also a difference in the emigration rate of complete broods soon after fledging. Drent (1984) has shown that males guided their broods to the area where they had foraged during the first month(s) after their own fledging, often outside the study area. This emigration of broods will be more marked in subareas without than with nestboxes. Because of the difference in the winter survival rate between these subareas the proportion of males without local early experience in foraging is the largest in the subarea without nestboxes (see 3.6).

4. DISCUSSION

4.1. ROLE OF CAVITIES IN TERRITORIAL BEHAVIOUR

The absence of suitable cavities (tree holes, nestboxes) for roosting and breeding did not affect territory settlement in September, when cavities are only of future value to the bird. Also in winter and spring, when cavities were directly needed for roosting and breeding, areas without cavities were settled. The number of new settlements in September was independent of the presence of cavities. The number of new territories was determined almost exclusively by the number of resident neighbours and rival candidates and thus, approximately, by the intensity of competition for vacant ground (Drent 1983).

The survival and reproduction rate of males with a territory without suitable cavities is reduced, but is better than that of nonterritorial birds in areas with an excess of nestboxes (see also Eyckerman 1974, Dhondt & Schillemans 1983, Drent 1984). Territorial ownership gives status and therefore success in competition for roosting and breeding cavities and food when these are in short supply both in and outside the territory. This effect fades out as the distance from the territory increases. Moreover, when an owner of a territory with cavities disappeared a territory owner without cavities improved the quality of his territory, leaving the poorer parts for the nonterritorial birds. Hence to be territorial in areas without cavities is more advanta-

geous than to remain nonterritorial or to give up the territory completely. The nearer it is to an area with cavities, the more profitable this strategy will be.

A cost-benefit analysis of territoriality in the Great Tit needs to include conditions in and outside the territory (Drent 1983). The distribution of food and water is often patchy and unpredictable in time. The same holds for the distribution of treeholes due to interspecific competition, weather conditions and forest management (Van Balen *et al.* 1978, 1982, own obs.). The territory as such has an important effect, as in it the owner reinforces its position in the hierarchy and this has a marked effect on the exploitation of resources elsewhere. This means that the competition for a territory, regardless of the distribution of resources within the daily activity range, will be great and thus mask completely a possible resource preference. Only after a territory has been occupied the tit could show a preference for locations with certain resources such as cavities. This preference will in turn be influenced by earlier experiences with cavities outside the territory. In September no direct need for cavities was observed and juvenile males have had no previous experience of cavities. Hence the distribution of cavities will be of minor importance for settlement when compared to food supply.

All the year the nonterritorial juvenile birds moved through plots with and without nestboxes. The greatest distance between a territory without a cavity and an area with nestboxes or a clump of tree holes was at most 300 m compared to the daily activity range of territory owners that was up to 600 m during late autumn, winter and spring. Therefore the results of this study should be applied with some caution to other areas without cavities, especially when the distance from areas with cavities exceeds the daily activity range of territorial and nonterritorial males. However, the marked shortage of tree holes in large areas of forests is a recent feature (Van Balen *et al.* 1982). It is likely that in the evolution of territorial behaviour tree holes were more abundant and irregularly distributed in the birds' main habitat (deciduous forest), which means that these results could apply to that situation.

4.2. DISTRIBUTION OF CAVITIES AND TERRITORY DENSITY

The density of new territories in September was determined by the number of resident males and rival candidates. The number and distribution of cavities did not directly limit the number of new territories. Therefore it is important to check whether the number of nestboxes influences the density of settled birds and rival candidates at crucial times.

The results show that both densities can indeed strongly depend on the presence of nestboxes. In areas without cavities the mortality and emigration rate (territory shifts) of territory owners was higher than in areas with cavities, resulting in a difference in the composition of the territorial population (age, duration of presence) and, if there were no more candidates, the density of territory owners changed. Pairs with a territory in areas without cavities were unable to breed in the territory. Therefore the reproductive successs was lower and will be even lower, if the density of breeding pairs at the location is high (Dhondt & Schillemans 1983) as well as when foraging conditions are poor (Drent 1984). These differences in composition and density of the territorial population and in the reproductive success per pair will mean that the density of juveniles will vary greatly in areas with and without cavities at the time that the young become independent (Drent 1984). If they do not disperse, this will have consequences for the density in September, the crucial time for settlement. Both effects will cause a difference in the density of new territories. Moreover in areas without cavities – the areas with the lowest local survival rate – the supply of nonterritorial birds after September will be less and, hence, exhausted earlier than in areas with cavities. The decrease in the density of territories during winter will therefore start earlier and be more pronounced than in areas with cavities. If there is no juvenile immigration there is a negative feedback between the effects of the absence of cavities on survival and reproduction. This will eventually result in very low densities of territories and therefore breeding pairs in areas without cavities.

4.3. CONCLUSIONS

Much more is known now about the effects of the distribution of cavities on survival, reproduction and territorial behaviour of the Great Tit. The Great Tit, when attempting to adjust his territory, takes into account the value of cavities (tree holes, nestboxes) in order to maximize his future chances of survival and reproduction. This however does not apply in September when the juveniles are settling. Since potential settlers and territory owners without a cavity in the territory have to compete with settled and candidate males, the final territory density will depend more on the outcome of this competition than on the overall abundance of cavities. The densities of settled and nonterritorial males, however, strongly depend on the distribution and number of cavities. Since the distribution of cavities causes marked differences in survival and emigration, the decrease in density of resident territorial males in winter was greater in areas without cavities. The degree to which this decline differs is strongly dependent on the difference in density of nonterritorial birds between the areas, which in turn is partly dependent on the difference in reproductive rate between areas without and with cavities. Therefore the differences in territory and breeding density between areas with and without nestboxes in the literature should be explained as a result of the effect of the absence of nestboxes on survival, emigration and reproduction and thereby on the densities of competing birds.

5. ACKNOWLEDGEMENTS

6. SUMMARY

From 1983 onwards a study on the importance of holes and their substitutes (nestboxes) on territory settlement, survival and reproduction has been carried out in different habitats, poor in natural holes. Territory settlement by juvenile males in September, which is the crucial period for territory density in years with a seed food supply in winter, appeared to be independent of the presence of nestboxes. The density of newly settled territories was determined by the density of adult territory owners and juvenile nonterritorial males. Occupation of vacant areas during winter and spring depended on the presence of nonterritorial birds. Marked shifts in the position of the area were only observed in males with territories in subareas without nestboxes and were directed towards areas with an excess of nestboxes. Earlier experiences with these boxes for breeding and roosting seemed to be important. In contrast to areas with nestboxes, most territory owners in areas without boxes roosted from October onward outside cavities in their territories. While in areas with nestboxes all territorial pairs used them for breeding, most of the territorial pairs from areas without nestboxes made breeding attempts in nestboxes outside territories and outside the area. This caused marked differences in breeding density and in the density of fledglings. The local survival rate of territory owners was markedly lower in areas without nestboxes than areas with nestboxes. This was due to emigration in summer and winter and to mortality in winter caused by predation, competition for nestboxes and unfavourable weather conditions.

The difference in the local survival rate between the areas caused a difference in composition according to age and duration of presence, in years with an excess of nonterritorial birds. Moreover it caused a difference in territory density in spring in years with a shortage of nonterritorial males.

From these results it is concluded that although Great Tits take into account the proximate value of cavities for roosting and breeding, the distribution of nestboxes (or natural holes) did not directly determine territory settlement and density. Territory settlement and density were dependent on the densities of resident territory owners and nonterritorial candidates. These densities were strongly influenced by the distribution of nestboxes, that caused differences in local survival rate and reproduction. Hence, the distribution of nestboxes indirectly determined the territory density.

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8. SAMENVATTING

Vanaf 1983 is in het terrein Buunderkamp het belang van nestkasten en natuurlijke holten voor de vestiging, overleving en voorplanting van de Koolmees bestudeerd in twee contrasterende habitats, beide arm aan natuurlijke holten, en deels wel, deels niet voorzien van nestkasten.

De vestiging van territoria door juveniele mannen in september bleek onafhankelijk te zijn van de aanwezigheid van nestkasten. De dichtheid van pas gevestigde territoria werd vrijwel geheel bepaald door de dichtheid van de nog aanwezige oude territoriumeigenaars en die van de juveniele candidaat vestigers. Het opvullen van vacante territoria in de winter en het voorjaar hing alleen af van de aanwezigheid van niet-territoriale mannen. Verschuivingen van territoria traden op in deelgebieden zonder nestkasten, en gingen in de richting van gebieden met een overmaat aan nestkasten. Daarbij speelden eerder opgedane ervaringen met deze kasten een rol.

In gebieden met nestkasten sliepen de meeste territoriumeigenaars in deze kasten, en gebruikten ze zonder uitzondering als nestholte. In gebieden zonder nestkasten sliepen de meeste van deze mannen wel in hun territorium, maar niet in holten, terwijl ze merendeels een broedpoging deden in kasten buiten hun territorium, in het aangrenzende nestkastgebied. Dit leidde tot grote verschillen in broeddichtheid en in dichtheid van de uitgevlogen jongen.

De locale overleving van territoriale mannen was in gebieden zonder kasten duidelijk lager dan in gebieden met kasten. Dit werd veroorzaakt door emigratie uit deze gebieden en door sterfte als gevolg van predatie, concurrentie om nestkasten en ongunstige weersomstandigheden.

Het verschil in locale overleving tussen gebieden met en zonder kasten leidde in jaren met een overvloed aan niet-

territoriale mannen tot verschillen in samenstelling van de populatie, voor wat betreft leeftijd en duur van aanwezigheid van de vogels. In jaren met een tekort aan niet-territo-riale mannen leidde het tot een verschil in dichtheid van de territoria in het voorjaar.

De conclusie uit deze experimenten is dat, hoewel Koolmezen rekening houden met de waarde van holten als slaap- en broedplaats, de verdeling van deze holten geen directe invloed heeft op vestiging en dichtheid. Vestiging en dichtheid van territoria worden bepaald door de dichtheid van eerder aanwezige territoriumeigenaars en niet-territoriale candidaten. Deze dichtheden worden sterk beinvloed door de verdeling van holten, die leidt tot verschillen in locale overleving en voortplantingssucces. Daardoor bepaalt de verdeling van nestkasten indirect de dichtheid van de territoria.