BLUE TIT TERRITORIES IN POPULATIONS AT DIFFERENT DENSITY LEVELS

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1. INTRODUCTION

Dhondt & Eyckerman (1980a) have shown that Blue Tit *Parus caeruleus* breeding density is influenced by interspecific competition with the Great Tit *Parus major* in winter. They provided experimental evidence that competition was over roosting sites in winter: after excluding the Great Tits from the nestboxes, Blue Tit numbers almost doubled in two experimental areas and remained at that level afterwards. Such an increase was not observed in the control area. They suggested that in the control area Blue Tit numbers were limited by interspecific competition with the Great Tit, but that in the experimental areas intraspecific competition among Blue Tits set a limit to the size of the breeding population. This intraspecific competition would either be for food, during winter, or for space, in spring (Dhondt & Eyckerman 1980b). From the knowledge that Blue Tit spring territories are small and of similar size in populations at low (Hinde 1952, Granitzer 1978) and high breeding densities (Schillemans 1979) and assuming that the breeding density, in a high density population, is limited through competition for space (Dhondt & Eyckerman's second alternative) we formulated the following hypothesis: in an area with a high Blue Tit breeding density territories are contiguous; in an area with a low breeding density open spaces should be observed between territories.

In a wood near Antwerp, repeating Dhondt and Eyckerman's experiment, we provided protected roosting sites for Blue Tits in one plot but not in another, to obtain Blue Tit breeding populations at different density levels. In the spring 1980 we studied Blue Tit territories in the two study plots to test our hypothesis.

2. MATERIAL AND METHODS

The "Peerdsbos" is an estate of *ca.* 150 ha near Antwerp (Belgium). A large part (111 ha) is covered with trees. A detailed description of the woody vegetation was made by Gillis (1975). In two plots of *ca.* 11 ha each we provided nestboxes during the winter 1978—1979. In plot T 80 boxes with an entrance hole diameter of 32 mm were erected. In plot B 59 large-holed boxes (diameter 32 mm) and 59 small-holed (diameter 26 mm) were erected. In the winter 1979—1980 an additional 59 large-holed nestboxes were provided in plot B. Both plots are similar in vegetation, being covered mainly with oak (*Quercus robur* L.) and beech (*Fagus silvatica* L.). They are 600 m apart.

Plot T is situated at the western edge of the estate and is surrounded with coniferous plots (east), villa gardens (north), open space and hedgerows (west). The vegetation along the southern edge is similar to that inside the plot. Plot B lies completely inside the wooded area. Only along the northern and part of the eastern edge conifers form a natural boundary. It is thus to be expected that some tits that are territorial outside our study plots would breed in the nestboxes inside our study areas if they are unable to find a suitable nestsite in their territory.

If the findings of Dhondt & Eyckerman (*op. cit.*) can be generalised we expect high breeding densities of the Great Tit in both plots, a high Blue Tit density in plot B, but a lower one in plot T. As the nestboxes were erected rather late during the winter 1978—1979, and that winter was extremely cold, we expected the differences between the density levels to be realized only from the second breeding season, *i.e.* 1980, onwards.

Through an intensive winter trapping programme most tits were colour-ringed in the spring of 1980. In the period February — April 1980 territorial brids were observed, identified, and their position and behaviour recorded on sketch maps in the field. Play-back of tape-recorded song together with a stuffed bird helped to delimit the territorial boundaries (Dhondt 1966). The field notes were combined to delimit the territory of each individual. Each bird that had at least one nestbox in its territory, even if most of the defended area was outside the plot, was included in our total count of territorial birds. Territory size was measured only for the birds whose territory lay completely inside a study plot. Captures of adults feeding nestlings confirmed the identity of the breeding pairs.

3. RESULTS

In Table 1 the number of breeding pairs in both years and in both study plots is shown. In 1979 similar numbers of tits bred in the two study plots. In 1980 the number of Great Tit breeding pairs was about double that of the previous year. However the number of breeding pairs was much higher than the number of terri-

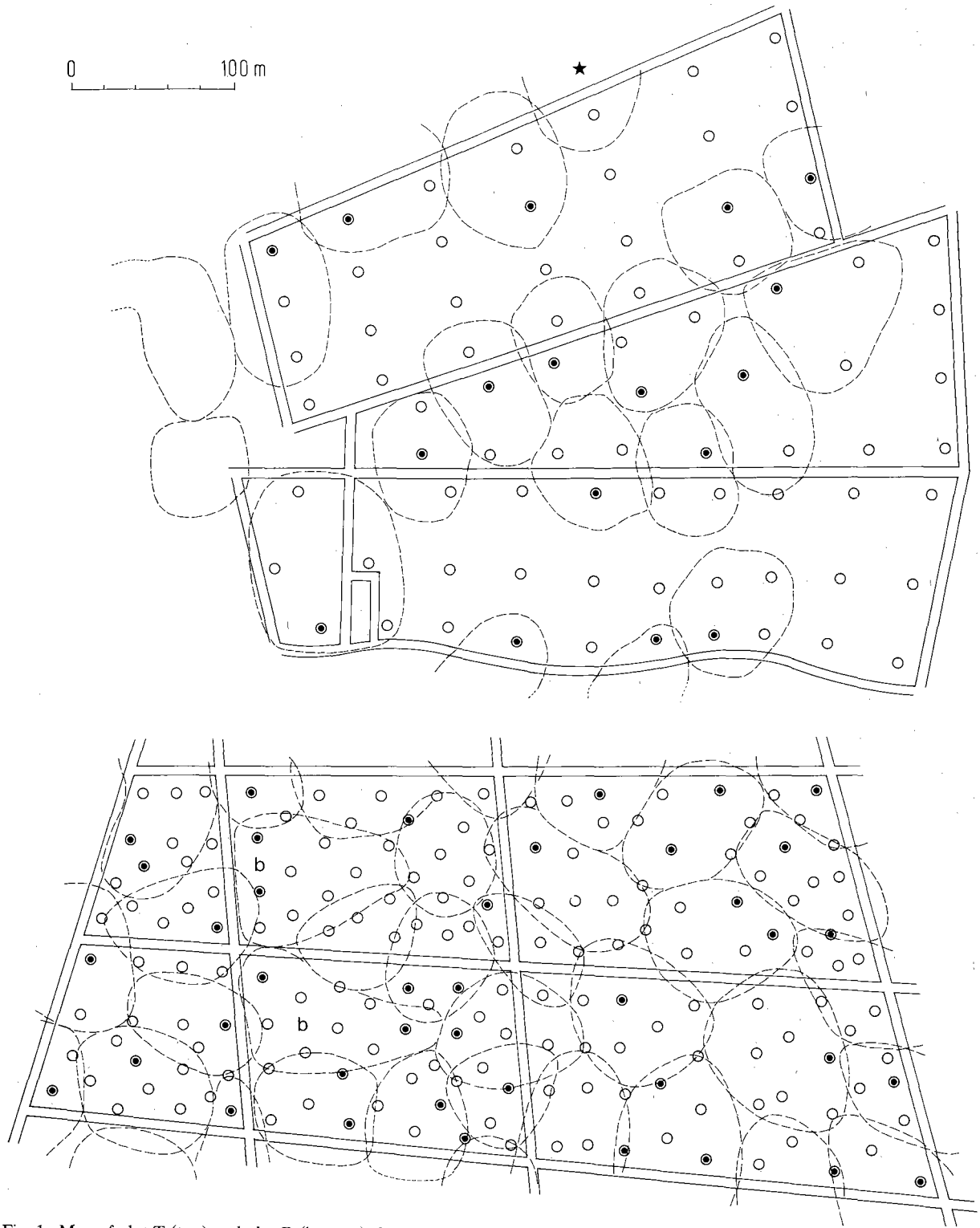

Fig. 1. Map of plot T (top) and plot B (bottom) showing the Blue Tit territory boundaries in 1980. Filled symbols represent nest-boxes occupied by Blue Tits. An asterisk denotes the breeding site of a Blue Tit in a natural cavity, and "b" marks the territories of two bigamous males.

Table 1. Number of breeding pairs in two study plots in the Peerdsbos. In brackets the number of territories delimited is given (see text)

	Great Tit		Blue Tit	
Plot	B	T	B	T
1979	19	16	20	20
1980	46 (27)	31 (25)	40 (34)	17 (18)

tories we had delimited, indicating that a large number of intruders had also reproduced. For the Blue Tit our data show a doubling of the number of breeding pairs in plot B from 1979 to 1980, but a similar number in plot T in both years. In plot B, but not in plot T, Blue Tit intruders bred. In plot B 34 territories had been delimited (Fig. 1): two were bigamous and two were not found in a nestbox giving 34 first clutches of territorial birds. Another 6 clutches were laid by intruding pairs. In plot T 18 territories had been delimited (Fig. 1). One pair was observed to breed in a natural cavity; the other 17 laid in a nestbox.

In Fig. 1 the territorial boundaries are shown for the Blue Tit in both plots. It is obvious that plot B is entirely covered with Blue Tit territories, whereas much open space remained in plot T. It is interesting to note that in plot T territories formed clumps, rather than laying isolated from each other. Territory size did not differ between the two plots, averaging about 0.5 ha in both (Table 2). In the course of our observations we had noted that boundary skirmishes were frequent in plot B but rare in plot T.

Table 2. Blue Tit territory size in two study plots of the Peerdsbos (spring 1980). The difference in territory size between the two plots is statistically insignificant ($t_{29} = 0.741$, $P > 0.4$)

Plot	T	B
Number of territories measured	13	18
Mean size in ha	0.53	0.50
Standard error	0.041	0.026

4. DISCUSSION AND CONCLUSIONS

Our study confirms Dhondt & Eyckerman's (*op. cit.*) experimental results: when Blue Tits are offered protected roosting sites in winter their breeding density increases as compared to an area where such roosting sites are absent. Our observations confirm the hypothesis formulated in the introduction: open space between territories was found in the low density area, plot T, but not in the high density area, plot B. Our assumption that spring territorial behaviour would limit Blue Tit density in the high density area but not in the low density one is further supported by the observations that (i) territorial skirmishes were much more frequent in plot B than in plot T; (ii) territory size in the low density area is not larger than in the high density area; and (iii) intruders were only observed in plot B, suggesting that some Blue Tits had not been able to settle there because of the territorial behaviour of the settled birds. It is puzzling, however, why Blue Tits, that are supposedly excluded from plot B, do not move to plot T. It is only 600 m away and much open space and empty nestboxes remained there. It should also be emphasized that bigamy was only found in the high density plot. As explained in more detail by Dhondt *et al.* (in print) this could be the result of females preferring to breed as a second wife to a territorial male, rather than remain paired to a non-territorial partner.

We thus conclude that our observations strongly support the idea that at low breeding density, *i.e.* when interspecific competition with the Great Tit is important, spring territorial behaviour does not affect Blue Tit numbers. When interspecific competition with the Great Tit is relaxed, intraspecific competition for space through spring territorial behaviour limits the size of the Blue Tit breeding population.

5. ACKNOWLEDGEMENTS

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