

Small habitat islands are inferior breeding habitats but are used by some great tits – competition or ignorance?

JON LOMAN

Department of Animal Ecology, Ecology Building, University of Lund, S-22362 Lund, Sweden (e-mail: jon.loman@zooekol.lu.se; fax: +46-46-2224716)

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Abstract. Great tit breeding performance in small habitat islands in an agricultural landscape was compared to that in large deciduous woods. Clutch size was similar in both habitats, but more nestlings starved and fledgling weight was lower in the small habitat islands. The area of wooded habitat in the territories of tits breeding in the small habitat islands was less than what is common to encounter in 'optimum' habitat, deciduous woods. I suggest that this may be responsible, ultimately or proximately, for the poor performance in the small habitat islands. Two possible mechanisms for this effect are discussed. It is possible that the small habitat islands were perceived as inferior by the tits and used by competitively inferior individuals that also were less successful in raising a brood. However, the results were obtained even when female age and weight were controlled for. Therefore, the competitive ability (and probably also young raising competence) may be the same for tits breeding in small habitat islands as for those breeding in optimum habitat. Such a pattern is conceivable if tits have been selected for maintaining a large territory as a response to the close presence of other tits and not as a means of securing a large feeding area. Historically, territories large enough to reduce predation or mate competition (or any cause of territoriality) may always have contained ample food. The presence of small islands, without close neighbours but with insufficient food, may be evolutionarily new. It is probably typical of modern agricultural landscape.

Introduction

Numerous studies have analysed the structure of bird communities in fragmented landscapes (e.g., Martin 1981; Nilsson 1986; Van Dorp and Opdam 1987; Hinsley et al. 1996). However, not only the pattern but also the processes that shape them need to be documented. This study is concerned with one process in this type of landscape, one of several possible behind the community patterns found.

This study describes the breeding performance of great tits (*Parus major*) in very small habitat islands. This tit is a small resident passerine which is strongly territorial during the breeding season. It is a woodland species, deciduous woods being the optimal habitat (Perrins 1979). It is a hole nester, readily accepting nest boxes. Most studies of tit breeding have been undertaken in continuous woods, much larger than those studied here. However, in modern agricultural landscapes, large forests become increasingly fragmented and in some areas, small patches are

Table 1. Habitat islands used in the study.

Size class	No. of islands	Range of sizes (ha)	Nest boxes per year	Mean island size (ha)
Small	23	0.03-0.40	70	0.13
Medium	3	1.2-2.5	56	1.98
Large	2	26-28	63	27.0

The value for mean island size is weighed by number of nest boxes in the different islands; each breeding contributes one value to the mean.

all that remain (Jennersten et al. 1997). Some studies of great tit breeding in woodland fragments have been made and they have usually found poorer breeding performance in these than in continuous woods (Krebs 1971; Møller 1987, 1991; Dhondt et al. 1990; Riddington and Gosler 1995; Hinsley et al. 1999).

This study documents breeding performance of great tits in habitat islands, including very small ones, in a south Swedish landscape. Is the difference in performance, that has previously been documented, only found because the fragmented habitat is inferior or is it also because it is used by less competent parents that for reasons of competition are excluded from optimal habitat? Therefore, also female age and size is recorded to find evidence for a possible difference in the characteristics of those females breeding in large and small forest fragments.

Methods

Study area

The study was performed in the southern part of the province Skåne in southern Sweden. This is to a large extent an agricultural landscape, dominated by cropped fields with cereals, rape and sugar-beet. In this open landscape there are islands of non-cropped areas, ranging in size from 0.01 ha and up. Only islands covered by deciduous trees are considered in this study. The habitat islands used are usually separated from other islands by more than 200 m. The islands used fell in three distinct size categories (Table 1). The islands studied constituted all habitat islands in four areas. They were thus a representative sample of islands of different sizes in the region. The four areas were situated in the vicinities of the estates Ellinge, Svenstorp, Trolleholm and the village of Sjöstorp.

Structural characteristics of habitat islands

The following variables that represent the vegetation of each island were recorded: (1) percent of the ground covered by the canopy of trees or bushes. (2) Total stem area (dm^2/ha) . (3) Mean canopy height (open areas excluded). (4) Number of different tree and/or bush species expected in a sample of five (estimated with rarefaction). The field procedure is described in detail by Loman and von Schantz (1991).

Field procedure

In February 1984, 189 nest boxes were put up in the habitat islands. In the small islands there were one to four boxes per island, with an average density of 25 boxes per ha. In the medium sized islands there were 10 boxes per ha, evenly spaced in the islands. In the two large islands there was only one box per ha. However, local density was higher as the boxes were put in lines, with a distance of about 30 m between them. During the springs of 1984 and 1985 the boxes were checked every few days during laying time. When a clutch was started, the box was again visited when the clutch could be expected to be complete. The box was next visited when the size of the nestlings. When the nestlings were about 8 days old, the female was caught at night, between 10 P.M. and midnight, when roosting on her nestlings. She was weighed and her age (1 year old or older) was determined (Svensson 1984). A final check of the number of nestlings was done when they were near fledging. The nestlings were also weighed at this time. Replacement and second clutches were excluded from the study.

In about half of the small islands, territory mapping (Anonymous 1970) was performed in both years of the study. This was also done in all three medium sized islands in 1985. This mapping was carried out by persons that were not involved in the checking of the nest boxes and provided an estimate of the actual number of birds nesting in the islands, both those in the supplied boxes and in natural holes.

Corrections

Female weight

All females were not weighed on exactly the same date, nor on the same day within the breeding cycle. Because females lost weight during the season (personal observation), their measured weights were corrected for these two variables before use in the analyses. A multiple linear regression of female weight (g) on the date of laying and on the day after hatching yielded the coefficients -0.023 and -0.042, respectively. These coefficients were used to estimate each female's weight on June 1 and at the time of hatching of the first egg.

Fledgling weight

All fledglings were weighed at least once between age 13 and 17 days, close to fledging. The mean value for each brood was used in the analyses. To compensate for growth during this period, brood data were fitted to a model allowing linear growth up to an age A and a constant size after that. Eleven broods were weighed twice between age 11 and 18 days. Their growth was fitted to this model. The best fit was for a slope of 0.919 up to age 13.3 days (A) and a constant weight after that. This compares reasonably well with previously published data (Gibb 1950; Henrich 1989). As all broods were weighed at or after day 13, no corrections were applied.

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Results

Habitats

Tree species diversity and total density of trees and bushes was almost the same for all categories of habitat islands (Figure 1, ANOVA, d.f. = 2:20, F = 0.55, P = 0.58 and d.f. = 2:19, F = 0.10, P = 0.90, respectively). However, small islands had less tree cover (ANOVA d.f. = 2:21, F = 6.95, P = 0.005) and the tree cover present had a lower average height (ANOVA, d.f = 2:21, F = 3.64, P = 0.044).

Tit breeding densities

The most abundant guest in the nest boxes was the great tit, but blue tit (*Parus caeruelus*) and pied flycatchers (*Ficedula hypoleuca*) were also abundant (Table 2). Both tit species were more abundant in boxes in large islands than in those in smaller islands. This could possibly have been due to differences in the nest-box density between islands of different size classes.

In the subset of islands where territory mapping was undertaken in addition to the checking of nest boxes, the number of territories was usually similar to the number of nest boxes known to be occupied (Table 3). One exception was the small islands in 1984, where only about half of the great tits breeding in nest boxes scored as valid territories. Possibly, tits breeding in small islands without neighbours are more silent and thus difficult to detect by territory mapping than are tits breeding in larger islands, with neighbours. However, although the result cast doubt on the accuracy of territory mapping, it does suggest that most tits breeding in the small and medium



Figure 1. Vegetation characteristics in habitat islands of the three size classes considered. The value for canopy height is only based on the parts of the islands where a canopy cover was at all present.

Table 2. Species occupying the nest boxes.

Island size class	Total nest boxes	Great tit (%)	Blue tit (%)	Pied fly-catcher	Starling (%)	Nuthatch (%)
Small Medium	140 112	21 22	4 8	1 21	0 2	0 1
Large	126	40	14	17	2	0

'Total nest boxes' refers to the combined number in both years.

Table 3. Number of tits breeding in nest boxes compared to the number estimated by territory mapping in the small (1984 and 1985) and medium (1984 only) sized islands.

	Year	Number of islands	Boxes used	Mapped territories
Small islands	1984	13	14	6
	1985	12	5	5
Medium islands	1984	3	15	13

Included are all those islands that were both supplied with nest boxes and territory mapped.

Table 4	<i>d</i> . Densities	(used	nest	boxes	per	ha)	of	great	tits	in	small	and	medium	sized	habitat	island	ls.
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	No. of islands	Total area (ha)	Nest boxes	t boxes 1984 1985			
				Nestings	Density	Nestings	Density
Small	27	3.1	70	22	7.1	10	3.2
Medium	3	5.6	56	15	2.7	9	1.6

No relevant data is available for large habitat islands, as these were not saturated with nest boxes.

Table 5. Breeding success of tits in habitat islands of different size.

	Small		Mediu	m	Large		Three-way ANOVA			Five-way ANOVA			
	Mean	п	Mean	п	Mean	п	d.f.	F	Р	d.f.	F	Р	
Day of 1st egg	15.56	18	21.67	15	10.86	35	2:50	4.30	0.019 ^a	2:32	3.47	0.043 ^b	
Eggs	8.76	29	9.21	24	8.55	49	2:80	0.69	0.50	2:55	0.63	0.53	
Addled eggs	0.22	23	0.38	24	0.43	42	2:68	0.46	0.63	2:54	0.48	0.62	
Hatched eggs	7.65	23	7.71	24	7.50	42	2:68	0.04	0.96	2:54	0.12	0.89	
Starved young (%)	17.3	18	7.40	19	0.41	32	2:49	8.89	0.001°	2:42	10.4	0.001^{d}	
Fledged young	6.09	22	6.81	21	7.40	35	2:57	2.17	0.12	2:49	0.81	0.45	
Weight of young (g)	16.47	20	17.55	18	18.37	34	2:52	5.59	0.006 ^e	2:45	4.45	0.017^{f}	

Significant (P < 0.1) contrasts (Tukey test) were found for the following tests: ^a M vs. L P = 0.015; ^b M vs. L P = 0.067; ^c S vs. L P = 0.005, M vs. L P = 0.003; ^d S vs. L P = 0.029, M vs. L P = 0.001; ^c S vs. L P = 0.004; ^f S vs. L P = 0.004; ^f S vs. L P = 0.001; ^c S vs. L P = 0.004; ^f S vs. L P = 0.0

sized islands did so in the provided nest boxes. It is therefore reasonable to assume that almost all tits breeding in small and medium sized islands investigated in this study did use nest boxes. Total breeding densities in all such islands in the study, not only those with territories mapped, can thus be determined. Breeding density varied

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Table 6. Female weight and age.

Island size	Female weight (g)	n	Female age	older			
			1 year old	older			
Small	18.72	19	16	3			
Medium	19.18	21	18	3			
Large	19.43	37	31	10			

between years, island size classes and species (Table 4). The highest densities were for great tits in small islands in 1984, 7.1 breeding pairs per ha.

Breeding performance and female characteristics

Breeding started earlier in large islands than in small and medium sized ones (Table 5). Also, there were fewer lost (and probably starved) young in large than medium sized and small islands and fledged young were heavier in large than in small islands. These significant effects of islands size class were found both when correcting for year and patch (nested under patch area class) only and when also correcting for female age and weight.

There was a tendency that female tits breeding in large habitat islands were heavier than those breeding in smaller islands (Table 6). However, this was not significant when tested with a three-way ANOVA (correcting for year and patch, nested under patch area class, d.f. = 2:58, F = 2.75, P = 0.072), nor with a five-way ANOVA (also correcting for female age and breeding time, d.f. = 2:32, F = 2.58, P = 0.091).

Also, there seemed to be a tendency for a higher proportion of female tits in large islands to be 2 years of age or older. This was, however, not significant (tested with a log-linear model that corrected for year differences in overall distribution of data on different size classes, $\bar{x} = 0.76$, d.f. = 2, P = 0.68).

Discussion

Breeding performance

Nestling survival was highest in the large habitat islands and fledgling weight was highest in these. Egg laying started earlier in the large islands. If there was an effect of island size on the timing of the first egg, this suggests that the adverse conditions in small (and medium sized) habitat islands operated already in the period before egg laying. The difference in number of eggs was, however, small and inconsistent. There was no significant difference in number of fledged young, despite the difference in number of starved young. This is partly because the latter effect was masked by a small (and insignificant) effect, in the opposite direction, on number of hatchlings.

Also other studies that have compared breeding great tits in woodland habitat

with that in habitat islands and hedgerows have found similar results. Pairs in the fragmented habitat tended to breed later (Riddington and Gosler 1995; Hinsley et al. 1999) and produce fewer and/or lighter fledglings (Krebs 1971; Riddington and Gosler 1995; Hinsley et al. 1999). Riddington and Gosler (1995) and Krebs (1971) (but as in the present study not Hinsley et al. 1999) in addition recorded smaller clutches in the fragmented habitat. A result similar to mine was also obtained by Møller (1991) for other species. In a landscape similar to the one studied here, clutch sizes of great tits, European blackbirds (Turdus merula), yellowhammers (Emberiza citrinella) and black-billed magpies (Pica pica) were not affected by habitat island area. However, the number of fledglings increased with increasing island size, suggesting a higher nestling survival in large islands. Huhta and Jokimäki (2001) studied redstart (Phoenicurus phoenicurus) and pied flycatcher and found that birds bred later in small forest patches than in large ones, but that there was no difference in clutch size and number of fledglings. In contrast, Matthysen and Adriaensen (1998) did not find an area effect on the breeding performance (including breeding date) of nuthatches. Their 'small' patches were, however, much larger (above 0.8 ha and on average about 5 ha) than those considered in the present study. A parallel to the present study, but contrasting other habitats, is that of Solonen (2001) where he found that the breeding performance of great and blue tits in urban habitats was less than that in rural ones.

Cause of differences in breeding success

Why did breeding tits perform less well in the small habitat islands? There were habitat differences between the islands of different size classes (Figure 1). However, I do not think these differences were necessarily the direct cause of the differences in performance found. There was no appreciable difference between the structure of medium and large habitat islands (Figure 1). Still, the difference in number of starved young between these two types of islands was significant. More important are probably differences in territory size (counting only wooded area) among patches of different size. In both years, the great tit densities were at least twice as high in small as in medium sized islands. The densities in the large islands were never determined but other studies in woods and larger habitat islands with similar habitats have reported average densities below those found in the small and medium sized islands of this study (Table 4). For example, Gustafsson (1987) found the combined density of great and blue tit to be 2.7 pairs per ha in each of two study years. The density of great tits in Marley wood in southern England varied between 0.5 pairs and 3.5 pairs per ha during the years 1948-1983 (McCleery and Perrins 1985). The second 'best' year had 2.0 pairs per ha. Källander and Karlsson (1981) report the breeding densities of tits in a deciduous forest in southern Sweden, actually one of the two large woods used in the present study. During the years 1969–1978 the densities varied between 0.8 and 2.5 (great tits) and 0.15 and 0.8 (blue tits).

However, it is not self evident that the territory size computed on the basis of patch area gives the full picture. It is possible that tits to some extent utilize also part

of the matrix habitat surrounding the patches or that they utilize neighbouring patches. Actually, tits were sometimes seen flying over the fields surrounding the patches. If so, territory sizes can easily be much larger for these tits than for those in medium sized and large patches, corresponding to what has been documented by Redpath (1995) in a study of Tawny Owls. On the other hand, utilizing the matrix or commuting to other patches probably leads to a less efficient foraging (Hinsley 2000), regardless of area available. If time available for foraging is limiting, this will reduce the amount of food brought to nestlings (Tinbergen and Verhulst 2000). Also, part of the border zone of the small patches was not wooded, as shows from the smaller canopy cover (Figure 1) of these patches. If the tits mainly use the wooded part of the patches, differences in territory size may actually be even larger than suggested above. Tentatively however, I assume that the combined area and allocation pattern for tits in small patches was less favourable than that for those in large patches.

Møller (1991) reaches a similar conclusion. He actually sampled food by sweepnetting but found no difference between small and large islands. Therefore, although he does not actually report bird densities in different islands, he concludes that birds breeding in very small islands have less food available because of the small area. In contrast, Zanette et al. (2000) found lower invertebrate densities in small than in large forest fragments and Riddington and Gosler (1995) found that the quality of food brought to their nestlings in marginal habitat (including small forest patches) was lower than that in woods.

Female behaviour and its cause

Which females (and males) settled in the small habitat islands? I see two basic possibilities. (1) Tits did not *a priori* prefer either one habitat (habitat islands class) over the other and thus, the tits breeding in the small islands were a random sample of all present in the region. The poor performance of those breeding there was due to some aspect(s) of the habitat and landscape structure, e.g., lower food availability (see above). (2) Breeding in small habitat islands is recognized as inferior by tits and those that breed there are in some respect competitively inferior to those breeding elsewhere. The poor performance is a combination of inferior habitat (in a wide sense) and poor breeding capacity correlated with poor competitive ability on part of the tits breeding there.

The second possibility certainly makes sense. However, there is not much support for it in the present data. The fact that great tits breeding in the small islands laid as many eggs as those in the large ones suggests that they were in equally good condition. Actually, they laid slightly more eggs despite the fact that they were breeding somewhat later than those in the large islands. Given that egg number decreases with time, in this study as well as in several others (Källander 1983 (blue tit), Perrins 1979 (great and blue tit), Verhulst and Tinbergen 1991 (great tit)) this stresses this point even more. Furthermore, young female great tits (which tend to be competitively inferior; Sandell and Smith 1991) usually lay smaller clutches than do older ones (Järvinen 1991). This supports my reluctance to believe that age differences and/or differences in competitive ability are important in explaining the lower breeding success in smaller habitat islands. Moreover, the most striking effects, those on weight of great tit fledglings and proportion of starved great tit nestlings, were significant also when the age of the female was accounted for.

True, females were lighter in the small habitat islands (Table 6) and although the difference was not significant, it may be numerically large enough to be important. Here, another complication must be considered. The females were weighed well into the breeding season. Even if they had only taken up their present home range just before breeding, they had themselves, by the time I weighed them, already suffered the adverse effects likely to be present in the small habitat islands. Thus, the weight differences found could well be due to the inferior quality of the habitat these females had settled in. Also females in small habitat islands were younger. Though not significant, this could contribute to the difference in breeding performance found. It should also be borne in mind that the effect of parent weight on breeding performance is complex. Actually, reduced weight during the breeding period might actually be an adaptation (Halpern et al. 1998). For example, Hinsley (2000) found that a low weight was a relative advantage for parents commuting between patches. However, the arguments in the previous section show that in addition to female size and age effects, more factors must be responsible for the differences in breeding performance found. Also in the study by Riddington and Gosler (1995) no difference was found in age and size between great tits breeding in woodland and marginal habitats.

Is it conceivable that the first alternative is valid; i.e. can the tits be ignorant of the difference in habitat quality and/or unable to respond accordingly? Because a landscape with small habitat islands (and nest boxes) may be new in an evolutionary sense, I think this is possible. It could be that territory size is to some extent determined by factors other than food supply, e.g., related to mate choice, mate guarding and nestling defence. If this assumption is true, it could be that total amount of food has not been the sole determinant of territory size in the evolutionary history of the species. Rather, a territory in a 'good' habitat (e.g., deciduous wood) that is large enough to satisfy area demands for mate guarding, nest defence etc., will automatically contain enough food.

This study only documents female size and age. Of course male characteristics may also have an influence. Lack of male data is due to the fact that the males are less easy to catch and to unequivocally assign to a clutch. However, it may also be that they are less important for the breeding result. Enoksson (1991) has shown that the age of female but not male nuthatches (*Sitta europea*) does affect time of breeding.

It may be argued that I created the artificial situation by providing a superabundance of nest sites in the small patches. Great tits readily accept nest boxes and breeding densities are usually increased by their provision (Dhondt and Eyckerman 1980). However, nest boxes in this study area resulted in increased breeding density in patches of all size classes (Loman, in preparation). Furthermore, also in the larger size classes, empty nest boxes were available. Also, the only factor manipulated was nest sites. If there are more nest sites available in an inferior habitat than in the unmanipulated case the question remains, why settle here when the habitat was less than optimal? Of course, it may be seen as doing the best of a bad job if the boxes were the only nest sites available. However, this explanation alone does not explain the patterns observed, why do females of all categories seem to accept these inferior nest sites as readily and why do the surplus nest sites provided in medium and large patches not yield a similar low quality of nestlings? It is also important to observe that these small patches were actually used also when nestboxes were not supplied. In a study of 135 patches without nest boxes, 0.01–24 ha in area, the smallest used by great tits was 0.19 ha (Loman, in preparation). Although nest boxes may be as evolutionarily new as small patches to great tits, there is no reason to expect an interaction of box breeding and patch size on breeding performance.

Basically, even small habitat islands are made up of 'good habitat' (but too little of it). Due to the landscape structure the spatial requirements for a nearest neighbour distance are satisfied by a small habitat island (if there is only one territory in it). When not subject to spatial competition, it may thus be that tits now accept territories that do indeed contain less than sufficient food.

There are several reasons birds lay more eggs than they fledge young. However, there is likely to be an optimum 'surplus'. I see no reason why tits in small islands should have higher optimum surplus than tits in larger woods. Thus, not only are they behaving suboptimally in the sense that they seem to breed in small islands without being forced by superior competitors. Also, they seem to behave suboptimally in the sense that they are laying 'too large' clutches. This could be explained by the same phenomenon. If the tits are not able to judge correctly the value of a territory when 'deciding' to settle there, they are probably also not able to correctly judge it when 'deciding' on the number of eggs to lay. A similar explanation has been put forth for super optimal clutch size of blue tits breeding in less productive Mediterranean woodlands (Zandt et al. 1990).

Alternatively, this behaviour can be explained by, and thus supports, a model by Dhondt et al. (1990). They claim that birds breeding in inferior habitats to a large extent are descendants of parents selected in a superior habitat (with a higher optimum clutch size). The model is supported by their field data and also by Matthysen et al. (2001), who found high immigration by great and blue tits into small patches. The argument by Dhondt et al. (1990) is similar (but not identical) to mine. Their model stresses clutch size as an inherited character while my hypothesis stresses evolution on the capacity to correctly evaluate the habitat quality (although my argument does not preclude a genetic component in clutch size determination). Their assumption that clutch size is inherited is supported by e.g., van Noordwijk et al. (1981). The argument of Dhondt et al. (1990) is valid in any stable landscape, with a mixture of good and bad patches. However, they do not explain why this gene flow should take place. I suggest a possible explanation that is valid in the particular landscape studied here. I stress that in a landscape where the inferior patches are 'new', they might not be discriminated against and, for the same reason, not give correct cues to clutch size. I think this is precisely the situation in the modern agricultural landscape.

In conclusion; there is an effect of landscape structure on breeding performance,

acting after the completed laying of the clutch. Small habitat islands do therefore constitute an inferior breeding habitat for great tits and possibly blue tits. Although the present study is insufficient for a conclusive inference, I argue that birds breeding in this inferior habitat may be ignorant, in an evolutionary sense, of this.

Consequences for population dynamics

Do the small patches represent a 'sink' habitat (Pulliam 1988) or pseudosinks (Watkinson and Sutherland 1995)? Because the young tits were not followed to adulthood it is not possible to estimate the difference in reproductive output between tits living in small habitat islands and in 'optimum' deciduous woods. It is possible that the small habitat islands, at least in some years, have a negative net reproductive output. This habitat may be dependent on a net influx from a donor habitat. Such a situation has been suggested for carrion crow *Corvus corone* populations breeding in Swiss valleys that rely on immigration from woodland hills (Tompa 1975). If the deficit is filled with a surplus from the optimum habitat, having no influence on its population density, or attracts animals that would otherwise breed in the 'donor' habitat is not clear. In situations like this, the former situation is the more likely. However, if the tits really are 'ignorant' of the conditions in the small habitat islands, it is possible that their presence in a landscape decreases the average population level in the optimum habitat (but not necessarily in the landscape as a whole).

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