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Nest predation and breeding success in Common Treecreepers nesting in boxes and natural cavities

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Most long-term studies of passerine life-history evolution have been based on species that breed readily in nest-boxes. Very few papers deal with data from natural holes. Here we compare the breeding success of the Common Treecreeper (*Certhia familiaris*) between special nest-boxes (southern Finland; 61°N) and natural nesting sites (Lithuania 55°N). The nest-boxes and natural nest sites did not differ in laying date or the frequency of the second clutches. Significant differences were found in clutch size, number of fledglings per breeding attempt and frequency of the replacement clutches. The reproductive rate was lower in natural sites than in nest-boxes, because of the higher nest predation in natural cavities (37% vs. 8% in nest-boxes). The higher predation in natural cavities led to greater frequency of replacement clutches in natural holes. This increased the clutch size, because the Treecreeper lays the largest clutches in the middle of its breeding period. The proportion of nests suffering predation did not vary seasonally. The observed difference in predation may bias conclusions regarding life-history evolution drawn from nest-box studies alone.

1. Introduction

Most long-term studies of the life-history evolution in passerine birds have been based on species that breed readily in nest-boxes. Very few papers deal with data from breeders in natural holes (however, see Alatalo et al. 1988, 1991). In consequence, it has been proposed that the results originating from nest-box studies are biased compared with those obtained from natural nest sites (Nilsson 1984a,b, Møller 1989a). Møller (1989a) presented four reasons why caution should be exercised in drawing conclusions from nest-box studies about life-history theory, quantitative genetics, population regulation and sexual selection: (1) the design of nest-boxes has reduced nest predation levels (see also Nilsson 1975, 1984a,b), (2) removal of old nests before the next breeding reduces ectoparasites, (3) nest-boxes make the breeding density abnormally high and (4) nest-boxes differ in shape from the natural cavities, often being shallower.

Here we compare the breeding success of the Common Treecreeper (*Certhia familiaris*, later

Treecreeper) nesting in nest-boxes (in Finland) with its success in natural nest sites (in Lithuania). We also compare our results with the results shown by the British nest cards (Flegg 1973), which results include breeding attempts in both nest-boxes and natural cavities.

The natural nest sites of Treecreepers are narrow vertical hollows between the tree trunk and partly detached bark, or other lengthy crevices in trees. Since modern forestry does not favour old forests and dead trees are removed, Treecreepers often nest in buildings and other artificial structures. Treecreepers seldom accept the usual nest-boxes designed for small songbirds, probably because of the difficulty of entering the box, but readily occupy a special nest-box (Kuitunen 1985, 1987, 1989, Kuitunen & Suhonen 1989, 1991). Here we focus on two questions regarding breeding Treecreepers:

Do the laying date, clutch size and breeding success differ between nests in nest-boxes and natural sites?

Do the predation rates differ between nests in nest-boxes and nests in natural sites?

2. Study areas and methods

The field work was carried out in two study areas: One was in southern Finland (61°10′ N, 24°40′ E; and the other in Lithuania (55°20′ N, 23°30′ E). The study area in Finland (5870 ha, in the years 1973–1983) is situated in the southern boreal coniferous zone and consists mainly (65%) of forested land. There are also small lakes, some larger bogs and dry forests not occupied by the Treecreeper. The forests are chiefly coniferous and consist of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*); deciduous tree species, birches (*Betula pendula* and *B. pubescens*), European aspen (*Populus tremula*) and grey alder (*Alnus incana*) are rare. The distribution of the forest types is normal for southern Finland. This study area has about 2.5 special nest-boxes per km^2 (for details see Kuitunen 1985), depending on the quality of the habitat. The mean distance between two boxes was about 400 m, ranging from 200 m to 1000 m. The number of boxes varied between years from 130 to 156. After 1978, the study area was fragmented by forestry and contained fewer boxes, with the result that in some of our tables only the years 1975–1978 are included. The ringed population breeding in nest-boxes varied between years from 34 to 86 pairs (for more details, see Kuitunen 1987).

The study area in Lithuania (1460 ha, in the years 1958–1984), which lacks nest-boxes, is situated in the hemiboreal vegetation zone about 670 km farther south. The forest (Šakiai forest) is chiefly mixed coniferous and broad leaf consisting of Norway spruce and Scots pine; deciduous tree species are more common than in southern Finland: birches (*Betula pendula* and *B. pu-*

Table 1. Data on Treecreeper nestbox numbers and occupancy in southern Finland.

	1975	1976	1977	1978	Total
Total number of boxes	130	156	154	144	584
Boxes occupied	99	120	112	57	388
% occupied	76.2	76.9	72.7	39.6	66.4
Breedings by:					
Certhia familiaris	99	121	106	58	384
Pairs	78	86	80	34	
Parus cristatus	1	6	3	2	12
Parus major	1	3	2	–	6
Parus ater	3	–	–	–	3
Parus sp.	–	–	–	1	1
Ficedula hypoleuca	–	–	2	–	2
Total number of breedings	104	130	113	61	408
Double breeding in the same box	5	10	1	4	20

bescens), European aspen, grey alder, English oak (*Quercus robur*), Norway maple (*Acer platanoides*), small-leaved lime (*Tilia cordata*) and common ash (*Fraxinus excelsior*). The number of nests found varied between years from one to fourteen.

3. Results

3.1. Occupation of the boxes

On average 66.4% (39.6–76.9%) of the nest-boxes were occupied by various bird species in 1975–1978 (Table 1). The Treecreeper was by far the most frequent species, with 384 nests (94.1% of all nests). The variation in the occupation frequency between years was due to fluctuations in the Treecreeper population.

3.2. Clutch size

In spite of the geographical distance between the areas, the laying dates of the first clutches were nearly the same in the nest-boxes and natural cavities (Table 2). Nor were there differences between the nest-boxes and natural cavities in the clutch size of the first clutches. However, if all clutches are included, the average clutch size was higher in natural cavities than in nest-boxes ($t = 4.0$, $df = 353$, $P < 0.001$, Table 2), presumably due to the greater proportion of replacement clutches in natural cavities than in boxes. In the middle of the breeding season, Treecreepers generally lay larger clutches than early in the season (see also Kuitunen 1987). The greater number of replacement clutches in natural cavities was due to the greater nest predation.

3.3. Reproductive rate

The reproductive rate (fledglings/breeding attempt) was higher in nest-boxes than in natural cavities (Table 2). The Treecreeper pairs breeding in boxes were more than twice as productive as pairs breeding in natural cavities. Of the breeding attempts in nest-boxes, 69.9% (n = 369) were successful (at least one fledgling) compared with 36.2% (n = 42) in natural nest sites. The difference is highly significant ($\chi^2 = 33.5$, $df = 2$, $P < 0.001$). The number of successful nests in nest-boxes may even have been underestimated, because a pair was considered as breeding if it had prepared a nest cup, but such breeding attempts are easily overlooked in natural nest sites. When only those nests where eggs were laid and incubated are included, the success rate in the nest-boxes was 85%.

3.4. Nest predation

In natural nest sites the proportion of the breeding attempts prevented by various predators was remarkably high (36.8%) compared with that of nest-boxes (8.1%; Table 3). The greater proportion of destroyed nests is also apparent from the larger number of pairs which laid replacement clutches in natural cavities (22.1%. n = 31) compared with the pairs breeding in nest-boxes (6.9%, n = 18). The number of second clutches did not differ between nest-boxes and natural cavities (Table 2).

The most common reason for unsuccessful breeding in Lithuania was predation by mustelids. In Finland this was only occasionally observed, although the density of mustelids does not differ greatly (e.g. Stubbe 1989). For the nests in boxes,

Table 2. The different breeding parameters compared between the two study areas.

	Nest boxes			Natural cavities		
	Mean	SD	n	Mean	SD	n
Laying date of first clutches	27 April	5.8	236	25 April	6.1	96
Clutch size, all clutches	5.43	0.71	299	5.82	0.66	56
Fledged young	3.03	2.51	427	1.50	2.04	116
Replacement clutches (%)	6.9	–	18	22.1	–	23
Second clutches (%)	34.5	–	90	32.3	–	31

the Great Spotted Woodpecker (*Dendrocopos major*) was the most important predator. It was able to make a hole in the box at the level of the calling fledglings and take them out. One pair of woodpeckers destroyed up to five nests located close to each other, perhaps after having learned to regard the boxes as a foraging place.

Nest predation did not differ seasonally. When we compared the number of unsuccessful nests in Lithuania between the first (59.7%, n = 40), replacement (75.0%, n = 12) and second clutches (52.2%, n = 12), there was not a significant difference ($\chi^2 = 2.12$, df = 3, $P > 0.50$). Nor were there any differences between the clutches laid in four different 15-day periods in natural cavities ($\chi^2 = 2.62$, df = 6, $P > 0.75$) or in nest-boxes ($\chi^2 = 5.26$, df = 4, $P = 0.26$). These results imply that predation is not important to the breeding schedule of the Treecreeper.

4. Discussion

4.1. Clutch size and breeding success

The laying dates and clutch sizes of the Treecreeper were similar in nest-boxes and natural cavities. However, due to predation the average clutch size is higher in natural cavities than in nest-boxes, where more of the first breeding attempts are successful. Clutch size has often been found to be smaller in natural cavities than in boxes (Karlsson and Nilsson 1977, Nilsson 1984a, Gustafsson and Nilsson 1985, Slagsvold 1987), but we found no differences in clutch size between boxes and natural cavities when the effect of the date of laying was eliminated. In the Treecreeper the effect of the laying date is the most important reason for the variation in clutch size, which typically shows an initial increase to a peak,

Table 3. Breeding success and reasons for unsuccessful breeding attempts in the Common Treecreeper in the study areas of Southern Finland (1975–1983) and Lithuania (1958–1984) and in the British Isles (Flegg 1973)

	Southern Finland		Lithuania		British Isles	
	n	%	n	%	n	%
Successful	369	69.1	42	25.8	93	52.5
Unsuccessful because	159	29.8	74	45.4	54	30.5
abandoned by unknown reason	64	12.0	6	3.7	1	0.6
disturbance by man	48	9.0	–	–	11	6.2
destroyed by Woodpeckers	23	4.3	5	3.1	1	0.6
destroyed by raptorial bird	–	–	10	6.1	–	–
destroyed by mammal	–	–	45	27.6	9	5.1
unknown nest predator	7	1.3	–	–	32	18.1
destroyed by ants *(Formica rufa* s. l.)	4	0.7				
adult killed by unknown predator	4	0.7	1	0.6	–	–
nestlings starved	6	1.1				
competition with tits (*Parus* sp.)	2	0.4				
female found dead in the nest	1	0.2				
sickness	–	–	1	0.6	–	–
fallen nest	–	–	6	3.7	–	
Uncertain outcome	6	1.1	47	28.8	30	17.0
Total	534	100.0	163	100.0	177	100.0

followed by a decrease during the breeding period (Kuitunen 1987).

The numbers of successful breedings recorded on British nest cards (Flegg 1973, 52.5%) fall between the numbers for nest-boxes in Finland and natural cavities in Lithuania. However, these results agree well with ours, as 13% of the nest card material consists of breeding attempts in nest-boxes (Table 3) and unsuccessful attempts may easily have been overlooked. In Michigan, 58% of the clutches in natural cavities were successful (Davis 1978). However, this sample was relatively small (n = 19).

According to Nice's (1957) review, the success of hole-nesting birds is on average distinctly higher than that of open-breeders. Most of the hole-nesting studies have been made with nest-boxes. The numbers given by Nice (1957) for open-nesting species resemble those for natural nest cavities in the Treecreeper, while the numbers for hole-nesting species resemble those for nest-boxes.

4.2. Nest predation

In nest-boxes the Treecreepers produced more fledglings than in natural cavities, the reason for the lower fledgling success in natural cavities being predation. If the predator learns that boxes contain prey, however, the predation rate can increase in nest-boxes, as we observed with the Great Spotted Woodpecker (see also Dunn 1977, Sonerud 1985 and Alatalo et al. 1991).

Passerine nesting success depends on the safety of the nest site. Kuitunen and Mäkinen (unpubl.) observed that Treecreepers choose the nest site for the first breeding in spring at least 100 m from the forest edge, in the interior parts of the forest. Beside being optimal for foraging and feeding of the nestlings (see Kuitunen & Suhonen 1989 and 1991), this may be a method of avoiding nest predation. Our results suggest that natural selection could favour pairs breeding further from the forest edge. Proximity to the forest edge has in many cases increased nest predation (e.g. Angelstam 1986, Møller 1989b and also experimentally: Andren et al. 1985, Andren & Angelstam 1988).

van Balen et al. (1982) found that the Treecreeper preferred nest-boxes to natural cavities. In our well-inspected nest-box study area, we have observed about five pairs of Treecreepers breeding in natural sites each year. In some cases the Treecreepers clearly preferred a natural site. In deciduous forest, the Treecreeper can probably find natural nestsites more easily than in coniferous forest (e.g. Flegg 1973).

Our results indicate that a nest-box is a more productive alternative for a Treecreeper than a natural cavity. In consequence, fecundity can easily be overestimated on the basis of nest-box studies. Comparison of the reproductive rate within populations is probably more reliable than between populations. However, nest-box studies have made a valuable contribution to the theory of life-history evolution, although the conclusions drawn from these studies may be biased by the differences in predation rate between nest-boxes and natural cavities.

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Selostus: **Pesäpredaation vaikutus pöntöissä ja luonnonkoloissa pesivien puukiipijöiden pesintämenestykseen**

Useat pitkäaikaiset lintujen pesintämenestystä selvittäneet tutkimukset perustuvat pöntöissä pesiviin lintuihin. Näissä tutkimuksissa saatuja tuloksia on viime aikoina arvosteltu (Møller 1989a), koska niiden on katsottu aiheuttavan vääristyneitä tulkintoja useilla biologian keskeisillä alueilla (elinkiertojen evoluutio, kvantitatiivinen genetiikka, populaatioiden säätelymekanismit tai puolison valinta).

Møllerin (1989a) mukaan pönttöjen käyttö aiheuttaa vääristyneitä tuloksia neljästä syystä: 1) Pöntöissä olevia pesiä ryöstetään vähemmän kuin luonnonkoloissa olevia pesiä. 2) Pöntöissä olevat pesät sisältävät vähemmän ulkoloisia kuin luonnonpesät. 3) Pönttöjen avulla saadaan aikaan suurempi populaation esiintymistiheys kuin luonnollisissa olosuhteissa. 4) Pöntöt ovat luonnonkoloja syvempiä ja tasalaatuisempia. Toistai-

seksi on olemassa vain harvoja tutkimuksia, joissa on verrattu saman lajin pesimämenestystä sekä pöntöissä että luonnonkoloissa. Tässä työssämme vertaamme pesäpredaation merkitystä puukiipijän pesintämenestykseen Etelä-Suomessa sijaitsevan pöntötetyn tutkimusalueen ja Liettuassa sijaitsevan luonnonkoloissa pesivän puukiipijäpopulaation välillä.

Muninnan aloituksessa tai toisten pesyeitten osuuksissa ei tutkimusalueitten välillä esiintynyt eroja. Keskimääräinen pesyekoko oli Liettuan luonnonkoloissa suurempi, mikä johtui uusintapesyeiden suuresta osuudesta. Pesyeet, joita puukiipijä munii pesimäkauden keskellä, ovat suurempia kuin aikaiset tai myöhäiset pesyeet. Toisaalta puukiipijät munivat uusintapesyeitä enemmän pesiessään Liettuan luonnonkoloissa kuin Etelä-Suomen pöntöissä, koska ensimmäiset pesät tuhoutuivat pesäpredaation vuoksi useammin Liettuan luonnonkoloissa (37%) kuin Etelä-Suomen pöntöissä (8%). Predaatioriski ei vaihdellut pesimäajan kuluessa. Pesäpönttöihin perustuvat tutkimukset saattavat aiheuttaa virhettä mm. tutkittaessa elinkiertojen evoluutiota, jos eroja luonnollisiin perintäolosuhteisiin ei oteta huomioon.

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