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Enhanced predation rates on cavity bird nests at deciduous forest edges – an experimental study

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The size of a forest tract influences the composition of the fauna. If forests become fragmented this will affect the fauna in several ways. One of the main effects is enhanced nest predation. Several studies which confirm this effect have been carried out, but none has used natural cavities. I tested experimentally whether the predation rate was higher in natural tree-holes close to the forest/farmland edge than in the interior of the wood. In a fragmented deciduous forest, fresh Quail eggs were placed in natural cavities at various distances from the edge. The eggs were exposed during a period corresponding in length to the egg and nestling period of a hole-nesting bird. In the beginning of the period, the predation rate was higher close to the edge (< 20 m) than further inside the wood. This result may indicate that a predator first searches the ecotone and afterwards penetrates deeper inside the forest. The results is in accord with earlier observations that nests in natural cavities seem to be less vulnerable than other types of nests.

1. Introduction

There is evidence that forest fragmentation affects both the community structure, i.e. species richness and diversity (Whitcomb et al. 1981, Ambuel & Temple 1983, Helle 1984, Zarnowitz & Manuwal 1985), and population dynamics of birds (Andrén et al. 1985, Wilcove et al. 1986, Andrén & Angelstam 1988). It is now generally accepted that bird species dependent on large intact forests are declining in numbers as forest fragmentation progresses (Whitcomb et al. 1981, Ambuel & Temple 1983), but the reason why species disappear chiefly from small fragments is not fully understood. A number of explanations have been suggested, including interspecific brood parasitism from outside habitat fragments (Brittingham & Temple 1983) and enhanced nest predation rates (Robbins 1980).

The nest predation hypothesis has furnished an explanation of the fragmentation on bird populations. For instance, it has been shown that predation rates in general are higher in small than in large forest fragments (Gates & Gysel 1978, Wilcove et al. 1986, Andrén & Angelstam 1988, Andrén 1989). Earlier studies have been carried out using artificial nests (Wilcove 1985, Yahner & Wright 1985), abandoned open nests (Gottfried & Thompson 1978), nest-boxes (van Balen 1973, Nilsson 1975, 1984, Kuitunen &

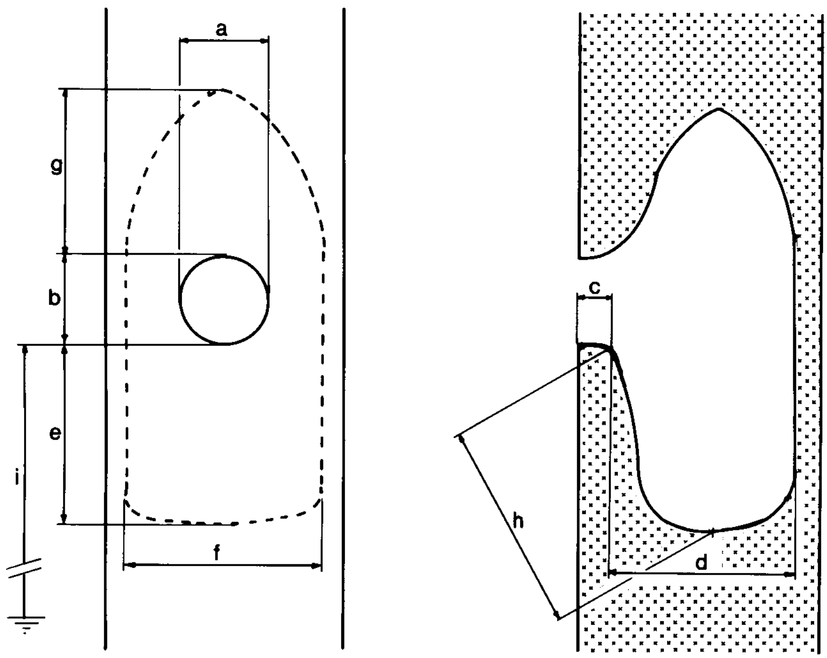

Fig. 1. Schematic representation of a natural cavity showing the variables measured. a: entrance hole width, b: entrance hole height, c: wall thickness, d: distance front to rear wall, e: hole depth, f: width of hole, g: height above entrance, h: distance of egg from entrance, i: height above the ground.

Helle 1988) or open nests placed on the ground (Andrén et al. 1985, Wilcove 1985, Angelstam 1986 (cup nests), Møller 1989), or by simply exposing eggs on the open ground, with no attempt at creating an artificial nest (Avery et al. 1989). The aim of this study was to establish whether nest predation in natural tree-cavities varies in relation to forest size or location of cavity tree in relation to edge.

2. Methods

The study was carried out in a deciduous forest north of Uppsala (Andersby, 60° 09' N, 17° 49' E), in south-central Sweden. The entire study area was 59.7 ha, of which 44.3 ha was covered with forest and 15.4 ha consisted of arable and pasture land. Of the forest, 56% (24.8 ha) had been thinned mainly in 1967/68, to re-establish former land use patterns. A smaller part (0.9 ha) of the forest included spruce *Picea abies*. The dominant deciduous trees, in decreasing order of occurrence, were oak *Quercus robur*, maple *Acer platanoides*, lime *Tilia cordata*, rowan *Sorbus aucuparia*, birch *Betula pubescens/verrucosa*, and aspen *Populus tremula* (Hytteborn 1975).

Thirty-nine tree-holes were utilized, at various distances from the forest edge. The distances from the cavity trees to the closest farmland-forest edge varied between 1 to 70 m and were measured in the field with a 50 m long measuring-tape. Two types of holes were used, viz. woodpecker holes and limb holes. For each cavity several variables were measured (Fig. 1, Table 1). The bottom area was estimated from the two diameters (d and f) measured at entrance height, using the equation of an ellipse ($\pi \times d/2 \times f/2$). The volume of the cavity was estimated by multiplying the bottom area by the total height (= e + b + g) (see van Balen et al. 1982). The direction of exposure for each cavity was recorded only in the four main quadrants, i.e. North – South – East – West. The following conditions had to be fulfilled for a cavity to be considered suitable: The bottom area should measure at least 22 cm^2, the smallest diameter inside the cavity had to be at least 4 cm and the entrance should have a diameter of at least 25 mm.

One fresh Quail *Coturnix coturnix* egg was placed in each cavity. The eggs had an average size of 30 mm x 23 mm and a weight of 10–11 g. They were whitish or creamy yellow with reddish brown or light brown blotching, which is slightly darker than the colour of the eggs of hole-nesting birds in the area (Nuthatch *Sitta europea,* Pied Flycatcher *Ficedula hypoleuca,* Great Tit *Parus major,* Marsh Tit *P. palustris,* Coal Tit *P. ater* or Blue Tit *P. caeruleus).* The eggs were placed in the cavities in the following way: Two strings were fixed to a small bag made of fabric, one to fasten the top and one to fasten the bottom of the bag. The eggs were carefully placed in position by lowering the bag with an egg in it to the bottom of the cavity whereupon the string closing the bottom of the bag was pulled, thereby releasing the egg.

The cavities were inspected on day 15 and day 30 after the eggs were placed in the cavity. A 30-day period is adequate for hole-nesting passerines having incubation and nestling periods of 28–30 days (e.g. Pied Flycatcher, Great Tit or Blue Tit). The cavities were inspected using a dentist's mirror fitted with a lamp. Predation was considered to have taken place if the egg had been removed from the cavity when it was inspected. No eggs were found broken or eaten in a cavity. It was assumed that the nests had been robbed independently.

The experiment was carried out during the early summer of 1989, from 13 June (= day 0) to 13 July. By this time, many hole-nesting birds either have nestlings which have left or are about to leave the nest, or are laying their second clutch for the season.

3. Results

During the experiment (30 days), 17 of the 39 cavities lost their eggs, the average daily predation rate being 0.014 nests daily. The predation rate for the first 15 days was 0.017 nests daily (10 eggs lost), being higher in cavities near (< 20 m) the forest-farmland edge than further inside (≥ 20 m) the forest or in the rest of the study

Table 1. Mean variables (± SD) of nests in natural cavities in the untouched and robbed groups. The probabilities (P) based on the Mann-Whitney U-test.

Nest variables	Untouched (n = 22)	Robbed (n = 17)	P
Entrance hole width (cm)	4.3 ± 1.4	5.1 ± 1.6	< 0.05
Entrance hole height (cm)	5.1 ± 2.4	8.2 ± 7.5	< 0.01
Wall thickness (cm)	4.8 ± 2.7	5.4 ± 2.2	NS
Distance front to rear wall (cm)	17.6 ± 9.2	19.6 ± 10.6	NS
Hole depth (cm)	13.0 ± 9.8	16.9 ± 8.4	NS
Width of cavity (cm)	11.7 ± 8.4	14.5 ± 7.0	< 0.05
Height above entrance (cm)	9. 0 ± 11.3	10.3 ± 12.0	NS
Distance of egg from entrance (cm)	15.6 ± 8.8	17.4 ± 9.4	NS
Circumference of trunk at hole(cm)	114.0 ± 53.2	130.6 ± 51.8	NS
Height above the ground (m)	3.5 ± 1.0	3.9 ± 1.2	NS
Bottom area (cm^2)	204.0 ± 272.6	229.8 ± 174.3	NS
Volume (cm^3)	7828.6 ± 17386.1	8157.4 ± 6236.4	< 0.05
Diameter of trunk at breast height (cm)	38.4 ± 15.1	49.6 ± 21.5	NS

period (days 16–30) (Fisher's exact probability test, $P = 0.03$). Of the plundered cavities, 53% were woodpecker holes and 47% limb holes; of the undisturbed cavities, 55% were woodpecker holes and 45 % limb holes ($\chi^2 = 1.15$, df = 1, $P = 0.28$). For all the cavity trees ($n = 39$) the corresponding figures were 54% and 46% respectively. The cavities suffering predation ($n = 17$) did not differ noticeably from the others ($n = 22$) in their distribution by tree species or the direction of their exposure. The cavities that were robbed had larger entrance holes (Mann-Whitney U-test, $P < 0.05$ (width) and $P < 0.01$ (height)), and a greater width and volume (Mann-Whitney U-test, $P < 0.05$ for both) (Table 1).

4. Discussion

In the beginning of the experimental period, this study showed a higher loss of eggs in cavities close to the farmland edges (< 20 m) than in cavities further inside the forest. Predators are supposed to concentrate their activities near edges (Gates & Gysel 1978, Brittingham & Temple 1983), and ecotones between two habitats are generally assumed to be richer in species and individuals than either of the two habitats alone (Odum 1971). In a conifer forest, Hansson (1983) showed that there were higher densities of birds in an outer belt of about 50 m than deeper inside the forest.

The timing of the experiment might be of importance, since it was carried out in the last part of the normal breeding season for hole-nesting passerines and the predators might have a time-dependent search image. This is most probably not the case, however, because, on the one hand, some species of hole-nesting birds may lay a second clutch, e.g. the Great Tit, and on the other, cavities are often used as night roosts. This means that for a predator it is always worth the trouble to search a cavity for food.

In the present study the cavities that were robbed had larger entrance holes than the others. This difference may have made it easier for a predator to locate the cavity and to enter it and remove the egg. This might have affected the result, but a more likely explanation is that a predator first searches the ecotone and afterwards penetrates deeper inside the forest. According to Wilcove et al. (1986; Figure 6, p. 251), the edge-related increase in predation may level off at approximately 300–600 m from the edge. An edge effect was also recorded here, although this study was carried out on a much smaller scale, most of the nests being at a distance (50 m) at which the edge effect is believed to be pronounced. Yahner & Wright (1985) obtained the reverse results in study in very small (1 ha) plots and believed that it was probably due to the small distances (< 50 m) of both the edge and centre nests from the edges of the plots. Studies in larger habitat patches than that of the present experiment showed that the predation rate within forest fragments increased with decreasing distance from the farmland-forest edge.

Møller (1989) found that the nest predation rate was significantly affected by distance from the edge and by the type of nest. During a period of 14 days, open ground nests had a daily predation rate of 0.039 inside a wood (> 100 m from the edge), 0.056 at the edge (from 25 m inside to 25 m outside the wood) and 0.020 in an open field (> 200 m from the woodland edge) (Møller 1989). For partially covered nests, the corresponding figures were 0.018, 0.030 and 0.021, respectively (calculated from Møller 1989).

This is in accordance with the observations of Wilcove (1985), who found that the predation rate was higher in smaller woodlots than in large intact forests. Wilcove (1985) also found that open-cup ground nests were more susceptible to predation than nests above the ground, and that experimental cavity nests were much less vulnerable than other nest types. Other studies with open-cup nests show similar patterns (e.g. Gates & Gysel 1978, Andrén & Angelstam 1988, Andrén 1989).

Cavity nests are thought to be less vulnerable to predators than open-cup nests (Lack 1954, Ricklefs 1969, Alerstam & Högstedt 1981). The present study showed a predation rate of 0.017 after the first 15 days and 0.014 for the whole period of 30 days which can be considered low compared with the rates recorded by Møller (1989) for open ground nests or partially covered nests. However, there is a danger in such a comparison, since predation rates depend very much on experimental procedures. Thus, for instance, the way dummy nests are hidden, how often they are inspected, etc., may influence predation rates. The results of this study concur with Wilcove's (1985) suggestion that nests in natural cavities are less vulnerable to predation than other nest types. Nest-boxes (e.g. Löhrl 1957, Nilsson 1975, 1984, Kuitunen & Helle 1988) show a lower predation rate than natural sites, but Nilsson (1986) found that the breeding success of open-nesting species did not differ significantly from that of hole-nesting species breeding in natural cavities. However, complete nest losses were higher in open-nesters than in holenesters. The low predation rate in this study is also noteworthy if the shape of the study area is taken into consideration. The area was rather fragmented with some long corridors and few circular areas, which means that a predator could easily penetrate parts of the area from adjacent habitats.

To conclude, this nest predation experiment is one of very few in which natural tree cavities were used. This makes it hard to reach any definite conclusions about the results and care should be taken when comparing them with those obtained using nest-boxes, dummy nests, etc. However, it can be noted that this experiment yielded results in accordance with earlier observations, viz. that nests in natural cavities seem to be less vulnerable than other types of nests and that nest predation is affected by distance from the forest/farmland edge.

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Sammanfattning: **Förhöjd bopredation i trädhåligheter vid kanter av en ädellövskog – en experimentell studie**

Storleken av ett skogsområde påverkar till stor del faunans sammansättning i området. Om skogar fragmenteras återspeglas detta i faunan på många sätt. En av de viktigaste följderna av fragmentering är en förhöjd bopredationsgrad som visats i ett stort antal studier, men ingen har använt naturliga trädhål. Jag har experimentellt testat hypotesen om predationsgraden är högre i naturliga trädhål närmare kanten skog-åker än längre in i skogen. I en fragmenterad ädellövskog placerades färska vaktelägg ut i trädhål med varierande avstånd från skogskanter. Äggen exponerades under en period som är relevant till den tid som hålhäckande fåglar har ägg och ungar. En signifikant högre predationsgrad närmare kant (< 20 m) jämfört med längre in i habitatet konstaterades. Resultatet kan indikera att en predator först avsöker ecotonen och därefter går längre in i skogen. Denna studie överensstämmer med tidigare observationer att bon i naturliga trädhål verkar vara mindre sårbara än andra typer av bon.

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