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What Happens to Old Nests in Natural Cavities?

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It is well known that old nest material accumulates in nest boxes and should be removed to keep the boxes usable. Perrins (1979) and Møller (1989) proposed that the removal of old material, via reduction of ectoparasites, could improve conditions in the boxes. This in turn could have profound effects on nest-site choice, mating success, and reproductive efficiency of the individuals that use the boxes.

Natural cavities are not cleaned by humans. Thus, by implication, conditions in them should deteriorate owing to the accumulation of old nest material. Indeed, Perrins (1979) stated that “. . . the nest material would slowly decompose within the chamber and presumably over a series of years the site might become filled with old nests.” I have tried to find support for this statement in the literature, but so far I have failed to find any information on this issue. Therefore, it seems that the information presented below, which indicates that old nest material disappears rapidly from natural cavities, constitutes the first data on this subject.

Study Area and Methods.—Data were gathered from 1992 to 1998 in the Białowieża National Park in eastern Poland, within which the last surviving fragments of European primeval lowland temperate forest are preserved. The tree stands of the park have never been cut, and the entire area has been strictly protected as a reserve since 1921. Hence, one can still observe cavities and cavity nesters in conditions free of direct anthropogenic disturbance. The forest consists of several types of old-growth stands (see Tomiałojć and Wesołowski 1990, Tomiałojć 1991, Wesołowski and Tomiałojć 1995), but most of the data were gathered in two types of chiefly deciduous stands. One was a stand of riparian trees composed mostly of alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), and Norway spruce (*Picea excelsa*); the other was a stand of upland deciduous forest composed of more than 12 species of trees, mainly hornbeam (*Carpinus betulus*), small-leaved linden (*Tilia cordata*), con-

tinental maple (*Acer platanoides*), pedunculate oak (*Quercus robur*), and spruce.

Since 1992, all cavities used by breeding birds within four large study plots (33 to 55 ha each; see Wesołowski 1998) and accessible from a ladder (up to 5 m above ground, in living trees) were marked and checked the following year (in the second half of April) to see whether old nest material was still present. For checking cavity contents, I used a small light bulb on a flexible wire and a small mirror.

The April inspections showed that cavities from previous years could be impossible for birds to use for several reasons (e.g. flooding, or being filled with rotten wood up to the cavity entrance). I have omitted these instances from the present analysis because they are irrelevant to the question at hand. If the cavity contained remnants of old material (e.g. moss and hair), it was classified as an “old nest.” If the cavity contained new material (e.g. fresh pieces of moss), it was classified as a “new nest” (the timing of the cavity inspections coincided with the nest-building phase of earliest breeding species in the study area; Wesołowski and Stawarczyk 1991, Wesołowski 1998). When a cavity contained no nest material and the bottom was covered with decayed material and rotten wood, or occasionally with a single fragment of leaf or piece of moss, it was classified as containing “no nest.”

Because the type of nest material could have influenced the rate of nest disappearance, I divided nests into two categories: (1) “tit” nests, which were constructed mostly of moss, wool, hair, or feathers and were made by *Parus major*, *P. caeruleus*, *P. palustris*, *P. ater*, and *Certhia familiaris*; and (2) “flycatcher” nests, which were composed mostly of dry leaves and other plant material and were made by *Ficedula albicollis*, *E. hypoleuca*, and *Erithacus rubecula*.

Results and Discussion.—No trace of the previous year's nest was visible in two-thirds of the cavities (Table 1), nor did cavities with new nests (ca. 20%) contain remains from the previous year's nest. As a rule, new nests were in the initial stages of construction, so any remains of old material would have been apparent. I found remnants of old nest material in

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TABLE 1. Contents of natural cavities in the second half of April in relation to the type of nest in the previous breeding season. Data are the number of cavities.

Previous nest	Cavity contents			Total
	Old nest (%) ^a	New nest (%) ^b	No nest (%)	
Tit ^c	5 (6.0)	19 (22.9)	59 (71.1)	83
Flycatcher ^d	24 (20.5)	20 (17.1)	73 (62.4)	117
Total	29 (14.5)	39 (19.5)	132 (66.0)	200

^a Remnants of old material still visible (e.g. moss and hair).

^b New material present (e.g. fresh pieces of moss).

^c Moss, wool, and hair or feathers; made by *Parus major*, *P. caeruleus*, *P. palustris*, *P. ater*, and *Certhia familiaris*.

^d Mostly dry leaves and other plant material; made by *Ficedula albicollis*, *F. hypoleuca*, and *Erithacus rubecula*.

only 6% of the cavities that originally had contained "tit" nests and in 20% of those that had contained "flycatcher" nests (Table 1). "Tit" nests vanished significantly more frequently from one year to the next than did "flycatcher" nests ($\chi^2 = 8.4$, $df = 2$, $P < 0.02$); consequently, dry leaves appeared to be more resistant to loss than did moss or substances of animal origin (see Table 1).

Causes of the disappearance of nest material are unknown. Nest material could have been removed by a non-human animal, or it could have decomposed *in situ*. In cavities that contained new nests, the remains could have been removed by the birds themselves; e.g. I commonly observed tits remove debris from nest cavities (Wesołowski 1998, 1999). Nest boxes in the managed part of the Białowieża Forest often contained nearly intact nests from the previous season. It is difficult to envisage why old material would be selectively removed from natural cavities but not from nest boxes. Therefore, I propose the alternative explanation that conditions in the cavities themselves, i.e. a favorable microclimate and a rich assemblage of decomposing organisms, result in high decay rates of old nest material.

Apart from cavities that were used for breeding in two consecutive years, numerous suitable but unused cavities were available in the study area (Wesołowski 1989, Walankiewicz 1991). Consequently, birds that were prospecting for new nest sites would have found traces of old material in cavities less frequently than the present data indicate, perhaps in less than 1 of 10 cavities.

Rates of disappearance of old material were similar in all study plots ($\chi^2 = 0.74$, $df = 3$, $P = 0.86$) and did not vary substantially among years ($\chi^2 = 3.37$, $df = 4$, $P = 0.49$). Given that the species concerned accounted for more than 80% by number of all secondary cavity nesters in the Białowieża Forest (Tomiałojć and Wesołowski 1990, 1996; Wesołowski and Tomiałojć 1997), my results are likely to be representative for the situation in this primaevial forest. However, it

is not known whether the rapid disappearance of old material is typical of most natural cavities, or whether it is only a local phenomenon. Nevertheless, my data indicate that contrary to the suggestions of Perrins (1979) and Møller (1989), it is the accumulation of old nest material, rather than the removal of such material, that distinguishes nest boxes from natural cavities.

The removal of old nests from boxes can reduce the load of ectoparasites whose survival depends on nest material (Rendell and Verbeek 1996). Whether parasite numbers would decline if nest material disappeared from decay is unknown. Clearly, additional information is needed on the relationship between parasite loads and the presence of old nest material in natural cavities.

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Natal Dispersal of Peregrine Falcons in Greenland

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Natal dispersal is female biased in most bird species in that proportionally more females than males disperse, or females disperse farther than males (Greenwood 1980). This pattern appears to be related to the amount of effort each sex spends in competing for territories or mates versus the amount of effort spent in raising young and choosing mates (Greenwood 1980). Presumably, males gain foraging and antipredator benefits that improve reproduction and survival when establishing territories in familiar areas. If males are philopatric, then females should disperse to avoid inbreeding (Pusey 1987) and to evaluate potential mates (Greenwood 1980). The effects of mating system and inbreeding avoidance on dispersal behavior are not mutually exclusive, and a combination of factors likely produces sex-biased dispersal.

Although some long-distance dispersers experience lower survival and reproductive success than their philopatric counterparts (Newton and Marquiss 1983, Nilsson 1989, Pärt 1990), others suffer no apparent costs (Arcese 1989, Plissner and Gowaty 1996, Miller and Smallwood 1997). Most investigations of natal dispersal have focused on species that breed at one year of age, have short lifespans, and nest in unpredictable environments. Few studies have examined dispersal in long-lived, long-distance migrants that nest in predictable environments. Individuals of these species typically spend several seasons exploiting different habitats over large spatial scales before settling to breed. Therefore, we might expect the benefits of short-distance dispersal

to males, such as higher productivity and lower mortality, to be less pronounced or absent, particularly if nesting habitat is not limiting.

We analyzed 20 years of Peregrine Falcon (*Falco peregrinus*) breeding data from Greenland to identify the proximate causes and consequences of natal dispersal associated with this long-lived, long-distance migrant. We determined if (1) sex ratio, survival, and population density affected natal dispersal; and (2) whether natal dispersal distance affected survival and subsequent productivity.

Study Area and Methods.—The study area encompassed approximately 6,000 km² in the widest part of ice-free land of western Greenland (66°45'N, 51°30'W). Most of the study area was rolling tundra (elevation up to 1,100 m) interspersed with nearly 1,000 lakes. Vegetation was dominated by willow (*Salix glauca*), dwarf birch (*Betula nana*), heaths (*Empetrum*, *Ledum*, *Cassiope*, spp.), and grasses (*Calamagrostis*, *Festuca*, *Poa*; see Burnham and Mattox [1984] for a more complete description of the study area).

From June to mid-August, 1978 to 1997, a variable number (two to five) of two-person teams backpacked across the tundra and visited cliffs that provided potential nesting habitat for Peregrine Falcons (Burnham and Mattox 1984). Teams observed cliffs for signs of breeding activity. If breeding activity was not evident after a minimum of 4 h of observation, the cliff was considered inactive. Observers recorded the presence of adult peregrines and attempted to classify individuals by sex at cliffs occupied by lone adults.

Banding teams either rappelled or climbed to eeries that contained young. Nestlings were individually marked with a Danish Zoological Museum num-

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