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Nest soaking in natural holes — a serious cause of breeding failure?

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Nest loss rates of four secondary hole-nesters — Pied (*Ficedula hypoleuca*) and Collared (*Ficedula albicollis*) Flycatchers, Marsh Tit (*Parus palustris*) and European Nuthatch (*Sitta europaea*) — due to soaking recorded during a long-term study in a primaeval temperate forest (Białowieża National Park, Poland) were low. Even during extremely heavy rains (> 74 mm in one day) they did not exceed 11%, far less than the loss due to predation. Soaking of nests occurred significantly less often in the late (flycatchers) than in the early breeding species (Nuthatches and Marsh Tits). In the latter species partial brood losses due to nest soaking were observed as well, the partial nest loss being more frequent in the rainy seasons. Interior walls of 8–40% holes were moist due to sap drain, but this only exceptionally led to the total nest failure. We suggest that the main function of bulky nest foundations in all these species may be protection against moisture.

1. Introduction

It has been assumed that one of the major benefits of hole-nesting, especially in tropical rain forests, is avoidance of soaking (Collias & Collias 1984). Though hole walls usually restrict direct access of rain water, tree holes are not always waterproof. Nest loss due to soaking has been observed in several groups of primary and secondary hole-nesters, such as parrots (Snyder *et al.* 1987, Rowley 1990), barbets (van Zyl 1994), owls, pigeons (Rudat *et al.* 1979), woodpeckers (Rudat *et al.* 1981, Wesołowski 1995, Lange 1996) or passerines (East & Perrins 1988, Wesołowski & Stawarczyk 1991). These scattered reports indicate that water in holes could constitute a problem, but it is difficult to assess the role of nest soaking in lowering productivity and shaping nest site use of hole-nesters.

Data gathered by us during long term studies of breeding ecology of four species of secondary hole-nesters — Pied (*Ficedula hypoleuca*) and

Collared Flycatcher (*Ficedula albicollis*), Marsh Tit (*Parus palustris*) and European Nuthatch (*Sitta europaea*) — provided a unique opportunity to record variation in the nest soaking rates across species and seasons. The study was done in the last fragments of primaeval, European lowland forest, preserved within the Białowieża National Park (hereafter referred to as BNP). The birds breeding in these pristine conditions could choose from a full spectrum of natural holes (Wesołowski 1989, 1996, 2001, in press, Wesołowski & Stawarczyk 1991, Walankiewicz 1991).

In this study we (1) describe nest loss rates due to soaking in different species and years, (2) attempt to relate this to the rainfall, features of the species biology and characteristics of used holes and (3) discuss possible role of nest soaking in shaping patterns of hole use in different species.

2. Methods

2.1. Study area

The Białowieża Forest complex is situated on the Polish-Belarussian border. Its western part (580 km^2, ca. 45% of the area) belongs to Poland. The Forest represents a remnant of the vast lowland forests that once covered great parts of temperate Europe. The majority of tree stands in the Polish part are now under management but a block of the best preserved primaeval stands has been strictly protected within BNP (47.5 km^2, ca. 52°42´N, 23°52´E).

Oak-lime-hornbeam stands (*Tilio-Carpinetum*) cover 44% of the strictly protected BNP area. They are composed of a dozen or so species of trees [hornbeam (*Carpinus betulus*), lime (*Tilia cordata*), pedunculate oak (*Quercus robur*), Norway spruce (*Picea abies*), continental maple (*Acer platanoides*)], that vary greatly with regard to age and size. In several stands the canopy is formed by trees over 200 years old, and often exceeding 250–400 years.

Swampy deciduous stands (*Circaeo-Alnetum*, *Carici elongate-Alnetum*), jointly 22% of the strictly protected reserve, are more uniform, their canopy being composed mostly of alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*) and spruce.

In the coniferous stands (*Querco-Piceetum*, *Pineto-Quercetum*, *Peucedano-Pinetum*), jointly 28% of the strictly protected reserve) the canopy is composed of spruce and Scot's pine (*Pinus silvestris*) with an admixture of birch (*Betula spp.*) and some oaks.

2.2. Data collection and analyses

We searched for occupied holes, finding almost all of them, mostly within the four permanent study plots. Three of them (plots C, M and W, joint area 152 ha) were situated in the oak-hornbeam habitat and one (K — 33 ha) in the riverine stands — see Wesołowski (1996) for details. To gather data on the course of breeding and fate of nests we regularly checked the breeding holes, mostly from the ground. We also inspected interiors of holes (using a small bulb on a bendable wire and a small mirror) to get data on clutch and brood size and cause of failure, where necessary. We were able to check contents of almost every hole in all species except the Nuthatch. In the latter species, due to technical problems, we could not access ca. 40% of holes situated in the thickest trees. During the interior checks, the humidity of hole walls was assessed as well. The observers looked at the illuminated walls and classified them as either dry (light colour of wood, no darker, mat patches), moist (wood dark, mat, strongly absorbing light) or wet (water oozing down the walls, shining in the light). This was done during the whole study period for the flycatchers but only in a single season for other species.

We treated all nests from which at least one young fledged as successful, all others as lost (Wesołowski & Stawarczyk 1991, Wesołowski in press, Walankiewicz 1991, Czeszczewik 2001). We checked holes with the lost nests to ascertain possible causes of failure. The nest was treated as lost to soaking when the hole was filled with water or a wet nest with intact eggs or dead young was observed.

We recorded also attributes of breeding holes (tree species, tree part and condition, hole type and origin, as well as entrance horizontal and compass orientations) — see Wesołowski (1989, 1996, in press) and Walankiewicz (1991) for details.

Data on rainfall were obtained from the Białowieża weather station, situated in the Białowieża glade, 1–6 km from the study plots. The readings from this the station seems to reflect fairly well the large-scale rainfall patterns over the Forest. However, brief, though often intense, thunderstorms can sometimes go undetected, as they happen to be very local, then only some patches in the forest get rain and the rest remain unaffected. All statistical procedures follow the formulas given in STATISTICA for Windows. All probability values are two tailed.

3. Results

3.1. Rains and nest soaking

3.1.1. Total nest loss

During six study years (1987–1989, 1998–2000, 300 nests) soaking of European Nuthatch nests after rain occurred only in 1988 and 1999 (Table 1). Additionally, a single clutch was lost due to nest soaking in 2000, though no rain fell during that period (see below). Soaking of Marsh Tit nests after rains was observed in four of 12 seasons (1987–1989, 1992–2000, 470 nests), including both years in which European Nuthatch nests were affected as well (Table 1).

The only Pied Flycatcher nest known in 1988 was soaked. Otherwise no soaking was observed in this species during seven years (1993–1999, 89 nests). Soaking of Collared Flycatcher nests occurred in two (Table 1) of 12 study seasons (1988–1999, 604 nests). Soaking in flycatchers was less frequent than in Marsh Tit — during four seasons in which soaking of nests of the latter species occurred, 47 Pied Flycatcher and 182 Collared Flycatcher nests were observed, yet only single ones were soaked (Fisher exact test, $P = 0.06$, and $P < 0.01$ respectively).

Overall, total nest loss due to soaking did not exceed 11%, even during extremely heavy rains in 1988, when 73.7 mm rain, almost equal to the monthly average, fell on a single day (Table 1).

3.1.2. Partial brood reduction

Several cases of partial mortality following soaking of the nest material were recorded in different years. For example in 1988, in an inundated European Nuthatch hole, a single young survived — it was standing on a raft made of the wet bodies of its sibs. In a second nest, incubation was prolonged by almost 50% and only a single young fledged. We could not prove in every case that the partial nest loss was due to nest soaking, but its substantially higher frequency in the rainy seasons indicates such a possibility. The partial nest loss in European Nuthatch occurred with the higher frequency in the "flood" years (Table 1) than in the "dry" (1998 and 2000) seasons — in 52% of 27 and 17% of 35 broods respectively (Fisher exact $P < 0.01$). Similarly, in Marsh Tit, brood reduction was more frequent in the "flood" years (one or more nestlings disappeared from 28% of 60 broods) than in the remaining seasons (15% of 99), the difference approached significance (Fisher exact $P = 0.07$).

Table 1. Total nest failures due to soaking by rain in relation to species, year and rainfall. Shown only years in which nest soaking occurred. Sample sizes refer to the number of active nests before the onset of rains.

Species	Year	Soaking dates (May)	Rainfall (mm)	n nests	n soaked	% soaked
Sitta europaea	1988	20–21	91.7	25	2	8.0
	1999	10–11	16.0	35	3	8.6
Parus palustris	1988	20–21	91.7	26	2	7.7
	1994	27	27.7	37	1	2.3
	1997	21	11.2[a]	28	2	7.1
	1999	10–11	16.0	65	7	10.8
Ficedula albicollis	1988	20–21	91.7	27	1	3.7
	1994	27	27.7	62	1	1.6

[a]strong local thunderstorms over the forest

3.1.3. Hole features and nest soaking

The probability of soaking was related to some aspects of hole localisation. European Nuthatch holes in trunks were more often soaked than ones placed in limbs (Table 2). Marsh Tit holes, on the other hand, were significantly more often soaked when their entrances were exposed to the south and upward facing, and when they were situated in knotholes (Table 2). The latter two variables, though, were correlated; 29% of knothole entrances were upward facing (Fisher exact $P = 0.03$). Other variables, such as tree species, tree condition or hole origin did not influence the probability of soaking.

3.2. Sap drain and nest soaking

In addition to stem flow of rainwater, sap drain from interior hole walls contributed to the moisture in holes. In only one case did it cause a total nest failure. A European Nuthatch female deserted her clutch after prolonged incubation in a hole situated in a trunk that was unusually out of the vertical; the nest material in the hole remained wet, despite no rain falling during that time. Also other data from the unusually dry spring of 2000, when hardly 5.3 mm of rain fell during the whole of May, indicate the role of sap. Despite drought, walls of almost 41% of European Nuthatch holes remained moist from inside (Table 3). Both total nest loss (4 of 16 in dry vs. 2 of 11 in moist holes) and frequency of brood reduction (3 of 10 in dry vs. 2 of 10 in moist holes) remained similar. Holes used by Marsh Tits in 2000, on the other hand, had mostly dry walls (Table 3).

Overall, about 16% of Pied Flycatcher and Collared Flycatcher holes had moist interior walls (Table 3). Pied Flycatcher breeding in such holes were as successful as the ones using dry holes (43 vs. 46%) the same was probably true of Collared Flycatcher (54 vs. 48%).

Pied Flycatcher holes with wet and dry interior were similar in all the measured variables. In the Collared Flycatcher, the entrances of wet holes were more often upward than downward facing or vertical (22% of 176 and 12% of 394 holes respectively, $\chi^2_1 = 8.95$, $P < 0.01$); they were also situated more frequently in living than in dead wood (17% of 536 and 3% of 64 respectively, $\chi^2_1 = 8.22$, $P < 0.01$) and they were more often of non-woodpecker origin (16% of 501 and 9% of 98 respectively, $\chi^2_1 = 3.28$, $P = 0.07$).

4. Discussion

Two points have to be kept in mind when interpreting these data: (1) estimates of the inundation rates are most probably conservative — checks of hole interior were infrequent, thus single cases in which nests were only briefly soaked could have escaped notice; the same could be true of some nests lost in inaccessible Nuthatch holes; (2) due to the small number of soaked holes, the power of detecting differences between features of "waterproof" and inundated holes is rather low.

The highest nest soaking rates so far found were observed in parrots: up to two-thirds of Galah

Table 2. Inundation frequency in relation to hole characteristics. Only holes found in seasons in which soaking occurred are included. Probability values refer to the Fisher exact test.

Variable	State	*Sitta europaea*			*Parus palustris*		
		n	% soaked	P	n	% soaked	P
Tree fragment	Trunk	92	13.0		150	6.7	
	Limb	33	0	0.04	24	8.3	0.66
Exposure	SW–SE	61	9.8		62	12.9	
	Other	64	9.4	1.0	111	3.6	0.029
Type	Knothole	67	10.4		26	19.2	
	Other	58	8.6	0.77	115	4.3	0.019
Orientation	Upwards	16	12.5		29	17.2	
	Vertical or downwards	98	9.2	0.64	140	5.0	0.035

(*Eolophus roseicapillus*) clutches in some areas could have been lost after heavy rains due to soaking or nest desertion (Rowley 1990) and problems with wet bottoms occurred in six of 25 nestings of Puerto Rican Parrot (*Amazona vittata*, Snyder *et al.* 1987). As soaking rates in BNP did not exceed 11%, these results suggest that nest soaking could be a more serious problem in the tropics than in the temperate areas. The soaking rates, at least in the Puerto Rican Parrot, could be inflated, as natural holes used by this endangered species were in short supply, so these birds could have been using suboptimal places (Snyder *at al.* 1987). The very high soaking rates found in Tengmalm's Owls (*Aegolius funereus*) using the old Black Woodpecker (*Dryocopus martius*) holes in Germany (23% of 53) were clearly due to the shortage of suitable holes (Rudat *et al.* 1979).

The nest loss rates of hole-nesters in BNP were usually high, in extreme cases approaching 70%. They were mostly due to heavy predation, in the four species studied predators were responsible for 64 (Nuthatch) to 91% (Pied Flycatcher) of total nest loss (Wesołowski & Stawarczyk 1991, Wesołowski 1995, 1998, in press, Walankiewicz 1991, Walankiewicz *et al.* 1997, Rowiński & Wesołowski 1999, Czeszczewik 2001). As nest loss due to soaking did not occur every year, and even in the seasons with heavy rains the loss rates were relatively low, soaking could be only a subsidiary factor, modifying the basic requirement of nesting in predator-proof holes (Wesołowski 1996, in press). In other words, a hole had to be first of all safe, and only in the second place should it be water-proof.

Flycatcher nests in BNP were less frequently lost to soaking than those of Marsh Tits or the Nuthatches. It would be difficult to account for these differences in terms of nest sites, as there were large overlaps in patterns of hole use — not infrequently the same hole was used interchangeably by different species (Wesołowski 1989, 1996, Walankiewicz 1991). However, these two groups of species differed strikingly in their timing of breeding, the flycatchers commencing breeding ca. three weeks later than Marsh Tits or the Nuthatches (Wesołowski & Stawarczyk 1991, Wesołowski 1998, Czeszczewik 2001, and W. Walankiewicz, unpubl.). As a consequence, during the rainy periods the flycatcher nests contained mostly eggs, whereas the other species were already feeding nestlings. Perhaps eggs were more resistant to chilling in temporarily soaked nests than were the young.

Marsh Tits in BNP bred in knotholes only infrequently whereas the Nuthatches used them regularly (13 and 41% of all nestings respectively — Wesołowski 1989, 1996). This was correlated with differences in inundation rates: breeding in a knothole significantly increased chance of nest loss due to soaking in Marsh Tits but not in the Nuthatches. The latter species' habit of plastering the hole entrance (behaviour non-existent in Marsh Tits) constituted an apparently efficient means of diminishing the inundation risk. The Nuthatches could thus afford to use knotholes in limbs, despite them often having upward facing entrances.

The species dealt with here bred almost exclusively (75–100%) in holes in living trees (Wesołowski 1989, 1996, unpubl.) Though nesting in holes with hard walls helped them in avoiding predators (Wesołowski 1996, in press), it demanded some means of coping with the risk of nest contents soaking by constantly flowing sap. It seems that the birds have managed to find the way out — they can breed successfully in holes with wet walls. Their bulky nests may fulfil this function, as all these species fill holes with a large amount of nest material — Pied Flycatchers can make nest foundation of up to 1300 dry leaves, bast and grass fibres (Stjernberg 1974), the Nuthatch can pile a 30 cm layer of nest material comprising 850 pieces of rotten wood and 11 440 bark flakes (review in Matthysen 1998) and Marsh Tits can accumulate up to 15 cm of green moss (Wesołowski 1996). Such thick water absorbing layers were apparently in most cases sufficient — their capacity was exceeded only from time to time during the heavy rains.

Table 3. Proportion of holes with moist/wet interior walls in different species.

Species	Years	N nests	% moist
Parus palustris	2000	48	8.3
Sitta europaea	2000	27	40.7
Ficedula albicollis	1988–1999	604	15.2
Ficedula hypoleuca	1988–1999	89	15.7

Woodpeckers do not use any nest lining, so one could expect their nests to be soaked very frequently. Contrary to this expectation, they are apparently soaked at rather low rates: Black Woodpecker — three of 70 (Rudat *et al.* 1981), one of 238 (Lange 1996), eight of 238 (old holes, Johnsson *et al.* 1993); Magellanic Woodpecker (*Campehilus magellanicus*) — none of ca. 40 holes (P. McBride, personal comm.); Yellow-shafted Flicker (*Colaptes auratus*) — three of 75 holes in one year, none in the next (K. Wiebe personal comm.). Woodpeckers probably avoid problems with water by making holes preferentially in dead wood, often in snags or broken limbs of living trees (Wesołowski 1989, 1995, Baicich & Harrison 1997). Though excavating a hole in dead, soft wood is most probably simply easier for birds (e.g. Schepps *et al.* 1999), making it in such a substrate simultaneously secures woodpeckers safety from sap flow and — especially when excavated near the top of snag — also strongly reduces a chance of hole soaking by stem flow. Few woodpecker species, which habitually excavate holes in living trees, have apparently solved the problem of keeping their nests dry in a different fashion. It remains to be seen how they achieve it.

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Selostus: **Pesän kastuminen — vakava syy pesinnän epäonnistumiseen?**

Kolopesinnän yhdeksi eduksi on esitetty sitä, että kolossa sijaitseva pesä ei kastu niin helposti kuin avopesä. Vaikka kolon seinät yleensä estävät veden suoran pääsyn pesään, eivät kolot kuitenkaan ole täysin vesitiiviitä. Kirjoittajat ovat keränneet aineistoa pesän kastumisen vaikutuksista kirjosiepon, sepelsiepon, viitatiaisen ja pähkinänakkelin pesätuhoihin Białowieżan luonnonpuistossa Puolassa vuosina 1987–1989 ja 1998–2000. Tutkijat pyrkivät löytämään neljältä koealueelta kaikki tutkimuslajien pesät. Pesän tarkastuksen yhteydessä arvioitiin kolon märkyys (kuiva, kostea tai märkä). Pesintä luokiteltiin onnistuneeksi, mikäli pesä tuotti vähintään yhden lentopoikasen. Muulloin pesintä todettiin epäonnistuneeksi. Tuhoutuneet pesät tutkittiin tarkemmin pesinnän epäonnistumisen syyn selvittämiseksi. Pesä tulkittiin tuhoutuneeksi kastumisen vuoksi, mikäli kolo oli täyttynyt vedellä tai koskemattomia munia tai kuolleita poikasia havaittiin märässä pesässä. Tulosten mukaan pesän tuhoutuminen kastumisen seurauksena oli harvinaista. Kastumisen vuoksi tuhoutuneiden pesien määrä vaihteli lajeittain 1,6–10,8 %. Joinakin vuosina pesiä ei tuhoutunut kastumisen vuoksi lainkaan. Myöhään pesivillä lajeilla (siepot) pesän kastumisen aiheuttamat pesätuhot olivat vähäisempiä kuin aikaisin pesivillä lajeilla (pähkinänakkeli ja viitatiainen). Noin 8–40 % tutkittujen kolojen seinämistä oli kosteita, mutta tämä aiheutti pesän tuhoutumisen vain poikkeustapauksissa. Koloissa pesivien lintujen pesän kastumisen vuoksi aiheutuneet pesätuhot näyttävät jäävän vähäisiksi.

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