SHORT COMMUNICATIONS

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THE LOSS OF AVIAN CAVITIES BY INJURY COMPARTMENTALIZATION IN A PRIMEVAL EUROPEAN FOREST[1]

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In a recent paper, Sedgwick and Knopf (1991) documented for the first time a formerly unrecognized aspect of avian cavity dynamics, i.e., the loss of avian cavities due to injury compartmentalization in a Colorado plains cottonwood (*Populus sargentii*) forest. Their results, over 15% of cavities in living substrate lost over a five year period, suggested that this process could potentially influence the abundance and distribution of secondary-cavity nesting birds.

Here, I provide data on the extent of this phenomenon in the Białowieża National Park (E. Poland), in which the last surviving fragments of the European primeval lowland temperate forest are preserved. The tree stands of the park have never been cut and the whole of its area has been a strictly protected reserve since 1921. Hence one can still observe here processes of cavity formation and loss in conditions free of direct anthropogenic disturbance. The forest consists of several types of old growth stands, both of deciduous and coniferous character (more detailed descriptions of study areas are given in Tomiałojć and Wesołowski 1990, Tomialojc 1991), but the majority of data were gathered in two types of chiefly deciduous stands. These were riverine stands—composed mostly of alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*) and Norway spruce (*Picea excelsa*), and upland deciduous stands—composed of over a dozen species, mainly hornbeam (*Carpinus betulus*), small-leafed linden (*Tilia cordata*), continental maple (*Acer platanoides*), pedunculate oak (*Quercus robur*) and spruce.

METHODS

Since 1979, all cavities used by birds for nesting found within the study plots were permanently marked in the field and their fate monitored. The majority of cavities were located only from the ground, without the observer's climbing trees. Hence, holes in trees were considered "cavities" only when some signs of their occupancy by the birds (bringing of nest material, changes of incubating birds, bringing of food for nestlings) were observed. Every marked cavity was checked, as a rule also only from the ground, at least once a year before the beginning of the breeding season to determine whether it was still available or perhaps had become unsuitable. The cavity was described as lost to tree compartmentalization when its entrance diameter decreased to such an extent that it was too small to be used even by the smallest cavity nesters (18 mm width of cavities with slit-like openings for Marsh Tit [*Parus palustris*]).

RESULTS AND DISCUSSION

My data pertain to cavities which were situated in living substrate, the fate of which was followed for at least one year within 1979–1993. Cavities in living substrate (n = 620) constituted 63% of all the cavities found (n = 983). Out of the total, 32 cavities (5.2%) were lost due to the compartmentalization. It took from two to 12 years (mean 5.3, SD 2.6 years) before a cavity was rendered unsuitable due to the entrance closure. Taking into account only the cavities observed for a longer time (i.e., those cavities which could have been monitored over a five year period) produced the same figure (n = 18 of 360, 5.0%).

There was no visible relationship between the frequency of cavity compartmentalization and bird species using it. When found, these cavities were used by Marsh Tit (n = 7), Blue Tit (*Parus caeruleus* [n = 7]), Great Tit (*P. major* [n = 2]), Collared Flycatcher (*Ficedula albicollis* [n = 4]), Pied Flycatcher (*F. hypoleuca* [n = 1]), European Nuthatch (*Sitta europaea* [n = 4]), European Starling (*Sturnus vulgaris* [n = 5]) and Great Spotted Woodpecker (*Dendrocopos major* [n = 2]). These are the more numerous secondary cavity nesters of the Białowieża Forest and the only woodpecker species regularly pecking cavities in living substrate there (Wesołowski 1989). In addition, cavity origin did not seem to influence its chance of being resealed, as the woodpecker- and non-woodpecker-made cavities were lost with almost identical frequency, 7/140 (5.0%) and

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TABLE 1. Frequency of cavity resealing by injury compartmentalization in different tree species in the Białowieża National Park.

Tree species	Number of cavities in living substrate	Number of re-sealed cavities	Percent-age of resealed cavities
Hornbeam (*Carpinus betulus*)	228	7	3.1
Alder (*Alnus glutinosa*)	118	10	8.5
Linden (*Tilia cordata*)	72	7	9.7
Ash (*Fraxinus excelsior*)	68	2	2.9
Continental maple (*Acer platanoides*)	56	1	1.8
Aspen (*Populus tremula*)	40	3	7.5
Pedunculate oak (*Quercus robur*)	22	1	4.5
Other	16	1	—
Total	620	32	5.2

25/474 (5.3%) respectively. Neither did the capability of trees to seal wounds depend on their size, though the trees with compartmentalized cavities were on average slightly smaller. Their mean breast-height girth was 130 vs. 139 cm in hornbeam, 150 vs. 162 cm in alder, 163 vs. 188 cm in linden. In no case were these differences significant ($P > 0.02$, t-test, sample size see Table 1).

However, the ability to heal the wounds appears dependent on tree species. Two groups of species are visible in Table 1, one composed of hornbeam, ash, and maple with loss rate below average and the other, consisting of alder, linden and aspen, with higher than the average frequency of cavity compartmentalization. The differences between these groups were statistically significant (goodness-of-fit test, $\chi^2 = -9.24$, 2 df, $P < 0.025$). This grouping could reflect real biological interspecific differences in the ability to heal wounds. All the species included in the latter group have soft wood and grow relatively fast, whereas the species in the former group have relatively hard wood and grow slower.

The process of injury compartmentalization could probably be slowed down or even totally prevented by activity of birds. Frequently, at reused nuthatch cavities, I noticed that fresh wood had been exposed at entrance rim due to pecking of bark. Similar phenomenon was also sometimes detectable when woodpeckers reused their old holes. Unfortunately, I have no quantitative data to evaluate the influence of this behavior on cavity longevity.

The frequency of using cavities in living substrate by secondary cavity-nesting birds in the Białowieża Forest 55–100% (Wesołowski 1989), is similar to that (49–100%) found by Sedgwick and Knopf (1991) in Colorado. However, cavity loss due to injury compartmentalization was three times less frequent in Białowieża Forest than in Colorado (5 vs. 16%). The loss rate was lowest in the oak-linden-hornbeam stands, where cavities in frequently resealing tree species constituted only 4–33% of those used (Wesołowski 1989). However, even in riverine stands, where cavities in more resilient alder constitute 52–90% of those used by the particular bird species (Wesołowski 1989), there is a turnover rate below 10% in a 5-year period. Considering that in this primeval situation there is a superabundance of cavities and their number exceeds the number of pairs of secondary cavity nesters at least two–three times (Wesołowski 1989, Wesołowski and Stawarczyk 1991, Walankiewicz 1991), we conclude that cavity loss due to injury compartmentalization cannot substantially affect the distribution and abundance of secondary cavity nesters in the Białowieża Forest. However, the results of the Colorado and Białowieża studies suggest that this process could locally assume more significance. Injury compartmentalization should be most important in relatively young stands, dominated by fast-growing tree species with easily molded wood, such as in riverine woods of the willow-poplar (*Salix-Populus*) type or in upland sites, and in stands developing in the early stages of secondary succession (primarily *Populus* and *Betula*) in central Europe.

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