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RESUMEN.—Una re-examinación de los dos especímenes conocidos de *Philydor hylobius*, ambos provenientes del Cerro de la Neblina en el sur de Venezuela, indicó que éstos pertenecen a *Automolus roraimae*. El tipo de *P. hylobius* correponde a un adulto de *A. roraimae* con predominancia de pigmentacion rojiza (eritrismo), y el otro especímen es un juvenil típico. Por lo tanto, *Philydor hylobius* Wetmore and Phelps es un sinónimo junior de *Automolus roraimae* Hellmayr.

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Evolution of Hole-nesting in Birds: On Balancing Selection Pressures

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It is generally accepted that the relative breeding success of hole-nesting birds is higher than that of open-nesting species (Lack 1954, Nice 1957). Holes may offer better protection from predators. Among hole-nesters about two-thirds, and among open-nesters about half, of the eggs laid produce fledged young. This "fact" has been used to explain life-history evolution among birds (e.g. von Haartman 1957, Lack 1968). Nearly all previous studies of the breeding success of hole-nesting birds, however, have been conducted using nest boxes where rates of predation and partial nestling losses are often lower than in natural cavities (Ludescher 1973; Nilsson 1975, 1984a, b).

I report here on the breeding success of six hole-nesting bird species in natural cavities and show, in contrast to previous reports, that the proportion of eggs laid that give rise to fledglings is about the same as in comparable open-nesting birds. Interference competition (van Balen et al. 1982, Nilsson 1984b), nestling losses due to hyperthermia (van Balen and Cavé 1970, Mertens 1977), and nest parasites (Winkel 1975) may be important factors that reduce breeding success in natural cavities more than in open nests. On the other hand, total nest losses seem to be higher in the latter (see below). Thus, selection pressures on open- and hole-nesting birds differ, but opposing factors seem to balance each other. This holds because there is a continuous transition from well-protected holes, for which competition is expected to be most severe, to shallow holes with wide openings. The latter may provide poorer nest sites than open nests.

I collected data on the breeding success of hole-nesting birds on two forest plots at Stenbrohult, south Sweden (56°37–38′N, 14°10–11′E) in 1973–1979. The nests were in deciduous and mixed deciduous/conif-

erous forest vegetation. The canopy trees are 75–100 yr old and mainly consist of oak (*Quercus robur*), beech (*Fagus sylvatica*), birch (*Betula* spp.), and spruce (*Picea abies*). The old-forest vegetation in both plots probably has regenerated naturally.

The breeding success of hole-nesting birds was studied in natural cavities using a mirror, supplied with a lamp such that when the nest contents were examined the lamp was shining from behind the mirror. Each nest was inspected about weekly, but more often near fledging. See Nilsson (1975, 1984b) for detailed descriptions of the study plots, sampling methods, sample sizes, predation rates, etc.

Breeding success, the proportion of the eggs laid that produce fledglings, was very similar (50–59%) in all six species nesting in natural cavities (Table 1). Comparable data for six hole-nesting species (five of them the same as in Table 1) breeding in boxes are available from Germany (Schönfeld and Brauer 1972). The breeding success averaged 82% (species range 75–90%), typical for other nest-box studies (Johansson 1972; van Balen 1973; Nilsson 1975, 1984a; Ojanen et al. 1979; Perrins 1979). For comparison, the breeding success in tree holes was 42% for *Parus major* and 55% for *Sturnus vulgaris* in a forest in Holland (Booij 1977). In a study of natural nests of *Parus palustris* and *P. montanus* in Germany, 55% and 61%, respectively, were destroyed by predators (Ludescher 1973). This means that the breeding success was below 45% and 39% in these two hole-nesting species. Results from Holland and Germany do not differ significantly from my results (Nilsson 1984b).

Several factors can bias estimates of breeding success of open nests. If only a proportion of the nests present in a study area is found, success could differ between nests found and those not found. For example, in deciduous forest, open tree nests initiated

TABLE 1. Breeding success of hole-nesting birds in natural cavities in forests and of open-nesting birds in habitats with forests and shrubs. For hole-nesters (except *Ficedula hypoleuca*) clutch size and brood size are means of yearly means (1973–1979; $n = 7$) of full clutch sizes and fledged brood sizes, excluding total failures. Productivity is the fledged brood size times the proportion of breedings found before the incubation stage that fledged at least one young. Breeding success is productivity as a proportion of clutch size. One standard deviation in parentheses. For open-nesters, only intensive studies over at least 2 yr are included.

Nest site, habitat, and species (source)	Clutch size	Brood size	Productivity	Breeding success (%)
Natural cavities in forests				
Sturnus vulgaris (this study)	4.8 (0.23)	3.2 (0.55)	2.41	51
Sitta europaea[a] (this study)	6.8	4.9 (0.64)	3.40	50
Parus major[b] (this study)	9.3 (1.27)	6.6 (0.67)	4.78	52
Parus caeruleus[b] (this study)	10.6 (0.78)	8.1 (0.61)	5.99	57
Parus palustris (this study)	7.0 (0.59)	6.1 (0.69)	4.14	59
Ficedula hypoleuca (Nilsson 1984a)	6.0	4.8	3.25	54
Open nests in forests				
Anthus trivialis (van Hecke 1979)	4.5	4.0	2.43	54
Sylvia atricapilla (Bairlein 1978)	4.5	3.7	2.28	51
Sylvia borin (Solonen 1979)	4.6	3.8	2.12	46
Pyrrhula pyrrhula (Bijlsma 1982)	4.7	4.0	2.34	50
Coccothraustes coccothraustes (Bijlsma 1979)	4.6	4.4	3.44	75
Open nests in habitats with shrubs				
Lanius collurio (Nilsson unpubl. data)	5.6	4.7	3.17	57
Sylvia nisoria (Neuschultz 1981)	5.0	4.4	2.35	47
Sylvia undata (Bibby 1979)	4.0	3.7	2.93	73
Serinus serinus (Gnielka 1978)	4.0	3.4	1.98	49
Carpodacus erythrinus (Stjernberg 1979)	5.1	4.7	2.98	58

[a] Although clutch size of *Sitta europaea* is based on only 6 clutches, the average was near the value in two other samples from Sweden where the average clutch size was 7.0 ($n = 10$; Durango and Durango 1942) and 6.8 ($n = 5$; H. Källander pers. comm.).

[b] Clutches of *Parus major* and *P. caeruleus* started in June or later are excluded (see text).

before the leaves unfold are easier to detect than later nests. This is likely to apply both to human observers and to predators. To get unbiased estimates of the breeding success of open-nesting birds for comparison, I used data only from intensive studies conducted throughout the breeding season in northwestern Europe. Studies in atypical habitats (e.g. in parks, in gardens, and on small islands) or of only one year's duration were not used. If observers suspected that visits to the nests lowered breeding success, that study also was excluded. My data on the breeding success of hole-nesting birds refer to small passerines in deciduous and mixed deciduous/coniferous forests. To get comparable data from open-nesting birds, I included only small passerines breeding in terrestrial habitats dominated by trees or shrubs.

I found 10 studies of open-nesting species that satisfied these stringent criteria. In these studies there was no significant difference in breeding success between habitats dominated by trees and habitats dominated by shrubs (Table 1). The relative breeding success of these open-nesting species did not differ significantly from that of hole-nesting species breeding in natural cavities (Table 2; Mann-Whitney *U*-test). However, the patterns of nest failures differed in the two groups. The percentage reduction from clutch size to brood size, excluding total failures, was about 24% (SD = 7.3) in the 6 hole-nesters but only 13% (SD = 4.6) in the 10 open-nesters, a significant difference (Mann-Whitney *U*-test, $P < 0.01$, two-tailed). This also means that the proportion of complete nest losses was higher, either in the egg or in the nestling stage, in open-nesters. Thus, lower complete losses for hole-nesters seem to be balanced by higher partial losses in natural cavities. Note that partial losses in boxes often are only about 10% (Schönfeld and Brauer 1972; van Balen 1973; Nilsson 1975, 1984a; Perrins 1979). Partial losses, therefore, seem to be about the same in open nests and boxes but higher in natural cavities. Nest parasites, which can cause nestling mortality (Winkel 1975), are more protected in nesting holes than in open nests, and they also can survive during winter in the hole. In most studies of birds breeding in boxes, the nest contents from the previous year were removed before each breeding season, probably reducing parasite populations in comparison with natural cavities (Perrins 1979).

TABLE 2. Comparison of clutch size and breeding success of hole- and open-nesting passerines, based on the data in Table 1. Values are means (1 SD in parentheses). Breeding success is productivity as a proportion of clutch size.

Nest site	Clutch size	Brood size	Productivity	Breeding success (%)
Hole	7.3 (2.1)	5.6 (1.7)	4.00 (1.27)	53.6 (3.5)
Open	4.7 (0.5)	4.1 (0.4)	2.60 (0.49)	56.0 (10.3)
Difference (%)	+55	+37	+54	−4

Predation is the major cause of total nest failures both in natural cavities (Nilsson 1984b) and in open nests (references in Table 1). The predation rates on nests in boxes are often lower than in tree holes (Ludescher 1973; Nilsson 1975, 1984a, b; R. V. Alatalo pers. comm.). The vulnerability of a nest in a tree hole depends on its position. Predation rates on nests in holes decrease strongly with increasing nest height for several species (Nilsson 1984b). For this reason severe interspecific competition for the safest, high holes is expected to occur if safe holes are limited. Such interference competition occurs and can reduce the breeding success of relatively smaller hole-nesting species (van Balen et al. 1982, Nilsson 1984b), diminishing a potential advantage of hole-nesting over nesting in an open nest.

My studies of hole-nesting birds were conducted in southern Sweden, whereas most of the studies of open-nesters used in the comparison were conducted further south in Europe. This is unlikely to have biased the comparison because the breeding success of hole-nesters in natural cavities in central Europe is similar to or even lower than my results (Ludescher 1973, Booij 1977). Furthermore, the breeding success of three open-nesting species (*Sylvia borin, Lanius collurio, Carpodacus erythrinus*) were studied in northern Europe, but their breeding success is not noticeably different from that of other open-nesters (Table 1).

The breeding success of hole- and open-nesting species does not balance equally throughout the breeding season of small passerines in northern Europe. Among birds nesting in boxes, breeding success is generally lower in late nests than in earlier ones (Klomp 1970). It is uncertain if there are true second clutches for any of the six species in the natural cavities I studied (Table 1). However, of 4 breedings of *Parus caeruleus* started in June none fledged young, and in 12 corresponding nests of *P. major* the breeding success was only 37%. On the other hand, the breeding success of small open-nesting passerines either shows no clear seasonal trend or increases over time (Lack 1954, Bairlein 1978, Bijlsma 1982). It is especially noteworthy that open nests started in April and early May, when most hole-nesters start breeding, have a very low success (Bijlsma 1982). Even nests with a dome, like that of *Aegithalos caudatus*, suffer from a high rate of predation at this time of the year (Perrins 1979, pers. obs.).

For birds that breed mainly in June or later, hole-nesting seems to be a poor strategy, possibly due to the risks of hyperthermia (van Balen and Cavé 1970, Mertens 1977) and attacks from nests parasites (Winkel 1975). On the other hand, these risks seem to be lower in April and May, a time when nests in holes also seem to be safer from predators than open nests. Prior to fledging, open nests suffer from a high rate of predation, and nestlings in them occasionally also have high thermoregulatory costs in spring, disadvantages that diminish in summer. Overall, the way in which different selection pressures change over a season can explain the association between early breeding and hole-nesting pointed out by von Haartman (1968).

Larger hole-nesting species dominate smaller ones in competition for nest sites, and the smallest species can in this way be relegated to inferior holes (Nilsson 1984b). Although competition from larger species is avoided partially by using small holes, overlap between species in nest sites used is high (Nilsson 1984b, unpubl. data). In this context it is interesting that the three smallest species breeding in northern Europe (*Regulus regulus, Troglodytes troglodytes,* and *Aegithalos caudatus*) start breeding early but do not nest in holes. It is possible that they cannot acquire good-quality holes in competition with larger species. Instead, all three have evolved remarkably well-camouflaged, dome-shaped nests that appear more difficult to find by predators and also conserve heat compared with cup-shaped, open nests. Furthermore, these three species have clutch sizes as high as those of hole-nesting species (von Haartman 1969). Therefore, one reason hole-nesting birds have larger clutch sizes than do open-nesting birds (Table 2) could be that the former breed early and feed nestlings at the time of seasonal peak of insect larvae in the foliage (van Balen 1973).

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