

and aviary birds (M. L. Petrak, Ed.). Philadelphia, Lea and Febiger.

ZISWILER, V., & D. S. FARNER. 1972. Digestion and digestive system. Pp. 343-430 in *Avian biology*,

vol. 2 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

Received 16 July 1985, accepted 30 October 1985.

***Philydor hylobius* Wetmore and Phelps is a Synonym of *Automolus roraimae* Hellmayr**

ROBERT W. DICKERMAN,<sup>1</sup> GEORGE F. BARROWCLOUGH,<sup>1</sup> PETER F. CANNELL,<sup>1</sup> WILLIAM H. PHELPS, JR.,<sup>2</sup>  
AND DAVID E. WILLARD<sup>3</sup>

<sup>1</sup>American Museum of Natural History, New York, New York 10024 USA,

<sup>2</sup>Colección Ornitológica Phelps, Apartado Postal 2009, Caracas, Venezuela, and

<sup>3</sup>Field Museum of Natural History, Chicago, Illinois 60605 USA

*Philydor hylobius* Wetmore and Phelps (1956) was described on the basis of two specimens, a tail-less adult (type) and an "immature" (= juvenile), collected at 1,800 m on Cerro de la Neblina in extreme southern Venezuela in January 1956. The two specimens are numbers 461696 and 461697, respectively, in the collections of the U.S. National Museum of Natural History. On the same trip 13 adult and 2 juvenile *Automolus roraimae duidae* (= *Automolus albicularis duidae* in the published list of birds collected on Cerro de la Neblina, Phelps and Phelps 1956) were collected. Mayr (1971) followed the describers and noted *hylobius* to be "Similar to and related to *P. atricapillus*." Mayr also cited a personal communication from C. Vaurie, who examined the two specimens of *hylobius*, and later wrote that it "... is only an isolated population of *P. atricapillus*, but not a distinct species" (Vaurie 1980). Note that the range of *P. atricapillus* along the southeastern coastal region of Brazil is approximately 2,700 km from Cerro de la Neblina!

In the ensuing years the Colección Ornitológica Phelps of Caracas obtained several additional collections from Cerro de la Neblina, but these included no new material of *P. hylobius*. During the period January 1984 to February 1985, eight ornithologists netted and collected extensively at elevations of over 1,200 m on Cerro de la Neblina. Twenty-three specimens of *A. roraimae* were obtained, but again, no additional specimens of *P. hylobius* were taken. In the field Barrowclough and Cannell noted that a juvenile *A. roraimae*, caught in the same mist net with its parent, resembled the description of *P. hylobius* in Meyer de Schauensee and Phelps (1978). Both specimens were collected and the juvenile matched well two juvenile specimens of *A. roraimae* in the collection of the American Museum of Natural History.

This renewed our interest in the original specimens, and Dickerman compared the three juvenile *A. roraimae* (including the above juvenile from Cerro de la Neblina) with the juvenile *P. hylobius* in the National Museum. The juvenile *P. hylobius* was found to be inseparable from them. It also differed markedly from every juvenile specimen of *Philydor*

examined (see acknowledgments) in having weak dusky scalloped edgings on the ventral feathers. The juvenile plumage in all species of the genus *Philydor* is very similar to the basic plumage and lacks any ventral barring or scalloping.

The tail-less adult of *P. hylobius* was compared with an adult *A. roraimae*. They were inseparable in wing length, in bill shape, and in size of the tarsi and feet. We believe the type of *hylobius* is actually an erythristic specimen of *A. roraimae*. The description of the type exactly fits an adult *roraimae* except for the "tawny" rather than cream-colored superciliary line, and the "ochraceous-tawny" rather than creamy-buff throat. However, below the right eye of the type of *P. hylobius*, there is a small patch of pale feathers that matches the throat color of *A. roraimae*.

In the original description, the authors wrote that they considered the most closely related species to be *Philydor atricapillus*, but noted differences in the more slender bill and heavier feet of *hylobius*. Indeed, the tarsi and feet of *hylobius* are heavier than those of any species of *Philydor*, but match well species in the genus *Automolus*. Furthermore, the wing formula of both *A. roraimae* and the type of *P. hylobius* is  $7 > 8 > 9 > 6 = 5 = 4 = 3 = 2 > 1 > 10$ , while the wing formula of *P. atricapillus* is  $6 > 7 > 8 > 9 > 5 > 4 > 3 = 2 = 1 > 10$ . We also note that no species of *Philydor* has an all-dusky ear patch, as do *hylobius* and *roraimae*, without some pale feathers included within the dark auricular area.

*Philydor hylobius* Wetmore and Phelps should be considered a junior synonym of *Automolus roraimae* Hellmayr. With this action, Cerro de la Neblina has no endemic taxa of birds above the subspecific level.

We thank M. Ralph Browning and Kenneth C. Parkes for making further comparisons of specimens in the U.S. National Museum of Natural History and the Carnegie Museum of Natural History, respectively. We thank Ms. Patricia Escalante for providing the Spanish summary. The biological exploration of Cerro de la Neblina was carried out under the auspices of the Fundación Para El Desarrollo de las Ciencias Físicas, Matemáticas y Naturales de Venezuela, and

was supported in part by NSF Biological Research Resources grant BSR-83-17687.

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* corresponde a un adulto de *A. roraimae* con predominancia de pigmentación rojiza (eritrismo), y el otro espécimen es un juvenil típico. Por lo tanto, *Philydor hylobius* Wetmore and Phelps es un sinónimo junior de *Automolus roraimae* Hellmayr.

#### LITERATURE CITED

- MAYR, E. 1971. New species of birds described from 1956 to 1965. *J. Ornithol.* 112: 302-316.
- MEYER DE SCHAUENSEE, R., & W. H. PHELPS, JR. 1978. Birds of Venezuela. Princeton, New Jersey, Princeton Univ. Press.
- PHELPS, W. H., & W. H. PHELPS, JR. 1956. Lista de las aves del Cerro de la Neblina, Venezuela y notas sobre su descubrimiento y ascenso. *Bol. Soc. Venezolano Cienc. Nat.* 23: 32-39.
- VAURIE, C. 1980. Taxonomy and geographic distribution of the Furnariidae (Aves, Passeriformes). *Bull. Amer. Mus. Nat. Hist.* 166: 1-357.
- WETMORE, A., & W. H. PHELPS, JR. 1956. Further additions to the list of birds from Venezuela. *Proc. Biol. Soc. Washington* 69: 1-12.

Received 4 October 1985, accepted 8 November 1985.

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

SVEN G. NILSSON

Department of Zoology, University of Uppsala, Box 561, S-751 22 Uppsala, Sweden

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