Association of open nests and sallying in the open in passerine families

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RESUMO. Associação de ninhos abertos e forrageio em vôo em lugar aberto nas famílias de Passeriformes. De modo geral, os Passeriformes que andam e trepam para bicar as presas têm ninhos em forno ou em cavidade, enquanto aqueles que voam para apanhar suas presas têm ninhos em taça. É possível que os primeiros possam enxergar melhor no escuro ou andar para dentro de seus ninhos, enquanto os demais têm asas muito longas para adentrar ninhos fechados, ou têm receio de fazê-lo (talvez por causa de olhos adaptados para enxergar longe ou com luz mais forte).

PALAVRAS-CHAVE: ambiente aberto, forrageio em vôo, forrageio pousado, ninhos, Passeriformes.

KEY WORDS: foraging, gleaning, nests, open habitat, Passeriformes, sallying.

Some birds build enclosed nests or nest in tree cavities, while others build open cup nests, at times prolonged into deep cups or pouches when at the tips of branches (Skutch 1976). Enclosed nests are well known to lower nest-predation rates (Ricklefs 1969) and to protect against rain and sun (Ricklefs and Hainsworth 1969). Cup nests presumably require little material compared to domed nests, and are not so restricted in availability as are cavity nests. Investigating distribution of cup and enclosed nests among families of the avian order Passeriformes, I discovered a previously unreported association between type of nest and foraging behavior: "intent" birds that creep or walk and peer at nearby or dense vegetation (or the ground or trunks) to glean food tend to have enclosed (cavity or domed) nests, while those "alert" birds that hop or fly to less dense foliage or to the air, sallying for prey and living in semi-open vegetation, tend to have cup nests. In brief, creeping birds have "creep-in" nests, while open-foraging birds have open nests.

I checked Harrison (1978) for information on nests and foraging for the approximately 66 families of Passeriformes (table 1). The original tally was made for other purposes, so that the association was not predicted (although it could have been). Enclosed nests are the principal type in 25 families; of these, 21 are of intent foragers and four (Eurylaimidae, Philepittidae (?), Nectarinidae and Ploceidae) are relatively

alert or distant foragers, although some can glean on the ground or in flowers. Cup nests are the principal type in 37 families; of these, 34 are relatively alert foragers, two (Meliphagidae and Icteridae) are rather intent foragers, and one (Neosittidae) quite intent. The three last families often live in sunny edges or canopies of vegetation (pers. obs., Americas and Australia). Both cup and enclosed nests are widely registered in four families, one being quite alert in foraging (Hirundinidae) and three (Timaliidae, Sylviidae, and Dicaeidae) variable. Excluding these four families, open nests are significantly linked with open foraging (χ^2 contingency-table=11.9, p < 0.01).

Exceptions within families with regard to nest type are sometimes birds that are exceptions with regard to foraging, or are probably derived from species that are not exceptions.

In the Parulidae, Seiurus spp. forage on the ground and walk to enclosed nests. However, Parula spp. have nests enclosed in epiphytes but are not intent foragers. Basileuterus spp. have oven-shaped nests, but some species (perhaps derived ones) forage alertly above the ground rather than on the ground.

In the Formicariidae, Myrmotherula gutturalis has a domed nest and does forage in dead leaves, while M. fulviventris also forages in dead leaves but has a transitional pouch-shaped nest (Oniki and Willis 1982). Oven nests occur in Pyriglena spp. (Willis 1981) and

Table 1. Normal nest type and foraging in Passeriformes.

Family	Nest ¹	Foraging ²	Family	Nest ¹	Foraging
	Е	I	Prunellidae	С	A
Pittidae	E	A	Mimidae	С	A
Eurylaimidae	E	ı,	Sturnidae	E	I
Dendrocolaptidae	E	7	Troglodytidae	E	I
Furnariidae	Č	1	Remizidae	E	I
Formicariidae		^	Aegithalidae	E	I
Conopophagidae	C	A	Paridae	E	I
Rhinocryptidae	E	I	Sittidae	E	I
Iyrannidae	C	A	Neosittidae	c	I
Cotingidae	C	A	Climacteridae	E	I
Pipridae	C	A	Certhiidae	Ē	I
Acanthisittidae	E	I	Dicacidae	CE	AI
Philepittidae	E	A?	Nectarinidae	E	A
Menuridae	E	I		č	A
Atrichornithidae	E	I	Zosteropidae	c	A
Alaudidae	E	1	Epthianuridae	c	AI
Hirundinidae	CE	Α	Meliphagidae	c	A
Motacillidae	E	I	Emberizidae	c	A
Campephagidae	С	Α	Parulidae		Ä
Pycnonotidae	С	Α	Vireonidae	С	AI
Irenidae	С	Α. Α.	Icteridae	C	A
Laniidae	С	Α	Fringillidae	C	ī
Malaconotidae	С	A	Estrildidae	E	_
Vangidae	C	Α	Ploceidae	E	A
Bombycillidae	C	A	Artamidae	С	A
Ptilogonatidae	С	Α	Grallinidae	C	A
Dulidae	E	I	Callacidae	· c	A
Cinclidae	E	I	Dicruridae	С	A
Turdidae	С	Α	Oriolidae	С	A
Muscicapidae	С	Α	Monarchidae	С	A
Maluridae	E	I	Cracticidae	С	A
Polioptilidae	C	A	Ptilonorhynchidae	С	A
Sylviidae	CE	AI	Paradisacidae	С	A
Timaliidae	CE	AI	Corvidae	С	A

¹C = cup; E = enclosed

Percnostola rufifrons (Willis 1982a), which hop in dense vegetation but sally short distances for prey, hence are not especially intent foragers. Myrmeciza or Myrmelastes ferrugineus walks on the ground but has a cup nest, as do Dichrozona cincta (Willis 1988) and the leaf-tossing Myrmornis torquata. These last three species are colored similarly to and perhaps derived from alert and ground-sallying antbirds of the genus Hylophylax (Willis 1984).

In the Tyrannidae, domed nests occur in some species that forage somewhat more intently than normal, as in Corythopis torquata (Oniki and Willis 1980), Pitangus sulphuratus, Pipromorpha macconnelli (Willis et al. 1978) or Todirostrum spp. but also occur in other species that sally well (Colonia colonus nesting in holes, Arundinicola leucocephala with domed nest, etc.). Exceptions within the family thus do not fit the general pattern.

In the Dendrocolaptidae, sallying *Dendrocincla* spp. and *Dendrocolaptes* spp. nest in tree holes (Willis 1972, 1982b) as do their intently-foraging relatives. It is likely that sallying species are derived, being ant-following specialists, or that use of open nests simply never arose in lines related to the nest-conservative ovenbirds (Furnariidae).

In the Emberizidae, several gleaning ground-hopping sparrows (Arremon, Myospiza, etc.) have domed or enclosed nests. Enclosed epiphyte-nesting Tangara spp. and Orthogonys chloricterus represent lines that peer under tree limbs, but are not so intent at foraging as are Furnariidae. Tiaris spp. with enclosed nests at forest edges are little more intent at seed eating than are Sporophila spp. of more open areas. A full analysis would be interesting in this and other large families.

In related orders, this correlation does not seem

²A = alert; I = intent

to hold. Piciformes and Coraciiformes nest in cavities, even alert flycatching families. Apodidae sometimes have domed nests, but all fly well. Trochilidae fly well and have cup nests, agreeing with Passeriformes.

Perhaps passerines that creep along the ground, trunks or foliage can easily enter a closed nest as if foraging, while passerines that fly about for food are often relatively poor fliers or too long winged to enter an enclosed nest directly. Where the birds fly very well, as in Hirundinidae and Tyrannidae, it is not so hard for an alert forager to fly into a nest hole.

Roberto Cavalcanti (in litt. 1990) suggests that, if the foregoing were the case, there would be no selective reason for intent foragers to avoid cup nests. He suggests that, since alert or flycatching birds normally forage in open vegetation, it way be hard for them to build covered nests. Another alternative is that alert or flycatching birds may be visually poorly adapted to dark or closed nest interiors, or to cluttered foliage, while dark-adapted or myopic gleaning birds could be better adapted. Obviously, birds that forage by gleaning require high densities of leaves or nearby continuous surfaces (ground, bark, etc.) and for this reason, tend to live enclosed by dense vegetation or on surfaces, while birds that sally tend to take rather open, often well-lighted sites from which they can see long distances (large surface areas). Furnariidae, Rhinocryptidae and Troglodytidae are examples of the first extreme, Tyrannidae and Muscicapidae the second, while Formicariidae and other families are intermediate. Intent Australian Neosittidae are actually light adapted, living on bright dead canopy limbs, and may need deep cup nests to avoid sudden visual adaptation problems.

Living in open vegetation may also make closed (large) nests too conspicuous to predators, although one could also argue that the conspicuousness and hot sun of open sites should favor closed nests that offer better protection.

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