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## OVERVIEWS

### NEST ARCHITECTURE AND AVIAN SYSTEMATICS

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ANYONE WHO TRIES to identify a bird nest, without seeing the bird that constructed it, enters the realm of avian systematics. The attempt to determine the identity of the nest leads immediately to an effort to categorize the nest according to its overt features: Is it in a hole? Is it on a branch? If the nest lies in a hole: Where is the hole located? How big is it? How was the hole constructed? For the nest itself: What material is it made of? How is the material fitted together? How is the nest lined?

Such quests to identify nests depend ultimately upon evolution and the "nested" nature of nest architecture. Members of a group of closely related birds tend to build their nests based on a common architectural theme, and subgroups "nested" genealogically within larger groups tend to build nests that are variations on the larger theme. By examining a nest, we can quickly assess the general type of bird that constructed it (oriole, swallow) by the basic theme (pendant nest, mud nest). Then, by following a route of subthemes (e.g. shape, location, construction method, materials, etc.), we can whittle down the list of possible builders. The reason for the "nesting" of nest themes is that throughout evolutionary history, birds have met ecological challenges (e.g. changes in climate, predation, and competition) by adapting their nests to each new situation. These adaptations tended not to be revolutionary, be-

cause of genetic and selective constraints on the morphology and behaviors associated with nest building (Winkler and Sheldon 1994). Instead, they tended to be slight modifications on the main nesting theme. For bird systematists, who are scientists interested in understanding evolutionary patterns, this adaptive tinkering has provided invaluable clues to the history of avian life. It has created a hierarchy of nest types that, when deciphered, can shed light on the phylogenetic (genealogical) relationships of birds, and it has left an evidential trail of the interaction between genetics and ecology, the driving force of evolution. Thus, even a rudimentary consideration of the possible owners of an unidentified nest delves into the methods and logic of avian systematics and yields insights into bird evolution.

An interesting example of "nested" nest architecture that we have studied concerns swallows of the genus *Hirundo* and their allies (Winkler and Sheldon 1993). This group includes Barn Swallow (*Hirundo rustica*), Cliff Swallow (*Petrochelidon pyrrhonota*), Cave Swallow (*P. fulva*), Common House-Martin (*Delichon urbica*), and about 32 other species. All build nests made of mud. The ancestral mud nest was a simple cup-shaped structure, like that of a Barn Swallow. A more derived (modern) nest from this group is a slightly enclosed cup, like that of a Common House-Martin. The most recently evolved nests are ornate, enclosed globes and retorts, sometimes with long entrance tun-

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nels, like those made by the New World Cliff Swallow and the "red-rumped" and "cliff" swallows of the Old World. The architecture of these mud nests provides strong clues to phylogenetic relationships of these swallows. For example, all 15 species that build simple mud cups are members of the same phylogenetic group as the Barn Swallow. All species that build retort-shaped nests with entrance tunnels are members of the same group as the Cliff Swallow. Moreover, the pattern of increasing complexity in nest structure through time, from simple cups to ornate retorts, corresponds with many other aspects of the group's ecology and behavior, including distribution, social structure, and breeding.

One might think that nest characters, as manifestations of behavior, are too plastic and unpredictable to provide a useful guide to phylogeny and evolutionary history. However, recent studies have shown that behavioral characters can be just as effective in reconstructing phylogenies as are morphological or molecular characters (e.g. de Queiroz and Wimberger 1993). The main problem with behavioral characters is not that they are unreliable, but that there are usually not enough of them to resolve phylogenetic relationships. Another problem is that most behavioral characters need to be observed in the field and are subject to a range of interpretations by different researchers. In this regard, nest characters taken from museum specimens present a distinct advantage. Nests can be lined up on a table and examined thoroughly by researchers and reviewers alike. This potential for scrutiny assures greater objectivity and discussion in choosing and interpreting nest characters than in using other behavioral characters.

Nest structure has been used for centuries to indicate bird relationships, but not in a rigorous way. In the past, ornithologists grouped species based on overall similarity of their nests. But similarity is difficult to quantify and, worse, it can result from convergent evolution as well as common descent. Many unrelated species of birds, for example, have adapted convergently to nest in tree holes because of the protection afforded by these sites. Fortunately, the problem that convergent evolution poses to phylogenetics has been alleviated, to some degree, by the development of cladistic analysis. This method determines the "nested" relation-

ships of groups of organisms by identifying derived characters that are shared among group members (synapomorphies) and not shared with members of other groups. The reconstruction of phylogeny from nest structure, therefore, should be simply a matter of coding architectural characters and identifying natural groups by their synapomorphies. However, ornithologists rarely do this, for several reasons. First, there are not enough data. This is especially true for tropical groups of passerines, for which many species' nests are undescribed or known from only a single example. To identify and code nest characters requires not only knowledge of the nest, but some notion of variation in the characters; a character that varies a great deal within a species is not likely to be helpful in phylogenetic work.

Another problem in coding nest characters concerns a lack of independence. It arises, for example, when nests built in holes are compared with nests placed on branches. Not only do these nest types share a limited number of characters because of fundamental differences in their sites, but some of the common characters will be strongly and jointly influenced by the site; they will not be independent indicators of phylogenetic relationship. For example, exterior nests are characterized by specific attachment methods and greater camouflage and strength than interior nests. The interdependence of characters associated with attachment, camouflage, and strength would not present a problem if the two types of nest builders were distinct phylogenetically. However, if some hole-nesting species were more closely related phylogenetically to branch nesters than to other hole nesters, phylogenetic analysis would probably fail. Unless the interdependence of nesting characters can be controlled by a weighting scheme (as commonly done in molecular phylogenetics), the hole nesters would appear as a group distinct from the branch nesters, and the phylogeny would be incorrect.

Given the pitfalls of nest characters, but also their great potential, Kristof Zyskowski and Rick Prum have accepted, in this issue of *The Auk*, the ultimate challenge in nest analysis: the reconstruction of ovenbird phylogeny. Members of the ovenbird family (Furnariidae) display more variation in nesting behavior than any other avian family, and because of their tropical distribution and diversity (240 spe-

cies), the furnariids are one of the most poorly understood major groups of birds in terms of phylogeny, ecology, and behavior. The large number of species assures a problem with missing data, which Zyskowski and Prum have done much to remedy. Moreover, the remarkable variation in nest architecture (e.g. self-excavated and adopted holes, nests attached to vertical and horizontal substrates, pendant nests, domed nests of vegetation or clay) also raises the specter of at least a poorly resolved, if not incorrect, phylogeny because of variation among nest types and resultant interdependence of characters within nest types. Finally, Zyskowski and Prum have no substantive study models from which to work. No modern workers have attempted to reconstruct a phylogeny of a family of birds based solely on nesting characters, let alone a family of such size and complexity. All recent studies have depended upon molecular or morphological data to complement and provide perspective on the nest data.

Despite these obstacles, Zyskowski and Prum have derived a reasonably resolved and logical family tree, based on a remarkable 168 species in 41 genera (ca. 70% of the ovenbirds). At this stage, we can only judge their success by intuition; to know the extent of their discoveries, or blunders, will require corroborating evidence from other phylogenetic data sets. However, intuition says that the "nested" nature of ovenbird nests has provided good phylogenetic signal, and that the Zyskowski and

Prum tree is largely on the right track (also see Vaurie 1971, 1980). Moreover, simply by virtue of its pioneering nature, the Zyskowski and Prum study has moved avian systematics substantially forward. Amassing such a large set of data and working through the process of coding nest characters, in themselves, are substantial achievements. We now have a foundation not only for future work on the ovenbirds, but also a guide for use of nest characters in systematic studies of other groups of birds.

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