Evolution of nest construction in swallows (Hirundinidae): A molecular phylogenetic perspective

(Aves/phylogeny/biogeography/behavior)

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ABSTRACT   Nest construction is more diverse in the Hirundinidae than in any other family of oscine birds. To explore the evolution of this diversity, we superimposed nest data on a DNA-hybridization phylogeny of 17 swallow species. Nest construction is tightly linked to the inferred evolutionary history. Burrowing appears to be the primitive nesting mode, and burrowing ancestors gave rise to cavity-adopting and mud-nesting clades. Obligate cavity adoption is mostly confined to a monophyletic clade in the New World, and the diversification of obligate nest adopters appears to be tied to the richness of forest habitats and recent active mountain building there. Construction of mud nests originated only once in the history of the group, and mud-nesters have diversified principally in Africa, where a drier climatic history has favored their mode of nesting. The use of pure mud to construct a hanging nest is unique among all birds, and we infer that mud nests have increased in complexity during evolution from simple mud cups to fully enclosed retort-shaped nests. This increased complexity appears to have been the critical precursor for the evolution of high-density colonial mud-nesters.

Swallows are popular subjects for behavioral ecological research (1–11). Their nesting habits are well known (1), and they are thus well suited for comparative analyses of nesting biology. The variety of nest construction in the family spans most of the general nest types observed in the order Passeriformes (which contains over half the world's bird species). The nests of swallows and martins vary from natural cavities in rocks and trees and long self-excavated burrows to mud structures attached to vertical surfaces. These mud nests vary from simple open or closed cups to enclosed retort-shaped structures, sometimes with long entrance tunnels. To study the evolution of nest construction in this group, we superimposed nest-construction data onto a DNA-hybridization phylogeny of 17 species (12). This phylogeny contains >20% of the species and all but two of the genera (1, 13) in the subfamily Hirundininae (typical swallows and martins).

When nest-building behavior is superimposed on the phylogeny (Fig. 1), a remarkable evolutionary conservatism is revealed. With the possible exception of the unresolved node bearing *Tachycineta bicolor* and *Riparia riparia*, there is no indication that any of the modes of construction arose more than once during the evolution of these species. To test for phylogenetic conservatism (19), we generated 1000 random character sets with the program MACCLADE (20) using the frequency of observed construction modes as the expected probabilities. By charting the number of changes required to produce the fit between the phylogenetic tree and each of these random character sets, we estimated that the number of changes required to fit the actual nesting data to the tree had at most a 0.04 probability of occurring by chance. This

provides objective evidence of phylogenetic conservatism in this group's nesting biology. As such, it supports Mayr and Bond's earlier use of nest types as the basis for phylogenetic inferences in the Hirundinidae (21). This study also corroborates recent demonstrations of the utility of behavioral characters in phylogeny construction (22, 23) and reinforces previous DNA-hybridization results (24) suggesting conservatism in behavioral evolution (25).

Each of the three basic modes of construction predominates in one of the three swallow clades. Mud-nest builders are restricted to the clade of *Hirundo* and its allies, and cavity adoption is the rule among New World members of the "core martin" clade. Nest excavators are divided between the third principal clade, *Psalidoprocne*, and the most basally branching Old World members (*Riparia* and *Pseudhirundo*) of the core martin clade. This phylogenetic distribution of nesting modes supports a coherent picture of the evolution of nest construction in the swallows (Fig. 1). Both New World adopters and mud-nesters were apparently derived from (different) burrowing ancestors. Within the mud-nesters there are actually three distinctive types of nests. From the perspective of parsimony alone, the historical ordering of these three nest types is not clear, since the same number of changes would occur, no matter which of the three mud-nest types was considered to be primitive. This ambiguity can be resolved by considering the process by which mud nests are constructed: The first step is a simple cup, as in the nests of *Hirundo* and *Ptyonoprogne*. This simple cup is closed by *Delichon* (1, 26). In the retort-nesters, the nest passes through the *Hirundo* and *Delichon* stages, with a closed mouth and tunnel added last (1, 27). From these observations, we assume that ontogeny of mud-nest construction recapitulates the phylogeny of nest types from open cups through closed cups to retorts.

Our hypothesis for the evolution of nest construction (i.e., that adopters and mud-nesters arose independently from burrowing ancestors and that mud-nesters evolved from a cup through a closed cup to a retort) corresponds to a five-state character tree. This tree is 1 of 235 other possible five-state nest-type trees (28), all but 1 of which would have an equivalent or poorer fit to the phylogeny. The unresolved node bearing *Tachycineta bicolor* and *Riparia riparia* is the only place in the phylogeny where our hypothesis may not be supported, and the observed fit, with at most one extra evolutionary change, is better than would be expected by chance ($P < 0.04$).

Contrary to our hypothesis, Mayr and Bond (21) suggested that cavity adoption was the most primitive state of nest construction in the hirundines. However, the more basally branching members of the core martin clade are burrowers (Fig. 1), as is *Psalidoprocne*, the sister taxon to the remainder of the subfamily. Moreover, the genus *Pseudochelidon* (river martins), which is thought to be the closest outgroup to the Hirundininae (29), is also a burrower (1). Finally, in Fig. 1,

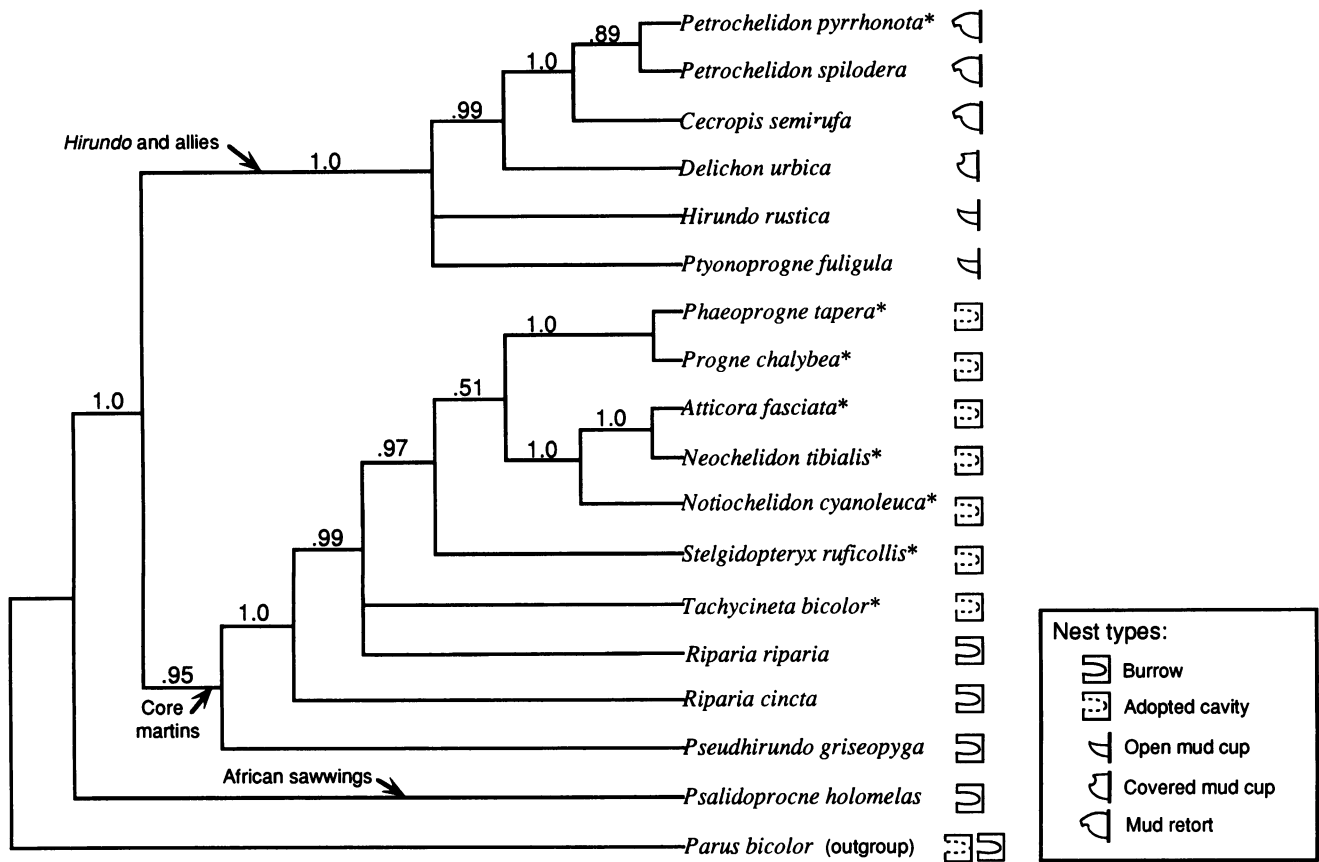†To whom reprint requests should be addressed.

FIG. 1.   Fifty-percent majority-rule consensus tree for 17 swallows and a titmouse (*Parus bicolor*) outgroup. The 18 × 18 matrix of single-copy nuclear DNA hybrids included replicate measurements in all cells (12), and the tree was produced from 1000 Fitch trees by the CONSENSE routine of PHYLIP (14). These Fitch trees were fitted from bootstrapped pseudomatrices of replicate melting temperature differences (15, 16), which were corrected to percent sequence divergence and for multiple mutations at single base sites (17, 18). The numbers at the bases of each tree node represent the proportion of the 1000 trees supporting that node, and nodes that were only supported in <50% of the trees are presented as polychotomies. The symbols at the far right indicate the type of nest built for each taxon, and two symbols are presented for *Parus bicolor* to signify the prevalence of both nesting strategies in that genus. Taxa that are exclusively New World in their distribution are indicated with an asterisk. Nest types were assigned on the basis of information in Turner and Rose (1), supplemented by our own field observations of African taxa. English names for the taxa are, from top to bottom, cliff swallow, South African cliff swallow, rufous-chested swallow, house martin, barn swallow, rock martin, brown-chested martin, gray-breasted martin, white-banded swallow, white-thighed swallow, blue-and-white swallow, southern rough-winged swallow, tree swallow, sand martin, banded martin, gray-rumped swallow, black sawwing, and tufted titmouse.

assuming that adoption was the primitive state would require three extra changes in nest type on the phylogeny and produce a fit no better than would be expected by chance (*P* > 0.30). It seems reasonable to conclude that the primitive condition is nest burrowing.

It is perhaps surprising that nest adoption is not primitive in the swallows, since adoption is their only mode of nesting that does not require special motor skills. If adoption was not the original mode of nest construction in the group, it would be expected nevertheless to occur frequently among swallows today. Many mud-nest builders and some nest burrowers are known occasionally to adopt old nests (1), but obligate nest adoption, like that in the New World martins, has been reported in only three other species (*Psalidoprocne fuliginosa, Phedina borbonica*, and *Petrochelidon nigricans*). These adopters are apparently the only species in the entire family that have nesting biologies different than those of their closest relatives in Fig. 1 (1). Each of these species appears to be distantly related from each other and from the New World adopters, and behavioral differences among them (1, 30) suggest that obligate adoption arose independently (and thus nonhomologously) in each. Even though there is not a large number of obligate adopters outside the New World martins, the fact that this nesting mode has apparently arisen four times whereas the others have arisen only once suggests that obligate adoption has indeed evolved more readily, as expected.

The occurrence of nonhomologous nest-adopting behavior within the family also raises questions about the homology of other nesting behaviors. Nest-burrowing among *Psali-doprocne* and the basal members of the core martin clade appears to be homologous, since it apparently arose only once in the phylogeny and the behavior used is similar: Both members of the pair excavate the nest by dislodging earth with the bill and pushing it out of the burrow with the feet (31, 32). Likewise, mud-nesting apparently arose only once, and virtually all members of the mud-nesting clade build their nests in similar ways. Both members of the pair bring mouthfuls of mud and add them to the nest, which always begins at its base with a small attachment to a vertical substrate and grows upward and outward from there (1, 32, 33). The use of mud by swallows appears to be independently derived from its use in nest building by other birds; swallows are apparently the only birds that build an elevated attached nest composed entirely of mud (33). This habit seems to be best developed in the more derived genera of the mud-nesting group (*Delichon, Cecropis*, and *Petrochelidon*), as several species of its most basal genus (*Hirundo*) mix the mud in their nests with grass and other vegetable fibers (1, 32). With the possible exception of *Hirundo atrocaerulea* and *Hirundo nigrorufa* (1, 32), however, all these swallows are distinctive compared to other birds in transferring pure mud in mouthfuls instead of transferring bits of vegetation to which the mud

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Table 1. Number of swallow species in each of four groups discussed in the text that breed in each of the principal biogeographic regions and the principal nest type in each group

	Nest type	Total species	Ethiopian	Oriental	Australian	Palearctic	Nearctic	Neotropic
Sawwings	Burrow	12	12					
Old World martins	Burrow	8	6	1	1	1	1	
New World martins	Adopted	27					4	24
Hirundo and allies	Mud	40	23	7	4	7	3	2

For exceptions see text. Species limits and distributions after Sibley and Monroe (13).

adheres (33). Thus, it appears that the style of mud-nesting used by the members of this family is an evolutionary innovation distinctive to this group.

The building of mud nests can be seen as a key innovation [*sensu* Liem (34)] allowing mud-nesters to occupy habitats lacking available nest cavities or substrates for burrowing. Given that over half of the species in the mud-nesting clade breed in Africa and that mud-nest builders are the predominant element of the hirundine fauna there (Table 1), it seems reasonable to conclude that they have been most "successful" on that continent. This higher success appears to be due to the historical prevalence of seasonally dry and lightly forested habitats in Africa (35, 36). Emlen (27) observed that the mud nests of swallows can crumble in conditions of high humidity, even without being directly moistened. It seems likely that this moisture sensitivity would prevent large-scale colonization and diversification in the humid tropics by members of the mud-nesting clade. It is not so clear why nest adopters have been so singularly successful in the New World. The high diversity of cavity adopters in the New World seems to be associated with the combination of extensive forest communities with a diverse fauna of primary hole excavators and the habitat (cliffs and talus slopes) and isolation provided by the disjunct areas of recent mountain building all along the north–south axis of both New World continents. It is difficult to understand, however, why cavity adopters have not colonized the Oriental region, where most of these factors have also been present.

If the evolution of mud-nesting in any form served as a key innovation in allowing *Hirundo* and its allies to colonize previously unoccupiable habitats, the increased development of the structure of the nest itself apparently served as a further innovation that allowed the elaboration of new social systems in this clade. The pattern of nest complexity in *Hirundo* and its allies (Fig. 1) is an interesting and straightforward example of increased development of a trait through a phylogenetic sequence. Lind (26) suggested that the closed nest cup of *Delichon* served to interfere with copulation attempts from neighboring males, since *Delichon* copulates in its nest, thus allowing the relatively dense aggregations of nests in this genus. Among the colonial retort nesters (i.e., *Petrochelidon* spp.), nesting densities are even higher, with many nests actually sharing common walls with their neighbors (1, 32). Members of these species also copulate in their nests (1), and we suggest that the progression to retort-nesting allowed the evolution of dense coloniality in the mud-nesting clade by providing a way to counteract the pressure of forced extra-pair copulation attempts (37). Factors favoring coloniality, such as increased foraging success and predator defense (2, 3, 38–41), may have supplemented the selective advantage of retort-nesting (unpublished data); however, the existence of several solitary retort-nesters (e.g., *Cecropis* spp., *Petrochelidon fuliginosa*) suggests that coloniality and the maintenance of retort-nesting are not necessarily linked. Coloniality with dense nesting aggregations appears to have arisen in response to the origin of retort-nesting, not vice versa.

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