

Hanging nests on a phylogenetic tree

Contrary to a common assumption, evolutionary sequences of complex behavioural patterns, such as nest building by birds, can be reconstructed by careful phylogenetic analysis.

Which characters are most useful for working out the evolutionary relationships among a group of species? Many would claim that molecules provide more reliable guides to the past than morphology, and that morphology is more reliable than behaviour. On the other hand, as long ago as 1959, Niko Tinbergen [1] argued that there is no reason why behaviour should be any less reliable than other traits for unravelling the past. Two recent papers provide strong support for Tinbergen's assertion [2,3].

The evolutionary tree, or phylogeny, of a group is reconstructed using characters shared by different species through common ancestry; such 'homologies' are keys to past relationships. Unfortunately, characters can also be shared because they have arisen independently in different evolving lineages; such 'homoplasies' are to be avoided in phylogenetic reconstruction. For example, many unrelated species of distasteful or poisonous insects ('Mullerian mimics') have converged on the same patterns of warning coloration, making colour patterns in those species a poor guide to evolutionary relationships. Behaviour will be more unreliable than other traits if it shows more homoplasy. But why should behaviour be more homoplastic?

Many biologists assume that behaviour is so evolutionarily labile that it provides little information about evolutionary relationships [4,5]. Perhaps it is easier to imagine behaviour evolving over short periods of time than morphology evolving over similar intervals. But imagination can mislead. de Queiroz and Wimberger [2] examined 22 phylogenetic studies in which both behavioural and morphological data were used and could find no significant difference in homoplasy between behavioural and morphological characters. Furthermore, in a separate comparison of 8 behavioural phylogenies with 32 morphological phylogenies, they again found no difference in homoplasy. In an earlier study, Sanderson and Donoghue [6] found that morphological phylogenies are no more homoplastic than molecular phylogenies. Taken together, these studies suggest that appropriately chosen behavioural, morphological and molecular data may be equally valid for phylogenetic reconstruction.

If behavioural traits are less evolutionarily labile than we might suppose, then it should be possible to use them to trace the evolutionary ontogeny of behavioural processes. A fine example of this approach is a recent study of the nest building behaviour of swallows [3]. Swallows' nests are as diverse in structure as those found in any family of the order Passeriformes, which contains over half the world's bird species. Swallows'

nests can be classed into three main types: excavated burrows, adopted cavities in rocks or trees, and mud nests ranging from open cups to enclosed retorts with necks (Fig. 1). To explore the evolution of this diversity, Winkler and Sheldon [3] superimposed information about nest structure onto a molecular phylogeny of 17 members of the subfamily Hirundininae (typical swallows and martins). Interestingly, the three principle phylogenetic groupings generally correspond to the three types of nest (Fig. 2). *Hirundo* and allies build mud nests; New World martins adopt cavities; and Old World martins, as well as the sole member of the African sawwings, dig burrows. The coincidence of nest structure with phylogenetic relationship is statistically significant. In short, far from being labile, the evolution of nest building in the 17 species of swallows is, in fact, remarkably conservative.

Winkler and Sheldon's study suggests that burrowing is the primitive form of nesting by swallows. Cavity adoption and mud-nesting evolved from different burrowing ancestors (Fig. 2). The mud-nesting lineage includes species that build three different types of nest: open cup, covered cup and retort-shaped cup. There is no most-parsimonious arrangement of the three cups; hence the authors arranged them on the basis of field observations suggesting that nest ontogeny recapitulates phylogeny. The most primitive type of mud nest is an open cup. Species building a covered cup must first construct an open cup. Species constructing a retort-shaped cup must first construct an open cup, which is then covered before the tunnel is added (Fig. 1).

The swallow study vindicates nest structure as a useful



Fig. 1. Cliff swallows (*Petrochelidon pyrrhonota*) build a retort-shaped nest of mud. Nest construction begins with an open cup that is then roofed over. Finally, a tunnel-like entrance-way is added. (Photograph courtesy of Charles R Brown.)

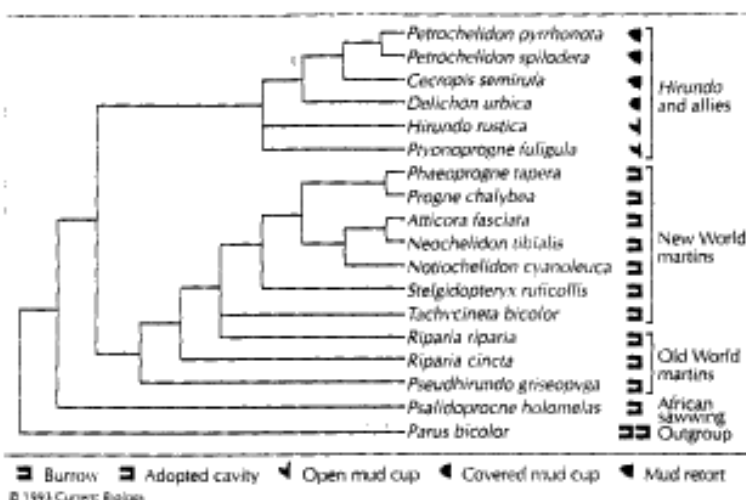


Fig. 2. Distribution of nest types for swallows in relation to their phylogeny reconstructed from DNA-hybridization data. (Modified from [3]).

trait in avian systematics [7,8], which may well help guide phylogeny reconstruction in other groups. Consider, for example, Asian cave swiftlets, which are best known as producers of saliva nests that are used to make Chinese bird's-nest soup. Cave swiftlets are also a source of considerable frustration for avian systematics: as Ernst Mayr lamented [9], "Every author who has ever worked with these small swiftlets of the Indo-Australian region will contend that their classification presents the most difficult problem in the taxonomy of birds". Three species of cave swiftlets (*Aerodramus*) are broadly sympatric. These species cannot be identified reliably on the basis of morphology, even when examined in hand by an expert [10]. Rather, they are identified on the basis of their distinct nests: *A. fucipagus* builds a nest of 100% saliva; *A. maximus* builds a nest from an eerie mixture of saliva and feathers plucked from its own body; and *A. vanikorensis* builds a nest of saliva and mosses. Hanging nests on this group's phylogenetic tree would certainly be a worthwhile replication of the swallow study.

There are still unresolved questions regarding behavioural characters in systematics. For example, behaviour has been used mainly for comparisons among lower taxonomic levels (species and genera). One reason for this is the unavoidable bias in the data sets. Behavioural data, which are often difficult to collect, tend to be available for domestic and semi-domestic species like waterfowl. Other groups are not so easy to observe because of their elusiveness and the broad geographic distributions of different taxa. It takes a good deal of time and money to collect behavioural data for large numbers of free-ranging species. Another problem, emphasized by de Queiroz and Wimberger [2], is that homoplasy varies with the number of traits and the number of taxa in a phylogeny. A more robust analysis of behavioural homoplasy would require a larger phylogeny than any of those compared to date.

These problems can potentially be overcome by going back to nest-building in birds. As the behaviour results in a physical object that can be preserved and studied

at will, it is possible to infer at least some behavioural information with relative ease. Data on nests are available for many taxa [11,12]. As nests are homologous structures, homologous components of building behaviour should be relatively easy to identify, even among higher taxa. Nest building is an excellent candidate for a large-scale phylogenetic analysis, possibly across all birds, thereby unravelling the evolutionary development of a particularly complicated behavioural process.

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