THE PHYLOGENETIC APPROACH TO AVIAN LIFE HISTORIES: AN IMPORTANT COMPLEMENT TO WITHIN-POPULATION STUDIES[1]

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Abstract. In recent years, two approaches have emerged for the analysis of character evolution: the largely statistical "convergence" approach and the mainly cladistic "homology" approach. I discuss the strengths and weaknesses of these approaches as they apply to phylogenetic analyses of life-history variation in birds. Using examples from analyses of character variation in swallows, I suggest that the phylogenetic approach yields distinctive insights into the selective role of the environment and other characters of the organism on the evolution of life-history traits. This view thus has the potential of bringing together micro- and macro-evolutionary views of life-history evolution.

Key words: birds, character evolution, life-history traits, phylogeny, swallows.

INTRODUCTION

The life histories of birds are fascinating because their study requires an integration of organismal and population biology. Here I relate some of my experiences in taking the phylogenetic approach to studying the evolution of avian life histories. I will mention briefly many dynamic areas: systematics is growing and changing rapidly, accumulating an immense literature and a great variety of ideas; comparative studies of the ecological characteristics of birds are increasing rapidly as well. My intention is to discuss briefly the ways that comparative methods can be applied to character evolution. I then give a few examples of how I have applied these methods to life-history traits in swallows. Finally, I conclude with a brief detour on another life-history trait, dispersal, which is suitable for analysis on several levels, including a comparative one. My goal is to demonstrate that comparative analysis provides an important tool for the study of life histories, as it provides the foundation for combining organismal and population perspectives.

Before proceeding, I must clarify the sense in which "comparative" is and has been used in biology. For decades, comparative anatomists have used comparisons among taxa as natural experiments to evaluate the mechanisms of or-

ganismal biology, and ecologists sometimes use similar comparisons among sites to evaluate the roles of various ecological processes. In the past 10 years or so, however, comparative studies have often been thought of as having an explicit phylogenetic component, and it is to that narrower set of comparative evolutionary methods for analyzing adaptation and character change that I limit my attention.

AN OVERVIEW OF THE METHODS

Two principal approaches to analyzing character evolution have found broad application during the last decade (Coddington 1994, Pagel 1994, Sheldon and Whittingham 1997). There is the *convergence approach* (also called the "functional" or "homoplasy" approach) and the *homology approach* (also called the "cladistic" approach). The convergence approach explores correlations among similar events across lineages. Methods have been developed by Ridley (1983), Felsenstein (1985), Grafen (1989), Harvey and Pagel (1991), Maddison (1990), Gittleman and Kot (1990), and Garland et al. (1992, 1999). These, and many other comparative methods that have been developed in the last 15 years, have the common feature that they attempt to draw inferences about the adaptive nature of character variation. They look *across* lineages at repeated changes in characters and correlate these with changes in ecological circum-

stances or with changes in other characters. Because these methods require statistical assumptions about the evolutionary process that are difficult to evaluate, I prefer the homology approach, which explores unique events within lineages. Homology methods are those of Wanntorp (1983), Padian (1985), Greene (1986), Coddington (1988), Carpenter (1989), Donoghue (1989), Lauder (1990), and Baum and Larson (1991)—many of whom are cladistic systematists as well. The homology approach explores unique events *within* lineages. Many convergence comparative methods have been created to solve the problem of pseudoreplication across taxa in studies of character evolution, and one could reasonably argue that the homology approach, instead of dealing with pseudoreplication, eschews any replication at all. Its greatest disadvantage is that it deals with single events. There is no pretense of a statistical interpretation of the variation in characters that we see. This approach does, however, have compensating merits.

Before exploring these, I will present a few examples and a few speculations on the history of these approaches as they pertain to life-history variation. I see the convergence approaches in ornithology as arising out of comparative analyses used by David Lack (1968) and Oscar Heinroth (1922) before him, in which mean life-history traits across species were plotted relative to some other feature of the organism or to some ecological circumstance. Phylogeny was usually dealt with graphically by plotting species in different taxa with different symbols and connecting them with different lines. So, in a sense, Lack and Heinroth attempted to control for phylogeny by highlighting the relationships that potentially differ between different groups. The more modern approaches have dealt with phylogeny either by analyzing characters according to the taxonomic rank of the groups possessing them, or by using phylogenetically based statistics (Felsenstein 1985, Garland et al. 1993, Martins and Hansen 1997).

Perhaps the earliest application of a homology-like approach to non-morphological traits in ornithology was Lorenz's (1941) attempt to analyze the evolution of waterfowl courtship. A modern example of the homology approach comes from Lanyon's (1992) work on brood parasitism in cowbirds (*Molothrus*). Lanyon constructed a phylogenetic tree for the cowbirds
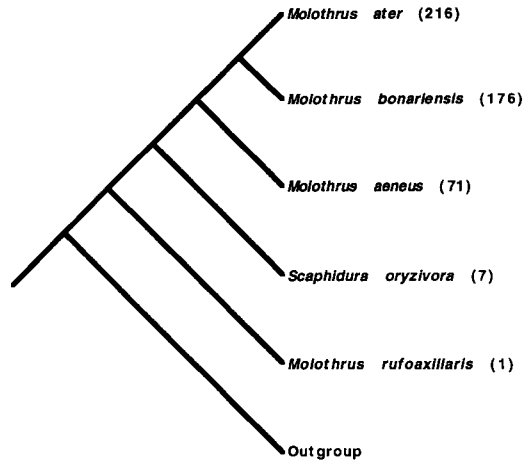

FIGURE 1. Scott Lanyon's phylogeny of cowbirds with his compendium of the number of hosts possessed by each species in parentheses for each taxon (after Lanyon 1992).

based on mitochondrial DNA variation and then mapped onto that tree the number of host species used by each of the cowbird species analyzed. He found an obvious trend within the cowbirds from basal species with few hosts to derived species with numerous hosts (Fig. 1). At first sight, this pattern of occurrence of host species across this phylogeny contradicts the predictions of the coevolutionary scenarios entertained by many evolutionary ecologists. According to these scenarios, as species coexisted with their hosts for longer periods of time, counteradaptations in the host would reduce the number of hosts that the parasite could utilize successfully over evolutionary time. Rothstein et al. (1997) criticized Lanyon's interpretation, pointing out that more primitive taxa could have been in contact with their host species for a longer period of time, thus losing host species as predicted by the co-evolution hypothesis. Regardless of its outcome, this issue has stimulated a healthy debate, which emphasizes the validity of the homology approach. It causes us to *focus carefully on the characters of interest and on the lineage of interest* and to think logically and explicitly about what kinds of forces may have produced the observed character distribution in that lineage.

Thus far I have glossed over the importance of constructing a phylogenetic tree. No evolutionary comparative analysis can be any better than the phylogenetic tree upon which it is

based. Unfortunately, the construction of a tree is not easy. There are many different types of data, each of which requires different assumptions in its analysis and different analytical methods. Cladistic methods involve many important decisions about character coding and weighting and combination of data sets, and the methods are being refined all the time. Also, increasing numbers of non-cladistic methods of increasing sophistication are being applied, especially to molecular data. In short, if you need a tree and are not a systematist, I suggest that you get help. However, I encourage population biologists and behavioral ecologists to get involved in the process of tree construction because it can be extremely informative. Not only is it interesting in its own right, but anyone who has worked on building a tree understands the limitations of that tree.

One more caveat should be made clear: *phylogenetic hypotheses are historical.* Each group of organisms has only one history, and the best we can do is to construct a hypothesis for its phylogeny. We can never subject phylogenetic hypotheses to experimental tests in the sense that we can test ecological hypotheses. We can add new information to an analysis to improve the resolution or robustness of a phylogenetic tree or of a character mapping. But ultimately we cannot do a manipulative experimental test. Equally frustrating for population biologists is the fact that phylogenetic analysis is relatively resistant to statistical evaluation. Clearly, we could deal with evolution statistically if we understood the evolutionary process. However, in a phylogenetic tree of any given size, it is likely that the blend of potential causative factors for character evolution has been different within every single lineage it contains. Thus, the search for one common statistical model of evolution for any group of organisms may be severely handicapped from the start. We may just need to accept from the outset that we will never know absolutely the history of a group or its characters, and we need to be cautious in our phylogenetic interpretations.

LIFE-HISTORY VARIATION IN SWALLOWS

For many years I have been interested in swallows, most specifically Tree Swallows (*Tachycineta bicolor*), but I have always felt that, in order to understand the ecology of one organism, it is valuable to consider the ecologies of its relatives. Swallows are an excellent group in which to interpret life histories using comparative methods. They are extremely conservative in their overall morphology and foraging ecology, but they are quite diverse in their nesting biology. Beginning in the mid-1980s, I have been working with Frederick Sheldon to study the phylogenetic relationships of swallows using DNA-hybridization (Sheldon and Winkler 1993), and we have been joined in mitochondrial sequencing work by Linda Whittingham (Sheldon et al. 1999).

Once we started getting phylogenetic trees, the phylogenetic hypotheses allowed us to make inferences about ancestral character states and the history of character change. There are three main clades of swallows (Fig. 2): (1) the African sawwings, (2) what we call the "core martins," and (3) a group consisting of *Hirundo* and its allies. Nest construction is more variable in the swallows than it is among any other family of oscine passerine birds; the nest construction of each of the terminal taxa is indicated on Figure 2. Species of swallows range from burrowers through a large group of cavity-adopters to mud-nesters that build either a simple cup, a closed cup, or a retort-shaped nest. Figure 2 also shows a reconstruction of ancestral characters for nest construction. A sense of how ancestral characters are inferred can be gained by considering the group of *Hirundo* and its allies. Notice that these species all make nests of mud, and within this lineage of "mud-nesters" we have plotted the reconstructions to indicate that cup-construction was the primitive state which gave rise to forms that made closed cups, which in turn gave rise to forms that made retorts. The strategy of ancestral character-state reconstruction is to minimize the number of changes in character state on the tree while producing the observed distribution of character states among the terminal taxa. In this particular case, for instance, the same number of steps (i.e., two steps from a primitive state to closed cup and retort) is obtained by assuming that the ancestral type was a retort: that a retort-maker gave rise to a cup-nester; that a retort-maker also gave rise to a closed-cup nester; and that the retort nest in the derived species represents the retention of the primitive character state. To circumvent this ambiguity of character state reconstruction, we observed that retort-nesting swallows, when they
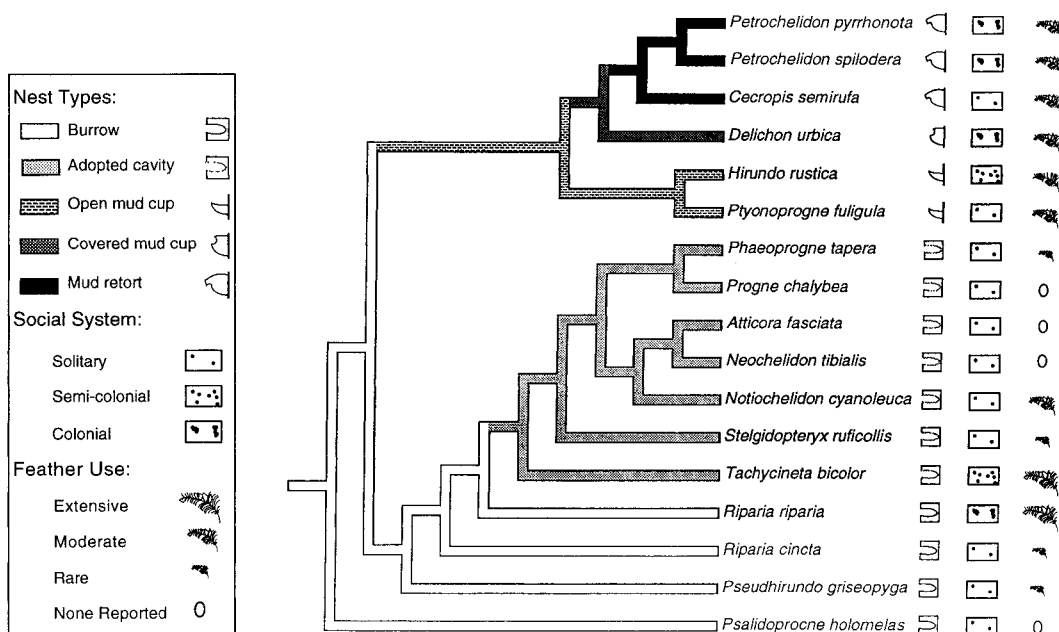
FIGURE 2.   Sheldon and Winkler's (1993) DNA-hybridization phylogeny of most of the putative genera of swallows, with the type of nest built by each taxon as well as their putative ancestors. Terminal character states for nest sociality and feather nest-lining, respectively, are added to the right of the terminal taxa. English names of taxa in tree, from bottom to top, are: Black Sawwing, Gray-rumped Swallow, Banded Martin, Sand Martin (Bank Swallow), Tree Swallow, Southern Rough-winged Swallow, Blue-and-white Swallow, White-thighed Swallow, White-banded Swallow, Gray-breasted Martin, Brown-chested Martin, Rock Martin, Barn Swallow, House Martin, Rufous-chested Swallow, South African Cliff Swallow, Cliff Swallow.

build their nests, proceed from a cup-shaped nest stage to a closed-cup stage, and then finish with a retort (Winkler and Sheldon 1993). We assumed that nest evolution proceeded in the same sequence of steps as does nest construction today. Character state reconstruction can be much more complicated (Cunningham et al. 1998), even for nests (Sheldon and Winkler 1999, Zyskowski and Prum 1999).

When characters are mapped on a phylogeny, we usually see immediately that different characters vary on the tree in different ways. For example, Figure 2 shows ancestral character state reconstructions for nest type, along with terminal states for sociality. The latter character has states ranging from territorial solitary nesters through semi-colonial nesters to colonial nesters. However, the distribution of these types is not so concordant with the tree as is nest construction. Specifically, highly colonial forms occur among both mud-nesters and burrowers. Elsewhere, Winkler and Sheldon (1993) have speculated about the origins of nest coloniality and how it relates to nest construction, and this

is an active area of research for us. Here the homology approach becomes very interesting: when we can examine the covariation of several traits on a tree and consider whether changes in one character state may have been antecedent to changes in another, we can begin to draw conclusions about the relative adaptive linkages between these different character states (Coddington 1988, 1994).

Tree Swallows line their nests with the feathers of other species (Winkler 1993), and mapping the use of feathers as nest-lining on the tree across the entire family (Fig. 2) is instructive. Like sociality, the distribution of the use of feathers in the phylogenetic tree is not concordant with the structure of the tree. Most of the mud-nesting swallows appear to use moderate numbers of feathers, although I think even this generalization might fall apart if we look carefully at more species. Within the cavity-adopters, there is generally relatively little use of feathers, although they are sometimes used by *Phaeoprogne* and *Stelgidopteryx*. But in *Notiochelidon,* they are used moderately, and in

Tachycineta bicolor and other *Tachycineta* species, they are used quite extensively. Within the burrowers, feathers tend not to be used much except in the Bank Swallow (*Riparia riparia*), which uses them extensively. There are a couple of points that I would like to make here. First, character coding can be extremely subjective, as the variation of this continuous character can be of two types: whether or not the birds use feathers at all, and if they do use feathers, how many feathers they use. For many species we have very few data, so it is hard to assign a character state for sure. Furthermore, if feather use had been scored in Figure 2 as a 2-state character instead of a 4-state character, the pattern of character variation on the phylogenetic tree would be very different.

The phylogenetic approach forces us to think hard about characters of interest and how we define character states. It also forces us to think hard about homologies across the group of interest. Consider the case of feather use by Tree Swallows and Bank Swallows, species which likely have independent evolutionary origins. In Tree Swallows, the feathers are placed in the nest lining with the feather shafts pushed down into the base of the nest and the vanes of the feathers overlapping so that the feathers form a discrete and continuous boundary between the nest contents and the grass nest itself. In well-feathered nests, the rachises of those feathers extend up and actually curve over the top of the nest so that it forms a canopy. Based on research done with Scott Turner, we know that this nest canopy is probably very important for thermoregulation in the nest (unpubl. data). In contrast, the Bank Swallow nest is essentially a flat platform at the back of the burrow on which feathers are placed rather haphazardly; there is none of the secondary structure that we see in Tree Swallow nests. The homology approach forced me to think carefully not only about whether or not the birds use feathers, but about the details of how they use feathers. It made me realize that the similarity in this character is likely convergent rather than homologous. This again, to me, is a great strength of the homology approach.

The phylogenetic approach, and especially the homology approach, highlights the inadequacies in our knowledge of groups of interest. For life-history traits, it is no accident that clutch size is the trait that has been subjected to most analysis over the years because clutch size is one of the few life-history traits one can measure in a collection. And it is one of the few life-history traits for which the quantification of the trait is fairly unequivocal. As soon as one attempts comparative analyses of life-history trait variation, one sees the need for more quantitative data on life-history variation among birds—such as is generated by the BBIRD program (Martin et al. 1997)—replicated with appropriate measurements for many groups of species around the world.

There has been an important debate over whether or not characters are phylogenetically constrained (Antonovics and van Tienderen 1991, McKitrick 1993), and the cladistic approach to tree construction causes one to realize that how we think about a character depends on our perspective within the tree. When one views the tree for swallows from the root looking out toward the branch tips, nest construction appears to be a flexible character, having changed many times during the diversification of this group. However, viewed from a branch tip back toward the root, nest construction appears quite conservative, having undergone few changes, and with no evidence of character reversal, over the history of a single lineage. Once a nest character has changed in this phylogeny of swallows (and it has very seldom changed), it has never gone back to its former state in the evolution of a lineage. So, even though nest-construction is quite variable when viewed from the root up, from the tips-down nest-construction appears conservative. So where do we stand on this notion of phylogenetic constraint? There is no strong evidence at any point in this tree of binding organismal constraints that have prevented evolutionary change in nest construction. Rather, at every step along the way there has been a blend of selective factors that has subjected nest construction to stabilizing selection. Occasionally, when swallows have colonized new habitats, stabilizing selection may have turned to directional selection and new modes of nest construction may have arisen. "Phylogenetic constraint" is too-strong a phrase that summarizes the history-dependency of character-state variation, and only by looking at a tree can we get a feel for the heritage of selective environments that have affected different characters. With a phylogenetic approach, one need not jump to the conclusion that a hard genetic constraint or lack of time for change has caused a trait's changes

to follow phylogeny. The phylogeny gives us a framework for evaluating the hypothesis that trait variation is the result of selection for "multiple adaptive peaks." Each character has an independent history, and we can view organisms as a suite of characters, each of which takes its own independent evolutionary path in responding to both the environment and to changes in other characters of the organism. Thus phylogenies, by teaching us about the histories of characters, can help us understand connections between life-history traits and responses to selective pressures.

One example of this has been extremely instructive to me in my studies of Tree Swallows. I believe that cavity adoption, which is the mode of nest construction in Tree Swallows, arose from an evolutionary heritage in which, for good selective reasons, nest-construction was a relatively conservative trait (Winkler and Sheldon 1994). Once cavity adoption existed, however, it could act as a selective influence on other characters. For example, I believe that cavity adoption selected for earlier breeding in Tree Swallows and more aggressive social behavior (Fig. 3). Earlier breeding has, in turn, led to selection for extensive feather nest-lining (for insulation) which has fed back on aggressive social behavior through competition for feathers. Earlier timing of breeding directly influences clutch size, chick survival and recruitment, and the feather lining has implications for chick growth. These four factors together are the principal contributors to fitness variation in Tree Swallows.

Notice that in considering interactions between characters and the influence of their variation on fitness, one shifts from between-species comparisons to between-individual comparisons, what some regard as the difference between macroevolution and microevolution. The transition between studying variation among species in character means and dissecting out individual contributions to variance in a life-history trait is an exciting and valuable aspect of the study of life-history variation. The comparative approach provides the phylogenetic foundation that makes us aware of this transition.

DISPERSAL AS A LIFE HISTORY TRAIT

When we think about micro- and macroevolutionary forces acting upon trait variation at the same time, it leads to some very interesting conceptual challenges. Consider for a moment an-
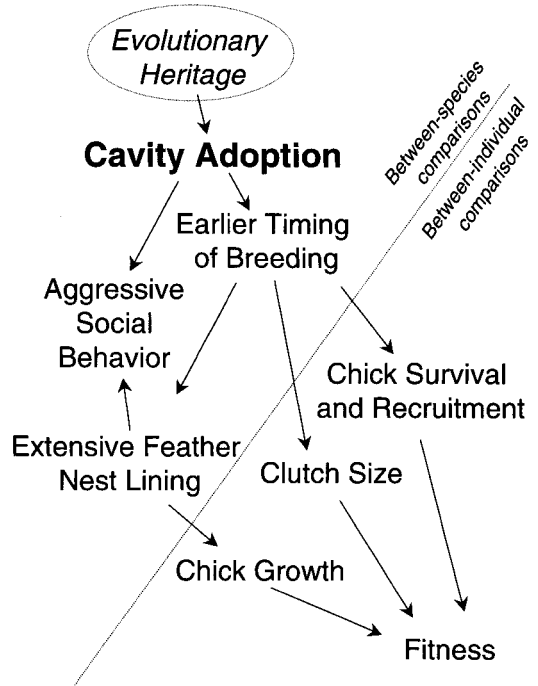

FIGURE 3.   A personal view of the connections between early-season life-history traits in Tree Swallows. For details see text.

other life-history trait that is of great interest: dispersal. Studies to date have been microevolutionary, but dispersal also can be approached from a macroevolutionary perspective. Levey and Stiles (1992) have suggested that long-distance seasonal migratory movements arose from seasonal food-driven shifts in distribution: does the same sort of gradation link aseasonal nomadic life styles with the shorter once-in-a-lifetime dispersal movements between natal and breeding sites that we observe in most birds? The fact that extreme nomadic dispersers are limited to a few phylogenetic groups (e.g., waxwings, Cardueline finches, and Australian honeyeaters) suggests that such a simple selective shift to nomadism is difficult to achieve. However, phylogenetic information is increasing for these groups, and it would be very interesting to see what their phylogenies can tell us about the interaction of ecological and organismal forces in the evolution of patterns of dispersal. There may also be some interesting feedbacks between dispersal and both speciation and extinction. Ornithologists might profitably follow the lead of Jablonski (1986) and Hansen (1978), who have

shown that patterns of extinction and speciation in gastropods can be affected strongly by the dispersal mode of their larvae. This is a fascinating case where the evolution of a life history trait at the micro level can have important effects on the macroevolution of the group.

CONCLUSIONS

The phylogenetic approach places organismal biology in a rich historical context. It helps us to clarify the likely roles of micro- and macroevolutionary forces on the evolution of any given character. I am often reminded of a joke that Fred Adler (a mathematician) once had on his office wall. Beneath a picture of a giraffe were the words "This is an organism; usually denoted X." In the context of life-history variation in birds, I feel that much of our failure to make progress in the elaboration and testing of life-history theory has been that we have often left organismal biology out of the mix. We have often thought we could have a life-history theory that applies equally well to blue whales and fruit flies. While the basic tenets of life-history theory must pertain to any animal population, a great deal of what we find of interest in life-history variation in animals includes a rich blend of the effects over history of both macro- and microevolutionary forces acting on character-state variation. By encouraging us to think carefully about many life-history traits and their interactions, comparative approaches bring the organism back into life-history studies. Comparative approaches will be an important tool for investigating life-history variation for a long time to come. They cannot replace detailed studies within single populations, but I see them as a necessary complement.

ACKNOWLEDGMENTS

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