

# Lifestyles and phylogeny explain bird life histories

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The evolution of life cycles, or life histories, is one of the most fascinating stories of Darwinian evolution. Natural selection has produced a stunning array of life histories, from tiny, rapidly multiplying bacteria and yeast to the large, long-lived albatrosses that produce only one egg every 2 y (1, 2). Life histories consist of species-specific vital rates: information about growth, reproduction, and survival. These species-specific traits describe the diversity of life and have strong associations with major events in the lives of organisms, such as metamorphosis and the onset of sexual maturity. In addition, such traits describe the fitness differences among individuals that produce evolutionary change, whether by natural selection, genetic drift, or other mechanisms of organic evolution. The genetic principles by which life-history traits translate into evolutionary change are the subject of quantitative genetics, a field that has produced insights into the way in which changes in such “fitness traits” within populations are produced by ecological processes (3, 4). For example, predation can favor a shortened juvenile period, leading to early maturity, increased reproduction, and shorter life span (5).

To discern the broad sweep of life histories across the amazing complexity of biological diversity, however, study of short-term genetic changes within populations may not be enough. Thus, ecologists and evolutionary biologists have turned to broad comparisons of many species, to view the evolutionary course of development of the diversity of life cycles (6). Given the complexity of this diversification, many attempts to find generality have failed. For example, the well-known hypothesis of *r*-*K* selection (7) was a generalization that was pleasing for a time, but then fell into disrepute, at least in part because there were so many exceptions to its predictions (1, 8). A subsequent paradigm has developed, however, that reflects general principles concerning the diversity of life histories. The first element of this paradigm uses the vast variation in body size among organisms, based on what are known as “mouse-to-elephant curves” that show the scaling of traits to body size (9–11). Some of the most basic changes in life cycles are due to the fact that it takes longer for larger organisms to develop than it does for smaller organisms. Thus, life spans are longer for larger species. If

the further assumption is made that life is a “zero sum game,” then long life (high “somatic” effort) should trade off with low reproductive rates (low reproductive effort) (12).

The second element of the life-history paradigm is also about the tempo of life, but focuses on shorter and longer lives when the influences of body size are taken into account (13–16). This “fast–slow

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continuum” reveals shorter and longer lives at a given body size and is thought to be due to extrinsic mortality differences among species. Thus, if mortality, especially juvenile mortality, were greater, the typical life span of a species should be shorter. Applying the zero sum game assumption, such species should balance shorter lives with greater reproductive rates. This element of the life-history paradigm does not specify the source of mortality and reflects a long concentration on demographic mechanisms within populations, rather than aspects of ecology of species (17). The next step in extending the life-history paradigm was the link to the environment and the discovery that different lifestyles could lead to similar life-history patterns (18). This insight came with a slight shift in focus from mortality to reproduction; but the upshot is that the “lifestyle hypothesis” replaces the fast–slow continuum as an explanation of variation in life histories, beyond that caused by differences among species in body size (19).

The lifestyle hypothesis is a “break-through” improvement in life-history theory, but it still does not use the full power of the comparative method for understanding a broad array of species. Previous advances in life-history theory have often ignored the use of the tree of life as a powerful predictive tool or have only partially used history by comparing major groups of organisms like the Families and

Orders of mammals (e.g., refs. 20 and 21). A major test of the lifestyle hypothesis by Sibly et al. (in PNAS) (22) uses close to 1,000 species of birds to examine the lifestyle hypothesis with explicit predictions. They also make a prediction about the constraining influence of historical time periods, specifically that an association of lifestyles and life histories should be conserved within closely related groups of species. To test this expectation, they have produced a supertree for the bird species and ask whether syndromes of lifestyles occurred in the ancestors of contemporary birds. The production of this supertree is a major achievement itself, but it is put to good use for testing the lifestyle hypothesis.

To examine the second axis of life history, the lifestyle, it is necessary to statistically control for body size. Changes in timing of life associated with body size need to be accounted for before changes in tempo due to lifestyles can be seen (19). It is these latter changes that the lifestyle hypothesis purports to explain. In addition, the tree of life can be used to study life histories in two ways: by making predictions about how lifestyles might be constrained over evolutionary history and by removing phylogenetic influences statistically to reveal “phylogeny-free” patterns. Sibly et al. do both. First, they use their supertree of the birds to ask whether there is strong phylogenetic signal in size-adjusted reproduction (termed “production”) of the bird species and find very strong historical influence on this important life-history and fitness trait. They illustrate the effect by showing how different orders of birds exhibit significantly different patterns of productivity for their body size.

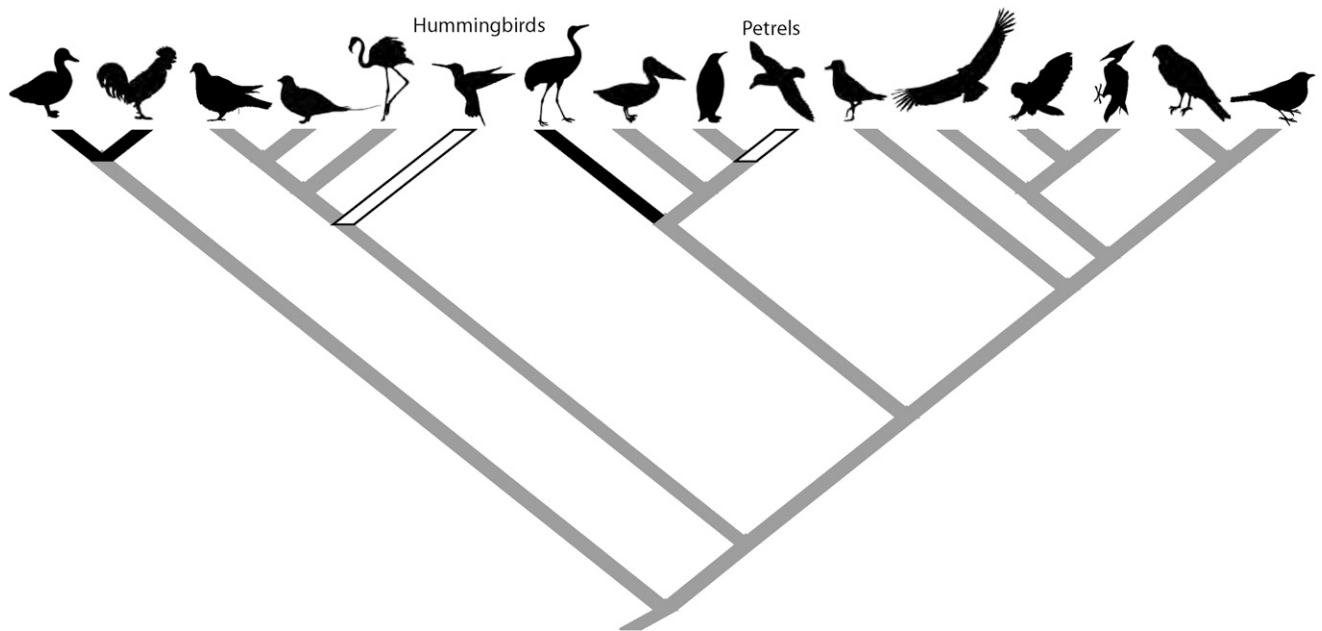
Second, they use a phylogenetic regression approach to statistically control for both body size and phylogeny, producing a test of the association of reproduction with several lifestyle traits. The body-size axis of life history has a strong influence on reproduction. However, in addition, several basic aspects of bird lifestyles were strong influences on reproduction, that is, the production of offspring: (i) Altricial species are less

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**Fig. 1.** Stylized phylogram of the birds, with silhouettes representing different Orders. The open branches are to Orders with especially low reproductive rates for their body size (i.e., low relative productivity), with examples of species (hummingbirds, petrels) labeled. The solid branches are Orders with especially high productivity, and other orders (shaded branches) show middling productivity.

productive than precocial species; (ii) monogamous species are less productive than cooperative breeders; (iii) resident species are less productive than migratory ones; (iv) several diet types differ, with nectar feeders the least productive; and (v) pelagic species are generally less productive than other birds. Different combinations of these variables can produce similar levels of reproductive investment and by extension similar life histories. For example, hummingbirds and petrels are exceedingly different in body size, diet, and habitat, but they both have low productivity lifestyles (associated with nectar feeding and pelagic foraging, respectively) and thus relatively low reproductive rates for their body size (Fig. 1).

Thus, the connection between the ecologies of the species, the historical similarities within groups of birds (e.g., albatrosses and petrels all lay only one egg at a time) (23), and the body size of the species interact to produce “syndromes” of life histories. These syndromes may appear similar for species that are in different high- or low-productivity environments or niches, but species in each productivity situation should have similar life histories. Life-history syndromes may change slowly over evolutionary time, producing guilds of species that share not only similarities of morphology and feeding styles, but also life histories. At the same time, niche expansion into high- or low-productivity environments should produce similar life

histories among divergent taxa through the process of evolutionary convergence, and in birds, Orders appear to provide good examples of this convergence. Further analyses of lifestyles in a variety of niches are likely to reveal those that promote or retard reproduction. Also, the scale at which life history is studied might also be expanded beyond “just birds” or “just mammals” as is common in past analyses. Eventually, testable hypotheses to explain variation in life cycles of such different organisms as bacteria and albatrosses might be produced!

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