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OVERVIEWS

RECONSTRUCTING THE EVOLUTIONARY ORIGIN OF POLYGYNY IN RED-WINGED BLACKBIRDS

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ONE OF THE CENTRAL GOALS of evolutionary biology is to explain the morphological and behavioral diversity that exists today. This challenge is particularly difficult for those of us interested in the evolution of behavior because by and large, behaviors do not fossilize. Thus, one cannot excavate through a few horizons and trace the historical record leading back from a modern behavior to its ancestral precursors. As a consequence, those studying the evolution of social behavior have been restricted mainly to examining the function of behavioral traits in extant populations. Such studies can yield important insights into the selective pressures shaping and maintaining particular behaviors. However, the origins of these behaviors are difficult to identify because the ecological and social milieu within which the trait evolved may be quite different from that which we see today. Such difficulties are particularly true for complex social behaviors that are likely to coevolve with other behaviors. For example, birds of many colonial-nesting species may obtain information from their colony mates regarding the location of unpredictable food resources (Brown 1986, Greene 1987). Does this mean that coloniality initially evolved in order for individuals to obtain such information, or that species nesting in colonies have secondarily evolved the capacity to take advantage of information from colony mates?

Recent advances in the analytical tools available for comparative analyses (see Brooks and McLennan 1991, Harvey and Pagel 1991) have made it possible to tackle these chicken-or-egg questions. Specifically, phylogenetic approaches are being used to reconstruct the character states, including behavioral characters, of ancestral species (e.g. Winkler and Sheldon 1993, Ryan and Rand 1995, Lee et al. 1996). Such reconstructions provide a crystal ball with which we can look back in time and address questions about the early origin of complex behaviors. In this issue of *The Auk*, Searcy et al. (1999) adopt this approach to reconstruct the ecological and social conditions under which social polygyny (i.e. multiple females pairing with a single male) originated in the ancestors of modern-day Red-winged Blackbirds (*Agelaius phoeniceus*).

The Red-winged Blackbird, a common North American species easily recognized by even the most casual birdwatcher, has a highly developed polygynous mating system. Male redwings defend territories, primarily in marshes, within which females construct nests and lay eggs. Polygyny is pronounced in all temperate-latitude populations that have been studied, and successful males in many populations can attract several mates, whereas other males remain bachelors throughout the breeding season

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(Searcy and Yasukawa 1995). In this respect, redwings are very different from most birds, the vast majority of which appear to be socially monogamous (the recent discovery of extrapair copulations, of course, is leading to a reappraisal of the genetic mating system of most birds).

Social polygyny has long posed something of a puzzle to behavioral ecologists. Although males are likely to benefit reproductively from such a social system, it is less clear that females will benefit. Indeed, females choosing to pair with an already-mated male face the likely possibility of reduced parental assistance, because the male will have to divide his parental duties among multiple nests and may even direct most of his care to the nest of his first mate (Verner and Willson 1966, Orians 1969). Several potential benefits may accrue to a secondary female that pairs with an already-mated male, including characteristics of the territory (e.g. safe nesting sites or abundant food resources) and male (e.g. "good genes" that may be passed on to the offspring), and possibly benefits of nesting near other females (e.g. group nest defense). Although these potential benefits may be important in some situations, none is automatic, and each is likely to be relatively small in most situations. Thus, because secondary females incur the cost of reduced parental assistance and relatively few benefits, social polygyny is expected to be rare and should evolve only when the costs of reduced male assistance are unusually low, or the benefits of nesting on the territory of an already-mated male are unusually high (Orians 1969, Altmann et al. 1977, Searcy and Yasukawa 1989, Webster 1991).

The Red-winged Blackbird is something of a "lab rat" for field ornithologists and has become the model system for studies of avian polygyny. Of the dozens of studies that have examined the causes and consequences of redwing polygyny across North America, most have provided support for a "low cost" model for the maintenance of polygyny (Searcy and Yasukawa 1989). That is, male redwings provide relatively little care, even at the nests of their primary mates, so the loss of male parental assistance appears to be of little consequence to a secondary female (Searcy and Yasukawa 1995). Thus, females are expected to pay little attention to the mating status of prospective mates and instead nest on territories that are (for example) relatively safe from predators.

But, as Searcy et al. (1999) correctly point out, therein lies the rub in understanding the *origin* of polygyny in redwings, because male parental care and polygyny are likely to coevolve. Specifically, as opportunities for polygynous matings increase, males are expected to invest more time and energy in mate attraction and less in parental care (Webster 1991). As polygyny develops, the cost to secondary females will decrease, leading to an even higher rate of polygyny and a lower dependence by females on male parental assistance. Thus, it is very difficult to draw conclusions about the early evolution of polygyny through detailed studies of extant populations (Searcy and Yasukawa 1995). Because polygyny and male parental care are likely to have evolved in concert, how can we understand the early evolution of such a system? Can we identify the ecological and social factors that are likely to have pushed the "proto-redwings" onto the coevolutionary trajectory that led to the well-developed polygynous mating system we see today?

To address these questions, Searcy et al. (1999) use a molecular phylogeny recently developed by Scott Lanyon from mitochondrial (cytochrome *b*) sequence data to examine the evolution of territorial polygyny in the lineage leading to Red-winged Blackbirds. They propose two alternative hypotheses for the early origin of redwing polygyny, each of which makes a different prediction about the behavior and ecology of the monogamous ancestor of modern redwings. Under one scenario, the ancestor resembled a modern-day monogamous *Agelaius*, such as the Yellow-shouldered Blackbird (*A. thilius*), in being marsh nesting but nonterritorial, and polygyny evolved through an increase in male territoriality. Under the alternative scenario, males of the ancestral species were territorial (like most modern songbirds) and did not nest in marshes, and the evolution of polygynous mating was triggered by a switch to nesting in marshes. By mapping information onto the molecular phylogeny, Searcy et al. found that the most-parsimonious description of the ancestral species is that proposed by the latter hypothesis; i.e. the monogamous ancestor of the Red-winged Blackbird appears to have been a territorial species that did not nest in marshes and in which parental duties were distributed relatively equitably between the sexes. Moreover, as predicted by the hypothesis that mating behavior and male parental care are likely to evolve in concert, polygyny and reduced male parental care were found to arise simultaneously at the same point on the phylogeny. In the end, Searcy et al. convincingly reject the model of an *Agelaius*-like monogamous ancestor and give some support to the hypothesis that polygyny in Red-winged Blackbirds was triggered by a switch to breeding in marshes rather than by an increase in territoriality. The apparent behavioral difference between ancestral redwings and modern *Agelaius* in South America also supports recent molecular evidence that the genus *Agelaius* is a polyphyletic pseudo-group rather than a monophyletic group of closely related species (Lanyon 1994).

Although painting a portrait of the probable ancestor of polygynous Red-winged Blackbirds, the study by Searcy et al. (1999) also points out several substantial gaps in our knowledge. First, Searcy et al. restrict their analysis to a subset of the subfamily Icterinae (grackles and their allies), because an unresolved polytomy at the base of the tree makes it difficult to include the other clades. Additional molecular data may help further resolve the phylogeny such that the entire subfamily could be analyzed. A fuller analysis would allow the emergence of a more general picture of the ecological and social traits that characterize the origins of polygyny (see Temrin and Sillén-Tullberg 1994). Second, the mapping of several traits onto the phylogeny (e.g. parental care patterns) resulted in several equivocal branches. This is in part due to the nature of parsimony analyses, but it is clear that a lack of knowledge about the basic natural history of many species hindered the analysis. Clearly, our knowledge of many species (e.g. those living in South America) is woefully inadequate, and more field studies of extant species will be necessary before general conclusions can be drawn.

Like any good study, Searcy et al.'s (1999) raises as many questions as it answers. For example, what is it about nesting in marshes that promoted polygyny in redwings? Is it that food abundance reduces the need for male parental care, or does the patchy nature of such nesting habitats increase the potential for polygynous matings (see Webster 1991)? Might safe nesting sites or group defense against predators be involved? If nesting in marshes promotes polygyny, then why are some marsh-nesting blackbirds, particularly those in South America, monogamous? And if nesting in marshes promotes polygyny in blackbirds, does it also do so in marsh-nesting species from other avian families? Finally, polygyny has arisen in several species of blackbirds that do not nest in marshes (Orians 1985, Robinson 1986, Webster 1992). Might the proximate factors that promote polygyny in these species be similar to those that do so in marsh-nesting redwings? The answers to these and similar questions likely will not arrive until we plug the gaps in knowledge that are outlined above.

The improved phylogenetic tools now available for comparative studies allow us to do more than statistically control for the confounding effects of history. Indeed, these tools enable us to gaze back in time and reconstruct the probable characteristics of species long gone. This backward-gazing crystal ball allows us to test competing hypotheses about the origin of complex behavioral traits. However, the reception on this crystal ball is a bit fuzzy, and we sometimes are not able to determine some of the key ancestral character states. In part, the clarity will improve with improved phylogenies and additional information about key extant species. However, the lack of clarity is also partially due to the analytical tools currently available, because they are unable to distinguish among competing historical scenarios that are deemed equally parsimonious. Additional advances in the analytical tools available to comparative biologists will further sharpen the clarity with which we can gaze back at our ancestral world.

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