

CHAPTER

18

Comparative Behavioral and Biochemical Studies of Bowerbirds, and the Evolution of Bower-Building

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Unprecedented human-induced changes in the environment are causing a rapid loss of species and their habitats. Common responses to the loss of biodiversity include habitat conservation and increased efforts to understand the origin and maintenance of biodiversity. While there is no doubt that these are critical activities, it is unclear the extent to which these and related conservation approaches can stem the tide of extinctions. Global threats such as climatic warming and ozone depletion place all species on the planet at risk and complicate attempts to determine the level of threat for particular species or communities.

There must be an intensive effort to collect information about species before they go extinct or are relegated to reserves in degraded habitats. Otherwise, we never will have detailed information about the life history, specialized adaptations, social behavior, or relationships with other species for the vast majority of species that go extinct. For those left close to extinction in degraded habitats, in zoos, or in preserves, our ability to understand their ecological and evolutionary relationships to other species and the surrounding habitat will be greatly compromised.

Wilson (1992) describes “unmined riches” locked in the diverse and poorly known biotas. He offers recent discoveries of natural seed stocks and the use of secondary compounds from plants as pharmaceutical agents as examples of such riches. But biologists have been less emphatic about the unmined intellectual resources that are lost with extinction. As species go extinct and habitats are degraded, the opportunity to use natural communities as sources of information about basic physiological, ecological, and evolutionary processes is lost forever.

As with basic research in other areas, the natural historical sciences also offer prospects for unforeseen intellectual and economically important discoveries.

The grim prospect of the loss of much biodiversity is tempered somewhat by the availability of many well-trained experts in a variety of natural historical fields, by the maturation of these fields in which intellectually significant issues have been identified, and the explosion of new tools to decode the information locked up in natural systems. Molecular methods for phylogenetic reconstruction, methodologies for comparative studies, and automated equipment that allows collection of data on diverse sorts of organisms all are becoming available and are being put to use in field studies. It is a sad coincidence that, as we are gaining sophisticated tools for exploring the natural history of organisms, there is a dramatic loss of species that can be studied. We are at a critical time when we have the opportunity to collect some of the most detailed and useful natural history information before many species go extinct. A broadly based biodiversity initiative that emphasizes both conservation and natural historical studies directed at species in still vibrant populations must be considered the only appropriate response to the loss of biodiversity.

EVOLUTION OF BOWERBIRDS

In this Chapter, I present information from a comparative study of bowerbirds (Ptilonorhynchidae) on the likely causes of the evolution of bowers. This work has been motivated by an interest in the causes of mate choice in species with extreme displays. It serves to illustrate the importance of studies that involve comparisons between species.

Bowerbirds occur across the Australio-Papuan region and are unique in that males build structures on the ground called bowers that appear to function in mate attraction and related activities. The first 7 years of my work on bowerbirds focused on the satin bowerbird (*Ptilonorhynchus violaceus*). Previously, there had been no detailed quantitative study of any aspect of bowerbird behavior. After those 7 years, I felt that I had a good understanding of typical bowerbird behavior. This belief was shaken after a preliminary study of spotted bowerbirds (*Chlamydera maculata*) that showed fundamentally different patterns of courtship and male interactions from those observed in satin bowerbirds. Since then, my students and I have studied nine additional species of bowerbirds.

As an example demonstrating the value of comparative studies involving a large number of species, this work shows that even among closely related species there can be very large differences in behavior. One cannot characterize a group like bowerbirds based on studies of single species, and there is no typical species that fully represents this group. Information from numerous species often is needed to understand the evolution of complex traits like bower-building.



Bower bird moving through undergrowth.

Mate selection in species with elaborate male display traits was a topic central to Charles Darwin's (1859, 1871) seminal writings on sexual selection. Prominent in his discussion of sexual selection were the bowerbirds and their unique behavior of building bowers. Bowders typically are made of sticks. In some species, bowders can reach 1.5 m high and are built near display courts decorated with more than 2,000 decorations. These elaborate decorated structures frequently have been described as one of the wonders of the animal world.

There are now numerous hypotheses explaining how extreme displays evolve, although clear answers remain elusive. "Good genes" models propose that extreme sexual displays function as indicators of male quality to females choosing mates (e.g., Andersson, 1982, 1986; Borgia, 1979; Hamilton and Zuk, 1982; Trivers, 1972; Zahavi, 1975). Alternatively, the runaway model (Fisher, 1930; Kirkpatrick, 1982; also see Lande, 1981) posits that female preferences can produce greatly elaborated male display traits without providing enhanced vigor to offspring. Other models include: passive choice (Andersson, 1982; Parker, 1983), intrasexual signaling (Halliday, 1978; LeCroy et al., 1980), proximate benefits (e.g., protection to females provided by well-constructed bowders; Borgia et al., 1985) and innate preferences (Burley, 1985; Kirkpatrick, 1987; Ryan et al., 1990).

Recent empirical studies have shown that elaborate displays in polygynous species are typically not single traits, but a complex sets of traits (Andersson, 1989; Borgia, 1985; Gibson et al., 1991; McDonald, 1989; Moller and Pomiankowski, 1993; Prum, 1990; Zuk et al., 1990). In bowerbirds, bowders and decorations are part of a generalized display that includes plumage, acoustical,

and dancing elements directed at females during courtship. Recent studies indicate that females prefer males with well-built and well-decorated bowers (Borgia, 1985; Borgia and Mueller, 1992), indicating that an important current function of bowers and decorations is to attract mates. The large number of models for explaining elaborated display traits, the lack of specific predictions from some of these models, and the complex array of traits involved in the display of polygynous species have made it difficult to develop clear-cut conclusions about the evolution of extreme male displays. Elsewhere it has been suggested (Borgia et al., 1985) that bowers may function in female assessment of male quality as sires (good genes), as a protective device for females being courted (proximate benefit), or as a structure with no direct functional significance outside the context of sexual selection (runaway or latent preference).

Comparative studies of the evolution of traits among related species can provide critical information about the sequential evolution of the components of display and their initial and derivative functions (Basolo, 1990; Brooks and McLennan, 1991; Kusmierski et al., 1993; Prum, 1990).

Several recent developments have made it possible to carry out a detailed comparative analysis of the function of bowers. First, the use of remote-controlled cameras aimed at bowers where males display and mate has allowed my students, field assistants, and me to simultaneously monitor all activity at as many as 30 bowers through an entire mating season. Because bowers are widely separated and the mating periods may last several months, it would have been impossible otherwise to obtain detailed information from numerous bowers. Second, the advent of molecular techniques has made it possible to build a phylogeny of bowerbirds based on mitochondrial DNA sequence information. The independent derivation of this phylogeny makes it possible to infer the historical pattern of the evolution of display traits by using maximum parsimony methods to map the distribution of particular male display traits and their occurrence in ancestors onto the phylogeny. By combining these techniques, my students, collaborators, and I have been able to gather detailed information on the display traits of bowerbirds and map this information onto an independently derived phylogeny of the bowerbirds.

Building bowers is restricted to the family Ptilonorhynchidae, which is made up of six genera. One genus, the catbirds (*Ailuroedus*, three species), is monogamous and does not clear a display court. Members of the remaining five genera are polygynous, clear a court, and typically build a bower. There are two major designs of bowers. Maypole bower-builders decorate a sapling with sticks. Males of species in the genus *Amblyornis* (four species) typically decorate a single spire surrounded by a mossy circular court, and two species build a hut-like dome that covers part of the court. *Prionodura newtoniana* builds a two-spired structure with a cross perch connecting the spires. Avenue-builders (three genera, eight species) build a two-walled structure with a display court near the end of the bower. Two other species, toothbills (*Scenopoeetes dentirostris*)

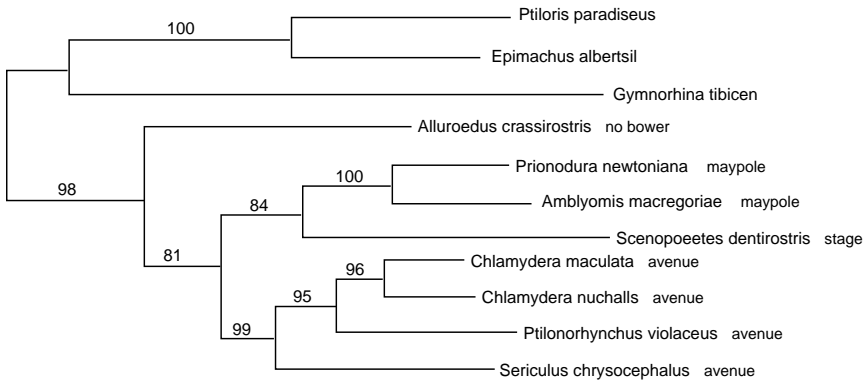


FIGURE 18-1 Phylogeny of the bowerbirds based on information from mt-DNA sequences taken from Kusmierski et al. (1993). The topmost grouping represents two Birds of Paradise (paradise riflebird and the brown sickelbill) and the Australian magpie. The bowerbirds are represented in three clades represented by the monogamous catbirds (*Alluroedus*) that build no bower, the maypole-builders (including the toothbill bowerbird, *Scenopoeetes dentirostris*), and the avenue-builders. Recent results (Kusmierski, personal communication, 1995) indicate that Archibold's bowerbird (*Archboldia papauensis*) is a member of the clade that builds maypoles. Like *Scenopoeetes* in the same clade, the most probable pattern of evolution is that Archibold's bowerbird has lost its tendencies to build bowers and these losses are independent. Numbers at nodes represents the percentage of times a group occurred in 1,000 bootstrap replicates.

and Archibold's (*Archboldia papauensis*), clear display courts but do not build a characteristic bower.

A phylogeny based on sequences of mitochondrial DNA from the cytochrome-b gene, developed in cooperation with Kusmierski and Crozier (Kusmierski et al., 1993), indicates that there was an initial separation of lineages that led to the monogamous catbirds and the remaining polygynous species. Later, a separation in the clade that led to bower-builders produced a lineage that led to the avenue-builders, and another that produced the maypole-builders (*Archboldia* and *Prionodura*) and the two polygynous species that do not build bowers (*S. dentirostris* and *A. papauensis*) (Figure 18-1). Because building bowers is the dominant pattern in both lineages and it occurs in no other avian family, it most likely evolved once, preceding the split of the ancestors of the avenue- and maypole-builders.

HYPOTHESES FOR THE EVOLUTION OF BOWERS

Many of the models of the evolution of extreme displays can be used to develop specific models for the origin and evolution of bowers. For example, the placement of sticks in an incipient bower could have been the result of an

arbitrary female preference (as part of a runaway or latent preference model). Such a hypothesis, however, posits no particular functional role for bowers apart from mate attraction and fails, by itself, to account for the variation in form of bowers. Evidence of a function for bowers, especially if it is consistent among different types of bowers, would weigh against this hypothesis.

Another possibility is that bowers could have functioned to provide protection from various threats (Borgia et al., 1985). Sources of threat include predators that might attack males and females, marauding males that force copulations on females while they view the court owner's courtship, and court owner himself forcing copulations on females not ready to mate.

The hypotheses of predation and marauding-males are not well supported. There is no evidence of predation on females or males while males are displaying on courts in more than 100,000 hours that cameras monitored the display courts of males. This is especially relevant because, in most species, males are not protected from predators by the bower during courtship. In addition, females are not protected in some types of bowers, including the open bowers of MacGregor's bowerbird (*Amblyornis macgregoriae*, which may be similar to ancestral bowers) and those of the streaked bowerbird (where the male occupies the covered part of the bower during courtship, opposite to what is predicted by the female protection hypothesis; Sejkora and Borgia, in preparation). Last, females change their behavior from being very reluctant to stand outside the bower before copulation to being quite willing to stand there afterward. The observations that many types of bowers do not confer protection, that the sexes stand in the wrong place, and that the female's behavior changes after copulation also fail to support the hypothesis that bowers provide protection from marauding males.

The remaining hypothesis, protection from the courting male, is not limited by these difficulties. Species from the two clades that build bowers show generally similar patterns of how they use bowers during courtships that lead to copulations. In both lineages, males display facing the female. The bower enhances the female's ability to escape unwanted matings by blocking the male's direct path to her and forcing him to run around the wall of the bower or maypole to mate. The increased distance that males must travel to reach a female enhances her ability to escape unwanted matings.

Several issues emerge in attempts to evaluate this hypothesis. First, why should males build a structure that decreases their prospects of forced copulation? If males are programmed to maximize their reproduction and forced copulations can contribute to their reproductive success, it at first seems counterintuitive for males to build a structure that limits this type of reproductive benefit. A plausible solution is that building bowers may offer a compensating benefit that outweighs losses from forced copulation. If the reduced threat of forced copulation causes more females to be attracted to courts with bowers than those without, then gains from increased visitation by females could more

than compensate for the lost ability to force copulations with females. Female attraction might arise for several reasons, as discussed above.

Second, how do we test the hypothesis that females prefer males with bowers that function to protect them from forced copulation? It is rather tricky to infer the function of a trait at its evolutionary origin, given no fossils or other record of the ancestral form of the bower. Information from observations of the different species of bowerbirds and knowledge of their evolutionary relationships can be used to establish likely hypotheses. The criteria that would strongly support a hypothesis for an incipient function of bowers are: (1) the proposed function should be consistent with the design of the likely ancestral bower, (2) this function should be significant across all types of bowers, and (3) species that do not build bowers should show alternative solutions to the problem solved by the bower. There is no guarantee that even the correct answer will meet all three criteria. It is possible, for example, that bowers could have taken on a variety of secondary functions that have replaced the incipient function of the bower.

In the following section, I present descriptions of courtship for four species, two with bowers and two without. Examples from two different types of bowers, avenue and maypole, illustrate how these bowers are used in courtship. The species described here characterize a modal type in their clades. For each, there are related species that show widely divergent behaviors but which are consistent with the use of the bower for protection.

Display in the Satin Bowerbird: An Avenue-Builder

Satin bowerbirds (*Ptilonorhynchus violaceus*) are representative of species that build avenues. They occur in rain forests that fringe eastern Australia. The bowers of satin bowerbirds have two walls of sticks separated by a central avenue where females stand and then crouch when they are courted. The bower is aligned in a north-south direction with a decorated display court on the north end. The male displays while facing the female from the display court with a decoration held in his beak.

The females visiting the bower and the court typically alight in the vegetation on the south side of the bower and then move directly into the avenue of the bower. Initial vocalizations consist of numerous guttural chortles and squeaks that progress into a typical call sequence that consists of an initial mechanical buzzing followed by mimicry of a kookaburra (*Declio gigas*), a Lewin's honeyeater (*Meliphaga lewinii*), and less frequently, a crow (*Corvus*) (Loffredo and Borgia, 1986). The buzzes in the mechanical calls occur in conjunction with rapid movements by the male across the north entrance of the bower accompanied by flicks of one or both of his wings.

Females signal their willingness to copulate by lowering from an upright stance to a crouch. To copulate, the male circles to the opposite side of the

bower to mount the female. After a brief (3-second) copulation, the female shakes intermittently in or near the bower for up to several minutes and then leaves. Females usually visit the bowers of several males, but mates with only one. The average courtship lasts slightly more than 4 minutes.

In satin bowerbirds and other avenue-builders, most courtships end with the female leaving from the north entrance of the bower as the male moves from the court toward the south entrance in his attempt to copulate. Only 9% of satin bowerbird's courtships are successful, although the most attractive males mate in 25% of their courtships. There is a significant relationship between the number of decorations and the mating success of males, indicating that it is important for females to enter the bower and see the display in order to assess the males.

Display in Macgregor's Bowerbird: A Maypole-Builder

Macgregor's bowerbird (*A. macgregoriae*) occurs at high elevations in the mountain ranges across central and eastern New Guinea. Its bower is a simple maypole, a sapling decorated with sticks and moss. Commonly, the sapling is rather thin and sticks are placed nearly horizontally, increasing the diameter around the sapling to approximately 25 cm. The low part of the maypole and the floor of the round court surrounding it are covered with a fine compressed moss mat that rises to form a circular rim approximately 40 cm from the may-



Bower of MacGregor's bowerbird.

pole. Many small decorations are used on the court, including insect parts and seed pods. Regurgitated fruit pulp is hung near the ends of the sticks of the maypole bower. Numerous large woody black fungi are arrayed on the rim of the court and on nearby logs.

Females arriving for courtship often land on the maypole, move down it, and then hop onto the court. The male usually is already present on the court and may have been calling prior to the female's arrival. The male positions himself on the opposite side of the maypole from the female with his chest pressed up against it and with his head plume concealed. He calls and, as the female moves around the maypole, he makes a counter move so as to keep the bower between him and her. Calling and counter moves continue for approximately 4 minutes before the male increases the intensity of display by expanding his bright orange head plume and violently shaking his head from side to side. The side-to-side shaking is associated with a rapid foot movement that appears to counterbalance the rapid movement of his head. Seen from the female's side of the bower, this display creates rapid orange flashes on each side of the maypole. After several bouts of head-shaking, the male moves around the bower toward the female in an attempt to copulate with her.

Although the shape of avenue and maypole bowers is fundamentally different, there is a striking similarity between maypole bowers and those of avenue-builders in the way in which the bower is used to separate the male and female. In each case, the male develops a prolonged courtship display. He watches the female and, when she signals her readiness to mate by crouching, he moves around the bower to mount her. If the female is not prepared to copulate, the bower serves as a dodge that allows her to leave from the opposite side from where the male is approaching.

Display in Toothbill Bowerbirds: No Bower with Leks

Toothbill bowerbird courtship is very different from that of other species of bowerbirds. Males clear courts but do not build bowers. Male courts are close together and aggregated into a lek (a group of displaying males not associated with resources needed by females). Males interact with frequent loud calls, with dominant males interrupting the calls of males on adjacent courts. Unlike other bowerbirds, they use large objects (e.g., leaves) as decorations on their courts. Courts surround several trees of small diameter, the bases of which have been cleaned meticulously of debris.

Females arrive on the court and stand very still, as if waiting for the male. Toothbill courtship is very brief. The male aggressively mounts the female with little or no display after she arrives on the court. The average time of courtship is 3.8 seconds. However, copulations are prolonged and violent relative to the brief and more cooperative behavior seen in other species. During these copulatory bouts, the male continues to display with characteristic low buzzing calls

and wing beats. Females leave the court immediately after mating without the prolonged flapping of wings that is characteristic of other species.

By far, toothbill males spend less time on their court than any other species, and it appears that the adjustments in their display and mating behavior reflect an especially high susceptibility to predation while they are on the ground. The aggressive nature of the courtship suggests that females might not be fully prepared to copulate when they arrive, but the need to reduce time on the ground has caused males to attempt to speed this process.

The loud vocal interactions of males on courts and the use of large decorations suggest that females can evaluate male qualities such as dominance before they arrive on the court. At lek centers, males that preliminary studies show are dominant in vocal interactions have the highest mating success. This correlation suggests that females are choosing mates. Observations by Cliff and Dawn Frith (1993) and our group show that males hiding behind a tree on their court sometimes call to females on nearby perches. However, we have not seen this calling lead to copulation.

In toothbills, if male calling interactions and large leaves allow females to choose mates before they arrive on the courts, then bowers may not be necessary. The female already may have selected the male before arriving at his court, so the prospect of forced copulation is not threatening. The capture of females by males indicates that forced copulations are possible in bowerbirds. The hiding of males behind trees during calling displays suggests a situation analogous to the initial condition of bower evolution in which females seek some protection from the courting male.

Archibold's Bowerbird: No Bower and No Lek

Archibold's bowerbird (*Archboldia papuensis*) is the other polygynous species that does not build a bower. Male Archibold's clear a large display court overlain with a mat of ferns where males place a variety of decorations, including snail shells, dark fruit, beetle wings, and King of Saxon Bird-of-Paradise (*Pteridophora alberti*) head plumes. Typically, small decorations are in piles near the fringes of the display court and are arrayed on the limbs overhanging the court. Male Archibold's bowerbirds neatly drape limbs that cross up to 1.5 m above the display court with a uniform curtain of flowerless orchid vines that nearly touch the display court and subdivide it. The cumulative array of the curtains provides a rather dramatic visual effect.

Male Archibold's bowerbirds are large and uniformly black, with a bright yellow head crest that extends from between the eyes, over the top of the head, to the neck. The crest covers more area on the bird's head than the crests in species of *Amblyornis*, but the individual plumes are much shorter.

Courtship in Archibold's bowerbird also is unique. Males chase females around the court. Occasionally the female pauses, and the male stops near her

and attempts to approach her with his body pressed close to the court. If the male is successful in approaching her, he faces toward the female with his head near the ground. He emits a chattering call and rapidly moves his head with slight side-to-side movements. If the female does not move after the initial frontal display, he slowly moves behind her while maintaining a position near the ground and then rises up to copulate. Copulation is brief and lasts only 3 seconds, as is typical for all bowerbirds except toothbills.

In Archibold's bowerbird, courtship is not constrained to a particular site, as it is in species with bowers. The preliminary phase of courtship involves chases about the court, and the large size of the court may accommodate these chases. The walls may function in constraining the direction females can move.

Male Archibold's bowerbirds have evolved an alternative solution to the problem of copulating with females in the absence of a bower. Unlike toothbills, they do not interact over long distances or have leks, and they do not attempt to grab and copulate females by force. Like most other bowerbirds, they have prolonged courtship and frequent female rejections, suggesting that choice occurs on the display court. The low position of males during courtship does not compromise the female's ability to escape the courting male, even when he is nearby.

One explanation for the loss of bower-building in Archibold's bowerbird may be related to the widely ranging displays that females use to test males. In most species of bowerbirds, males can be directly compared because they compete by stealing their competitor's decorations and destroying their bowers. Visiting females may assess male competitive ability by the quality of his display (Borgia, 1985; Borgia et al., 1985). In *Archboldia*, the bowers are spread very far apart, and the possibility of male interaction is low. The frequent chases may be a means by which females test male athleticism. Elsewhere I have suggested that intense displays which span large areas in male spotted bowerbirds function similarly for female assessment (Borgia and Mueller, 1992; Borgia, 1995). In *Archboldia*, where the bowers of males are spread apart in small forest islands, there may be a similar need for males to demonstrate fitness in athletic rather than interactive components of display. Comparisons among all of the species of bowerbirds that I have studied indicate that the two species with interbower distances of >700 m (*Archboldia* and *Chlomydera maculata*) have especially large display courts and male displays that range over these courts, whereas the displays of the remaining nine species with bowers that are closer together have relatively small courts and male display is restricted to these courts ($\chi^2=3.14$, $df=10$, $p=0.02$).

A MODEL FOR THE EVOLUTION OF BOWERS

The hypothesis that protection from the courting male is important in the evolution of bowers is supported by the patterns of evolution in bowers and its consistency with the diversity of types of bowers. The ancestor to the lineage

that led to modern species that build bowers probably displayed on a decorated ground court. Females favored courts with a natural barrier, such as a sapling, that separated them from males during courtship because it allowed them to approach the male and closely observe his display and decorations while still retaining the ability to leave if not stimulated by the display. Males who enhanced this barrier, e.g., placed sticks around the sapling and enlarged its diameter, offered females a safer vantage point for observing display. Males could gain from this elaboration by exploiting the female preference for mating in a protected environment. Increased female visitation and lessened threat during courtship contributed to an overall increase in matings over what might be achieved by forced copulations. Gains for females from the avoidance of forced copulations might include eschewal of genetically inferior males and reduction of direct physical costs (e.g., parasite transmission and time lost in remating). Remating of females which have been forced to copulate with other males would lower the value of forced copulations to court owners and may have caused males to shift efforts toward attraction of females.

The simple bower described above is similar to the bower built by MacGregor's bowerbird. Once the tendency to use sticks to build a bower evolved, however, it was possible to build a bower that functioned in female protection but did not require a central sapling. The loss of dependence on the use of saplings could have allowed males more freedom in selecting sites for bowers, in orienting their decorations, and in displaying their decorations. The ancestors of avenue-builders probably added a second barrier because it oriented females toward illuminated parts of the court where males could concentrate their decorations on a well-lit stage. The orientation of bowers in a north-south direction, the consistent placement of most decorations on the north side, and the clearing of leaves over display courts support this hypothesis.

This hypothesis is consistent with all types of bower-construction and our observations of how bowers are used in courtship. In both avenue and maypole bowers, males are forced to run around a barrier in order to reach the rear of the female where they can copulate. The delay caused by this extra traveling time gives females an opportunity to escape males that are unattractive to them. The behavior of the two species that do not build bowers also is consistent with the protection hypothesis. In toothbills, there is no bower, but because females appear to move to the ground for copulation only after they make their mating decision, they leave the court without mating proportionately less often than females in other species (Borgia, in preparation). In Archibold's bowerbird, by lying close to the ground as they approach females, males are not threatening as forced copulators.

CONCLUSIONS

We rarely can be sure about the evolutionary origins of a trait, but we can use information from comparisons among extant species to formulate reasonable

hypotheses. In the case of the hypothesis that bowers provide protection from courting males, the great diversity of behaviors among species of bowerbirds with very consistent elements within species gives surprisingly strong support for this hypothesis of the origins of bower-building. This work has the added benefit of suggesting an important role for models of proximate benefit in explaining elaborated male traits. This work could not have been accomplished had the number of species of bowerbirds available to study been limited by extinctions. This places an immediate imperative on carrying out detailed comparative studies of behavior before there are large reductions in numbers of species. It also suggests that attempts to preserve representative species may not be productive because there are no typical species.

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