

Why Do Bowerbirds Build Bowers?

Females prefer to visit courtship areas that provide easy avenues of escape, thereby protecting them from forced copulations

Gerald Borgia

Male bowerbirds of Australia and New Guinea clear and decorate courts and build bowers at display sites where they mate. Bowerbird species, however, differ in several characteristics, including the type and color of court decorations and the form of a bower, if one is even built. Moreover, some male bowerbirds possess bright crest and body plumages, and others do not. Charles Darwin's observations of satin bowerbirds—in the Blue Mountains of Australia during his round-the-world journey on the HMS *Beagle*—contributed to the then-controversial central element of his theory of sexual selection called female choice. The highly sculptured structure of a bower and a male's use of brightly colored decorations suggested to Darwin that female bowerbirds might shop for the most attractive bower, thereby directing the evolution of these display traits.

Nevertheless, several other mechanisms could have driven the evolution of bowers. The so-called good-genes model, for instance, suggests that male-display traits, including bowers, might indicate a male's vigor and, ultimately, his quality as a sire. That is, more vigorous males might have better bowers. A bower could even directly benefit a female, perhaps protecting her from threats, including predators that might attack her during mating or

males that might try to force her to copulate. Bower building could even arise from an arbitrary or pre-existing female preference, such as an attraction to nest-like structures.

I have used Darwin's method of comparisons of related species to reconstruct the evolution of bower building. My work on several species of bowerbirds confirms the existence of female preferences for males with well-built and highly decorated bowers. The origins of bower building, however, can be best explained as a trait that attracts females because of the protection it provides them from forced copulation by bower owners.

Evaluating Bower-Building Hypotheses Picking one model of bower-building evolution over another proves difficult because of several problems. One cannot always reconstruct what happened long ago, especially for display behavior that leaves no fossil record. Moreover, bower building may have evolved over a period of time, and different stages of its evolution may have served different functions. Although experiments can show the plausibility of a particular evolutionary process, understanding the origins of traits can best be accomplished by careful comparisons between species whose relationships are known.

Such an analysis depends on accurate and detailed descriptions of bowers and how they are used in courtship in modern species. Obtaining detailed quantitative information on courtship and mating through direct observation proves nearly impossible, because bowers are separated widely, the mating period may last several months and a large proportion of males do not or rarely copulate. Remote-controlled cameras aimed at bowers where males perform their dis-

plays and mate, however, have allowed intensive monitoring of more than 30 bowers for a single species through an entire mating season. That information has provided a direct measurement of male attractiveness and detailed information on how males and females use a bower during courtship. For most of the species that my colleagues and I have studied, we were the first to see these bowerbirds perform successful courtships, which ended in copulation.

By comparing mitochondrial DNA sequences, my colleagues, Robert Kusmierski and Ross Crozier, and I have developed a highly reliable bowerbird phylogeny, which shows evolutionary relationships among species. Our phylogeny indicates, in contrast to some earlier speculation, that all 18 species of bowerbirds evolved from a single ancestral species. Three species branched off from others long ago, and they employ the predominant avian pattern of monogamy with both parents caring for their offspring. All other bowerbirds are polygynous (males mate with more than one female), and they create elaborately decorated display courts. All but two of the polygynous species build bowers. The second major divergence developed between species that build avenue bowers—two vertical stick walls, separated by a central avenue—and those that build maypole bowers—sticks woven around a sapling to create a decorated pillar. It appears that bower building evolved once and then diverged into two types of bowers. The two species that do not build bowers, toothbill and Archbold's bowerbirds, apparently lost bower-building behavior, but they do clear and decorate display courts. Comparisons of bowers and relationships among living species suggest that a

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R. Brown, Vireo

Figure 1. Male bowerbirds build bowers, where they court and mate with females. Some species, such as this satin bowerbird, build avenue bowers, made of two freestanding stick walls. Others build maypole bowers, in which sticks are placed around a central sapling (Figure 3). In addition, a male may decorate his bower with a variety of objects, including the pieces of blue plastic shown here. This complex behavior of building and decorating prompts a fundamental question: How did it evolve?

decorated sapling—similar to a simple maypole bower—may represent the ancestral bower type.

Several criteria can be used to evaluate hypotheses for bower evolution based on mating behavior and the evolutionary relationships among species. To the extent that these criteria are met, we can identify the likely initial causes of bower building. First, the proposed function of incipient bowers should be consistent with the design of the supposed ancestral bower. That is, the bower type that appears most consistent with the ancestral bower type should be capable of functioning in accordance with the hypothesized cause of bower origins. Second, the proposed function of the earliest bowers should be consistent with the design of modern bower types. The persistence of bower building among the polygynous species suggests that ancestral functions may remain important. If a consistent function exists for modern bowers, it would be a likely candidate for the ancestral function. Third, species that do not build bowers should possess alternative solutions to the prob-

lem solved by a bower. These species should possess compensatory behaviors, which work in the absence of a bower to protect females from forced copulations by the courting male.

Avenue-Bower Builders

The group of avenue-bower builders consists of three genera and eight species, including the satin bowerbird. Satins inhabit rain forests along the



Figure 2. Inside an avenue bower, a female satin bowerbird observes a male's courtship display. A male flits back and forth across the avenue opening, flicks his wings, mimics the calls of other birds and performs other displays. When a male runs to the rear entrance of the avenue to mate with a female, she either waits to copulate or departs through the front opening.



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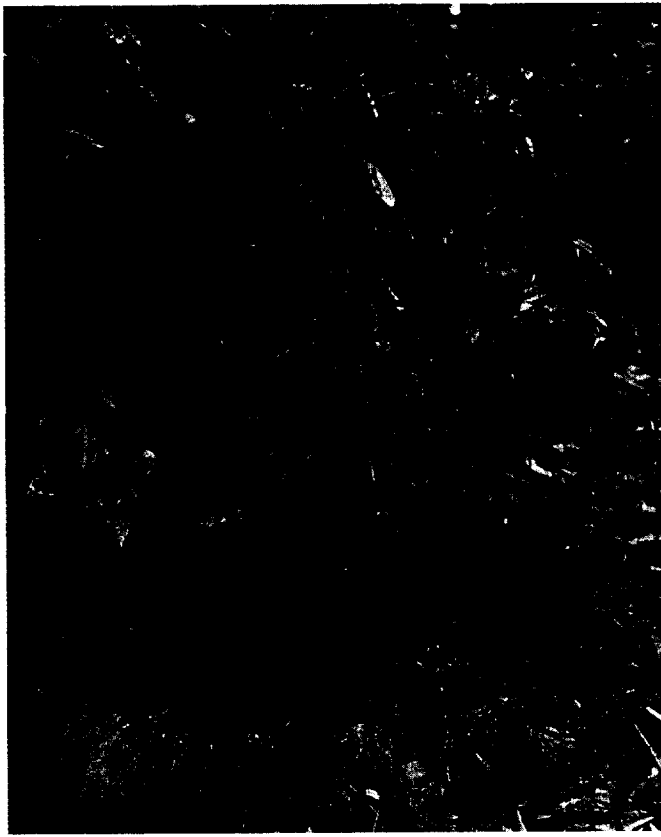
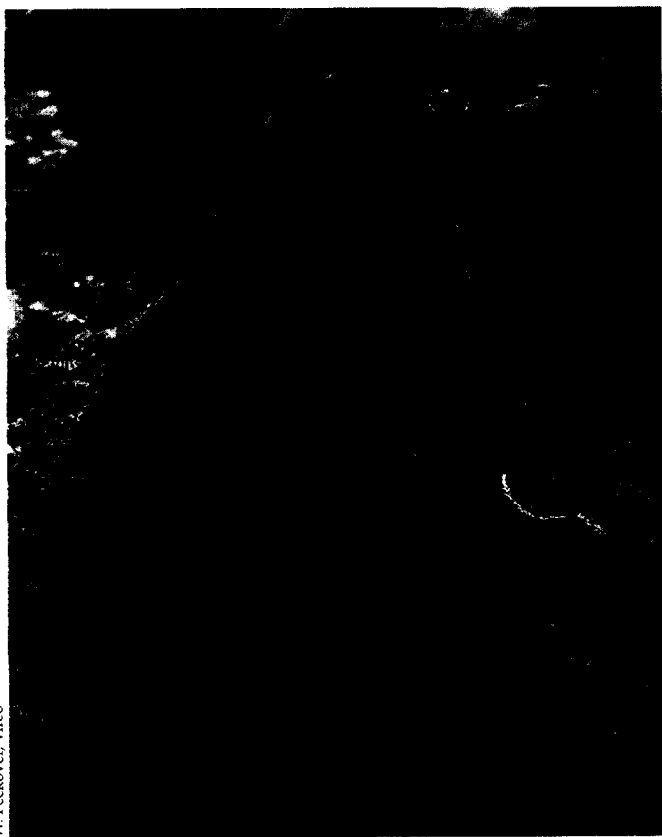


Figure 3. Macgregor's bowerbird (*left*) constructs the simplest maypole bower (*right*). A male selects a thin sapling, stacks sticks around it and covers a surrounding display court with a compressed-moss mat. In addition, he decorates the court.

eastern fringe of Australia. A male aligns his bower along a north-south line, with a display court at the north end. He decorates his display court with blue, yellow and white objects including feathers, flowers, leaves, snail shells and, where available, plastic and paper, over a background of yellow straw. The male trims leaves from above the court, and the northern orientation causes the sun to illuminate the decorated site, perhaps making it more attractive. Males of several species destroy each other's bowers and steal decorations.

A visiting female usually lands in cover south of the bower and then moves rapidly into the avenue between the two stick walls. On the display court, a male makes vocalizations, including guttural chortles and squeaks that progress into a typical call sequence: initial mechanical buzzing followed by mimicking a kookaburra, a Lewin's honeyeater and less frequently a crow. During the buzzing, a male moves swiftly across the northern bower entrance and rapidly flicks one or both wings. When he begins mimicking other birds, he stops at one side of the bower entrance, puffs up his body feathers, holds his wings at his side,

faces the female with a small decoration—usually a yellow leaf—in his mouth and performs a series of knee bends. After that, he usually moves away from the bower, makes several harsh calls and then returns to the bower for more displaying.

In courtships that lead to copulation, a female in the bower avenue crouches deeply as courtship progresses, and a slight lifting of her tail signals her willingness for mating. A male circles around to the opposite end of the bower and mounts her for a three-second copulation. After mating, a female shakes and flaps her wings in or near the bower for a few minutes before leaving. Although a female may visit several bowers, she usually mates with only one male. The average courtship lasts about four minutes. If a male moves to the southern end of a bower before the female is ready, she escapes through the northern exit.

Females exert strong preferences in mating, and only a small proportion of males achieve most of the matings. Males with high quality bowers—with symmetrical walls formed from thin, densely packed sticks—and many decorations on their courts mate most often. Although only nine percent of

satin courtships lead to copulation, the most attractive males mate in 25 percent of their courtships. The higher rate of courtship success by specific males, the significant effect of small decorations and the fine details of bowers on mating success, and the changes in a female's behavior that indicate her readiness to mate after she arrives at the male bower indicate that a female makes her mating decisions after she arrives at the court.

Maypole-Bower Builders

The other major group of bower builders make maypole bowers—a central "pole" surrounded by a circular display court. Some maypole builders cover part of the display court with a hut-like structure. The simplest structure, however, comes from Macgregor's bowerbird, which lives at high elevations in the mountains of central and eastern New Guinea. It decorates a sapling with sticks and moss. This bower may be most similar to the ancestral one for all bowerbird species.

A male Macgregor's bowerbird selects a thin sapling, usually from three to six centimeters in diameter, and surrounds it with horizontal piles of sticks, which increase the pole's diameter to about 25

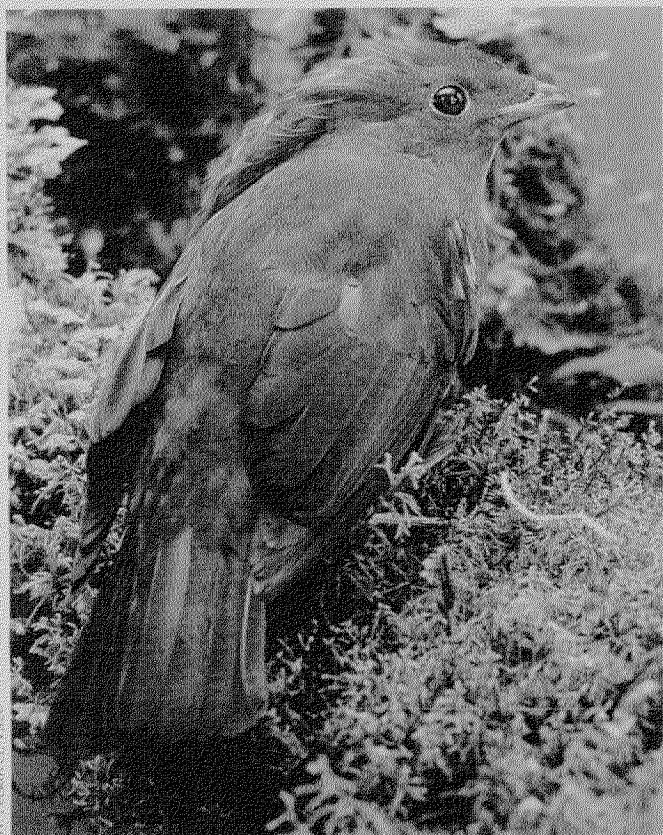


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centimeters. He covers the lower part of the maypole and the court floor with a fine compressed-moss mat that rises up to form a circular rim about 40 centimeters from the pole. He decorates the court with small objects including seeds, and he hangs regurgitated fruit pulp near the ends of the maypole sticks. On the court's rim and nearby logs, he adds woody black fungi.

We have observed young male Macgregor's bowerbirds clearing courts around the naked trunks of small trees. A selected tree's diameter usually approaches that of a fully developed maypole, which is much larger than the saplings selected by an adult male. This shows a functional correspondence between the trees used by young males and the size of maypoles built by adults.

A female arriving for courtship on an adult male's bower usually lands on the maypole and then hops down to the court. The male moves to the opposite side of the maypole with his chest close to it. He calls, and as the female moves around the maypole, he makes a countermove to keep the maypole between them. Calling, moving and counter moving go on for one to two minutes. Then the female stops moving, and the male expands his bright orange head plume and shakes his head from side to side, giving the female a view of rapid orange flashes on alternating sides of the maypole. While shaking his head, the male moves toward the female to copulate. In some cases, the male may charge the female without prolonged head shaking, causing her to escape around the opposite side of the maypole.

Bowerbirds without Bowers

Two species of bowerbirds, toothbill and Archbold's, clear and decorate courts, but they have lost their bower-building behavior. The unique mating tactics of each of these species suggest functional alternatives to bower building.

Archbold's bowerbird has lost bower-building behavior. Instead, it clears a display court that is about four meters long and 2.5 meters wide, and it covers the court with a thick mat of ferns. A male decorates his court with beetle wings, dark fruit, King of Saxon (a bird of paradise) head plumes and snail shells, and he places smaller decorations in piles near a court's edge and on limbs that overhang a court. A male also drapes orchid vines on numerous

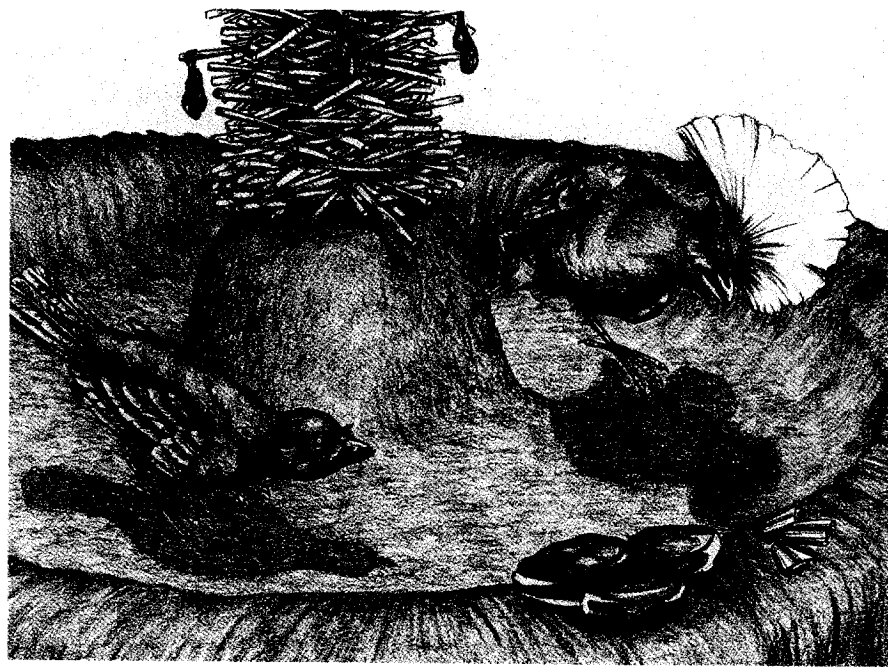


Figure 4. Macgregor's bowerbirds dodge around the maypole during courtship. A male calls, a female moves around the pole and the male makes a countermove to keep the pole between them. If a female wants to mate, she stops moving, allowing a male to approach her.

overhanging limbs, making a set of curtains that crisscross and nearly touch the display court.

Archbold's bowerbird courtship begins with a male chasing a court-visiting female. He flies and hops low, close to the court surface, beneath the vine curtains. After repeated chases, a female stops moving, apparently signaling the male that he may approach her. The male then presses his body close to the fern mat and moves toward the female. With his head near the ground, the male faces the female and makes a chattering call, during which he moves his head rapidly with slight side-to-side movements and occasionally jerks up his head and tail. If the female remains stationary after that frontal display, the male moves behind her, staying near the ground, and then rises rapidly to perform a brief copulation. The low position of the male held throughout courtship, in part assured by the low-hanging vine curtains, reduces his opportunity for forced copulations by jumping on the female.

Male toothbills clear courts that are about two meters in diameter. A court encompasses several small trees, and their bases are cleaned meticulously. Unlike other bowerbirds, a toothbill decorates its court with large objects: fresh leaves turned upside down so that their light undersides are showing. Although not visible from adjacent

courts, the courts of different males are aggregated, in a so-called *lek*, and are often less than 30 meters apart allowing them to interact through loud calls. Dominant males interrupt the calls of males on adjacent courts. In addition, toothbills spend little time on the ground and far less time on their courts than do other species. Males at the center of an aggregation—the birds that preliminary studies show to be dominant in vocal interactions—have the highest mating success.



Figure 5. Toothbill bowerbirds clear courts but do not build bowers. A male decorates his court with large leaves, which he turns upside down. The rectangular pieces of paper on this court were added in an experiment to test the colors of artificial objects males would use. (Photograph courtesy of the author.)

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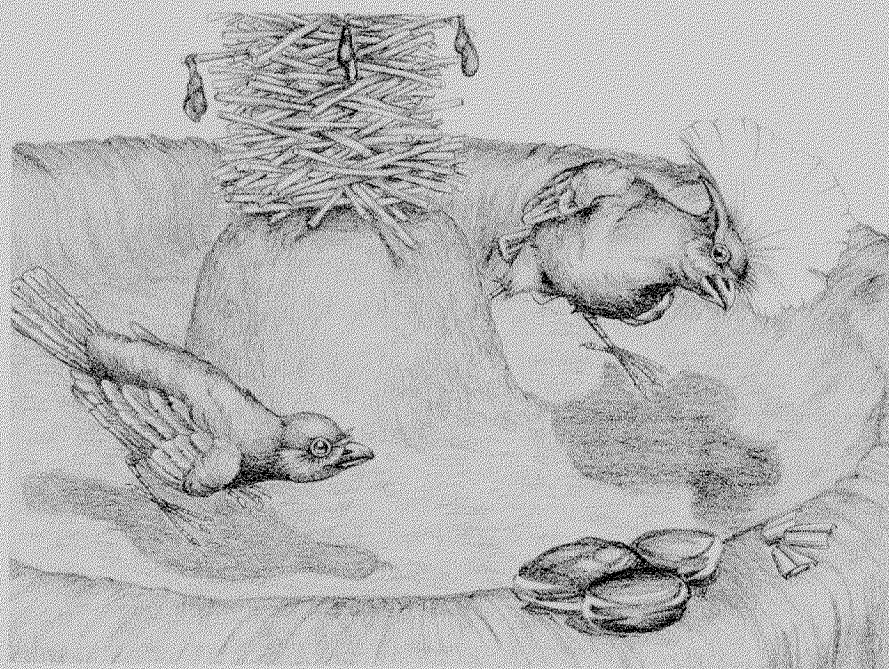


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Figure 6. Archbold's bowerbirds also build bowerless courts. A male approaches a court-visiting female with low-level flights or hops. He also makes calls and jerks his head from side to side. The female either remains stationary for mating or escapes.

During courting, a female arrives on the court and stands still, as if waiting for a male. After little or no display, the male aggressively mounts the female. The longest observed courtship lasted just 3.8 seconds. Toothbill copulation, however, lasts longer and appears violent compared with the brief and cooperative mating of other bowerbirds. During mating, a male toothbill makes low buzzing calls and beats his wings. After mating, a female leaves immediately. The use of exceptionally loud calls and large decorations and evidence of a female preference for central males on leks suggests that toothbill females may assess males before arriving on the court. If a female chooses a mate before arriving on a court,

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Why Build Bowers?

Although avenue and maypole bowers differ in form, observations of courtship behavior at bowers show that both provide a barrier that protects a visiting female from forced copulations by a courting male. Both avenue- and maypole-building males perform prolonged and active courtship displays. A male watches a female until she signals her readiness for mating, then he moves behind her to copulate. A female not prepared to mate can escape while an approaching male moves around a barrier created by a bower wall or maypole. A bower also allows a female to observe court decorations from close range with a reduced threat of forced copulation. The freedom from forced copulation offered by the bower may explain the high degree of elaboration of the decorated ground that has evolved in this group, including the use of small decorations on a ground court.

The two species that build courts without bowers offer alternative solutions to the problem of restricted mate choice because of forced copulation. Toothbill females select desirable mates before arriving on a court, so they do not need the protection of a bower. The low position of an Archbold's bowerbird male while courting allows a female to escape an unwanted copulation.

Males of many species gain reproductive success through forced copulation, so why would male bowerbirds build a structure that limits their opportunities for this behavior? The pro-

tection of a bower probably attracts females and increases their visitation, which more than compensates a male for losing forced copulations. Given that female bowerbirds choose the courts they visit, they should prefer the ones that provide protection from forced copulations. A female that freely chooses her mate should also be less likely to mate with another male. That combination of behaviors provides bower-building males with increased visitation by females and a high chance of being a female's only mate.

In some bowerbird species, males attack visiting females during courtship, and a bower might protect a female from such a threat. A maypole bower could serve that purpose. At avenue bowers, on the other hand, a male faces a female during courtship, so the bower offers no protection. Moreover, a female confined inside avenue-bower walls makes a susceptible target; she could only escape by moving backward, because the walls prevent her from moving sideways or turning around. If bowers served originally as protection against aggressive attacks from courting males, the evolution of the avenue bowers would require the loss of that function and replacement with others. Although the prostrate position taken by a courting male Archbold's may provide protection from attacks, no such behavior has been observed in toothbills. Overall, it seems unlikely that bowers initially evolved to protect females from attacks by males.

The good-genes hypothesis gains support from some observations, including the tendency of females to choose vigorous males and the intense, athletic displays of males in species with widely separated bowers. These characteristics, however, may derive from the origins of male courtship "dances" and vocal behavior rather than from bower building. In some modern species, a female might assess a male's genetic quality from his ability to maintain his bower in the face of destruction by rivals, but such a process seems unlikely early in the evolution of bower building, when only a few males had bowers. Assessing male quality by his bower probably arose as a secondary function after bower building evolved.

The so-called runaway model suggests that female preferences and male traits evolve together, driven by a mating advantage gained by males that possess



B. Chudleigh, Vireo

Figure 7. Great bowerbirds build avenue bowers and decorate them with green objects and shells. A male great bowerbird organizes the decorations strategically, such that they contrast with his lilac crest during his display. The combination of decorations and behavior may enhance a female's interest.



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The so-called runaway model suggests that female preferences and male traits evolve together, driven by a mating advantage gained by males that possess



B. Chudleigh/Viro

Figure 7. Great bowerbirds build avenue bowers and decorate them with green objects and shells. A male great bowerbird organizes the decorations strategically, such that they contrast with his lilac crest during his display. The combination of decorations and behavior may enhance a female's interest.

an extreme version of a trait, such as bower building. No evidence, though, suggests that males with large bowers mate more. In addition, recent versions of the runaway model expect high costs for a trait that confers a strong mating advantage. In an intense study of satin bowerbirds, I found no evidence of high cost, despite strong effects of bower quality on male mating success.

Several other hypotheses also lack support. The predation hypothesis seems unlikely, in part, because no example of predation on females or males appeared during more than 100,000 hours of monitoring bowerbird display courts in 10 species. That result proves especially relevant given that males of most species are not protected from predators during courtship. In addition, neither major bower type protects a female from behind, where a predator or a marauding male seeking forced copulation might approach.

Evolution of Bower Building

Determining the evolution of many traits requires an explanation of how incipient stages could be used. Our work suggests that the first bowers consisted of a sapling on a display court. If that is correct, why might a female prefer a male that has a sapling on his display court over ones with other attractive attributes that might benefit her or her offspring? Maybe females simply sought protected courts. A court with a natural barrier, such as a sapling, could separate a female from a courting male and allow her to closely observe the male's display and decorations without committing to mating.

By placing sticks around a sapling a male would be less constrained by sapling size and location. He could utilize a much wider range of saplings and ones in particularly suitable locations, by enhancing the diameter of a maypole to an appropriate size with a stick covering. In addition, the soft edge created by a stick maypole allows males and females to observe each other and anticipate each other's moves, which would be more difficult around a tree of equal diameter. In this scenario, stick-built bowers would have been an improvement on a previous practice of using natural barriers on courts. It might have begun with the rearrangement of fallen sticks that were already present to enhance a court's protective qualities and led to a simple maypole bower.

Once the tendency toward stick-built bowers evolved, two trends could emerge. First, bower form could diversify to serve other functions. Second, free-standing stick barriers would allow males even more freedom in selecting bower sites and in concentrating decorations in advantageous locations. The transition to avenue bowers required losing the use of a sapling as a bower support and the addition of a different barrier. The two-walled barrier oriented a female toward parts of a court where a male could concentrate his decorations on a well-lit stage and arrange the decorations to his best advantage. Many avenue-building males separate decoration types in zones around a bower in an apparently functional manner. Male avenue-building great bowerbirds, for example, place green objects beneath the spot where they display their lilac crest. The decorations are a complementary color to a male's crest and probably increase the contrast of his display. The hut-like cover on some maypole-bower courts also orients a female to a male's display.

No one knows whether bower building or decorating came first, but it appears that the development of complex bowers may have strongly influenced the use of decorations and the evolution of male plumage. The late E. Thomas Gilliard of the American Museum of Natural History argued that the degree of male head-crest elaboration correlates inversely with bower size and the number of decorations in maypole bowers. He suggested that plumage characteristics were transferred to the bower and its decorations, but offered no explanation for the transfer.

Observations of how bower shape constrains a male's display may reveal a relationship between plumage, bowers and display areas. Around the simple maypole of Macgregor's bowerbirds or the large bowerless court of Archbold's bowerbirds, decorations are spread widely around the bower. The males of both species possess well-developed crests, which they use actively during displays. That behavior contrasts with most avenue builders, which have either a reduced or no crest and build more complex bowers that orient a female toward a more limited area where decorations can be concentrated and kept in her view. In most polygynous avian species, including

bowerbirds with simple or no bowers, the position of males and females varies during displays, and for females to see bright colors males must carry bright plumage. In bowerbirds with more complex bowers, which focus a female's attention on concentrations of decorations, costly bright plumage may be replaced by strategically located arrays of decorations.

The combination of analyzing bowerbird behavior and constructing a phylogeny produces an unexpectedly coherent picture of bower function, despite the diversity in structural form. All types of bowerbird behavior indicate that females seek protection from unwanted mating. No other hypothesis proves consistent with current bower function, the function of a presumed ancestral bower and novel behavior in derived bowerless species. The significance of protection from a courting male suggests an important role for models that predict direct benefits that females might gain from elaborate male traits.

Acknowledgments

This research was supported by the National Science Foundation and the University of Maryland. The New South Wales and Queensland National Parks, The Australian Bird and Bat Banding Scheme, and the PNG Wildlife and Conservation Department provided permits. R. Crozier, J. Dimuda, G. Harrington, L. J., N. and M. Hayes, J. Lauridsen, M. J. Littlejohn, J. Kikkawa, M. Raga, J. Hook, and M. and J. Turnbull provided important support. C. Depkin, D. Bond, K. Collis, R. Condit, A. Day, J. Helms, I. Kaatz, C. Loffredo, J. Morales and D. Sejkora participated as team leaders and/or co-investigators. More than 100 volunteers provided excellent field assistance.

Bibliography

- Borgia, G. 1995. Threat reduction as a cause of differences in bower architecture, bower decoration and male display in two closely related bowerbirds *Chlamydera nuchalis* and *C. maculata*. *Emu* 95:1-12.
- Borgia, G. 1985. Bowlers as markers of male quality. Test of a hypothesis. *Animal Behavior* 35:266-271.
- Borgia, G., and U. Mueller. 1992. Bower destruction, decoration stealing, and female choice in the spotted bowerbird (*Chlamydera maculata*). *Emu* 92:11-18.
- Kusmiński, R., G. Borgia, R. Crozier and B. Chan. 1993. Molecular information on bowerbird phylogeny and the evolution of exaggerated male characters. *Journal of Evolutionary Biology* 6:737-752.