Is Beauty Only Skin Deep?

Biologists probing puzzles of evolution find two families of exotic birds excellent subjects for their search

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Second of two articles

Bowerbirds (Ptilonorhynchidae) and birds of paradise (Paradisaeidae) are among the strangest and most mysterious of all birds. To researchers, they represent a special challenge and an opportunity. One question still to be answered is the basis of these birds' strange mating systems.

A unique trait of these two families is that the majority of species within them are polygynous (one male mating with more than one female) and not pair bonding. Most birds are monogamous and maintain long-term, or even life-long pair bonds.

"We assume that the particular mating system adopted maximizes reproductive output," says Mary LeCroy, an American Museum of Natural History ornithologist who studies birds of paradise. Although biologists are just beginning to uncover ecological conditions that make polygyny a better option, one important prerequisite seems to be a food source that is either very abundant or distributed so that one male alone could never monopolize it.



Lesser bird of paradise (Paradisaea minor), upright wing pose.



Pair of satin bowerbirds (Ptilonorhynchus violaceus) with decorated bower.

"If the male's help [rearing the young] is not necessary, then there's no reason to form a pair bond," says Gerald Borgia, an evolutionary biologist at the University of Maryland, who studies bowerbird courtship and mating. He suggests, in this case, that the male's time is better spent passing on genes to new females.

"For example, there are oodles of insects around when the satin bowerbird [Ptilonorhynchus violaceus] reproduces. The female has no trouble getting enough of them to feed the young on her own." In addition, he notes that the chances of predation may be reduced if only one adult is there to attract attention to the nest. "The female must assess the costs, as well as benefits, of the male sticking around," Borgia says.

Another — and even more curious characteristic of bowerbirds and birds of paradise is that males within polygynous species exhibit bizarre behaviors - building stick structures called bowers and displaying bright exaggerated plumage both of which are used only in courtship related activities (SN: 9/4/82, p. 152). These traits evolved, according to Charles Darwin, "not from being better fitted to survive in the struggle for existence [through natural selection], but from having gained an advantage over other males. ... called this process sexual selection. Darwin named two distinct kinds of sexual selection - the evolution of features that help males defeat or drive away their rivals and of those that attract females.

While Darwin's theory still enjoys widespread acceptance, many mysteries remain—including the relative importance of the two forms of sexual selection and why females choose males with particular, often strange, characteristics. Some biologists maintain that these traits are signs of male vigor or dominance, while others believe they are just accidents of the evolutionary process.

Darwin noted that birds in polygynous mating systems, like bowerbirds and birds

of paradise, are more modified through sexual selection than are monogamous presumably because males are able to copulate with an unlimited number of females and traits evolved through sexual selection give them an advantage over their rivals. A female in this kind of mating system, who receives neither the labor nor resources that most female birds get from males, would be wise to choose a mate with "good" genes to sire her offspring. After all, a male's only contribution to her is his genes, and if they are "bad" she may waste her entire reproductive effort. Important as picking the best male may be in theory, however, whether or not females actually do this remains unknown.

"Female choice itself has been well documented in many species," says Borgia. In addition, it's "common for just a few males to do most of the mating" in some of these species, including the satin bowerbirds he's studied. But criteria of choice, as well as the quality of the male chosen, are still not clear. Borgia believes that females choose the most vigorous, or behaviorally dominant, male and that secondary sexual characteristics—fancy plumage or a good bower, for example—are signs of physical superiority over other males. He calls this the "male dominance" theory.

Alternatively, female preference for these or other male characteristics may be an accident of evolution, he suggests. A few females may have once begun to prefer males with a particular trait that had evolved through natural selection and, through a "runaway" selection process (proposed by Sir Ronald Fisher in 1930)—where the male trait and female preference for it reinforce each other over and over again — that now-meaningless characteristic was passed on to future generations.

Bowerbirds are "well suited for testing hypotheses concerned with the evolution of male display and female choice," says Borgia, because variables of the male's display can be quantified and manipulated

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Male Count Raggi's bird of paradise (Paradisaea raggiana) displaying.

without disturbing the bird. Also, bower decorations, ornamental plumage and other products of sexual selection are seen as evolutionary equivalents.

Last summer, Borgia spent five months on the east coast of Australia near Brisbane studying the satin bowerbird—an irridescent blue-black bird about the size of a pigeon. He divided 22 bowers and their owners into two groups: experimental and control. In the experimental group, Borgia removed all bower decorations, except for three yellow leaves. He and his assistants then watched the bowers 7 hours a day and took movie exposures every 15 seconds. They found that males in the control group mated "significantly more often" than those in the experimental group. Thus, as Borgia expected, bower decorations are essential to a male's mating Success

When they went one step further and statistically correlated the number of each kind of decoration with the number of matings, they found something even more interesting. Of all the decorations (blue feathers, yellow leaves, snail shells, yellow blossoms and miscellaneous natural objects - mostly "insect parts"), "only the number of blue feathers is strongly correlated with male mating success." This finding may be significant, says Borgia, because blue feathers are the only objects that are uncommon in the surrounding forests. "The relative rareness of feathers provides females with an indicator of male aggressive dominance," he says. "A male who can accumulate rare blue feathers and prevent them from being stolen is demonstrating his physical superiority over other males." Thus, the finding could support the male dominance theory of female choice.

"The explanation usually advanced [for

blue color preference in Ptilonorhynchus violaceus] is simply that blue matches the adult male bird's eyes, bill and plumage," says Jared Diamond, a physiologist and ecologist with the University of California at Los Angeles, who studies bowerbird behavior. He notes, however, that the aggressive male bowerbird spends much of his time wrecking the bowers of his rivals and stealing their decorations. Thus, an intact, well-decorated bower could serve as a "surrogate" for good genes as Borgia believes. "The female may hope that the male with better bower decorations is a superior male who had to chase away others in order to get them," says Diamond, but "the proof is lacking."

Even if a good bower turns out to be a sign of male aggressive dominance, the female is only "guessing," he says. Not all good genes go together. He draws an analogy to a woman who chooses a "big, strong, sexy man" for a mate, hoping this means he'll be a good husband and father, but ends up disappointed instead. "There's a risk involved in sexual selection," says Diamond.

Another possibility is that a trait getting an evolutionary start by serving as a sign of male dominance could proceed to become more and more exaggerated through runaway selection — losing its original relationship to fitness in the process. "Runaway selection is a likely component of sexual selection," says Diamond. He notes, however, that while the size of a physical trait may increase through this process until it becomes a handicap to its wearer (tails of peacocks, pheasants and some birds of paradise, for example), an equilibrium between natural and sexual selection will limit its ultimate size.

Borgia concurs that the runaway model

"could operate hand in hand with the male dominance theory." But, he asks, "is runaway selection alone enough to describe the fantastic characteristics we see? My bias is that of a field biologist... animals are so incredibly well adapted that it's hard for me to accept that anything's an accident."

LeCroy agrees that the exaggerated secondary sexual characteristics of male birds of paradise are probably no accident. But she differs from many others in her interpretation of their significance. "The plumes have primarily evolved in response to male-male interactions in setting up a dominance hierarchy," she says. The female is relatively passive ... she mates with the male at the top but is not actively selecting him." She cites her own research on several Paradisaeidae species where she found "no evidence" that females pick and choose among males. The dominant males chase away subordinates and set up their hierarchy before she arrives. Thus, fancy plumage would have evolved through Darwin's first, rather than second, kind of sexual selection - similar to horns and antlers used in the physical fights of other species.

She suggests a similar system may have evolved in the birds' bowerbuilding relatives. Diamond, too, thinks that "a lot of what goes on between bowerbirds is male-male interaction." He again notes the amount of time males spend wrecking other birds' bowers and stealing their decorations. These activities "directly prevent other males from wooing females," he says. "A sure way to destroy a rival's sex appeal is to destroy his bower."



While Darwin recognized that sexual selection could take two forms, he seemed to place more emphasis on female choice and even hinted at Borgia's interpretation when he wrote that "the best armed" and "the more attractive" males were "at the same time more vigorous." Most evolutionary biologists also have emphasized female choice, although there is little agreement on how a particular preference evolves. Birds of paradise and bowerbirds are a "perfect package for studying all this," Borgia says. "While I'm out in the field watching some really fascinating birds, I can also think about these important issues in evolutionary biology."

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