

Sexual Selection in Bowerbirds

The bower, or mating site, of these extraordinary birds of Australia and New Guinea is the center of intense competition among males. The female's mating choice is based on its architectural adornment

by Gerald Borgia

Naturalists have long been captivated by the complex and highly elaborate bowers of bowerbirds. Charles Darwin approvingly quoted the contemporaneous assessment of the ornithologist John Gould: "These highly decorated halls of [bowerbird] assembly must be regarded as the most wonderful instances of bird-architecture yet discovered." The interest of the two men is not hard to understand. The bowers of bowerbirds are found from dense forests to open grasslands in New Guinea and Australia, and they have no parallels in the animal world.

There are 18 bowerbird species, and the males of 14 of them decorate clearings or build bowers. There are several kinds of bower. The avenue bowers are formed of two vertical walls of sticks built on a broad platform base. In most species the end of the avenue opens onto a display area where decorations are exhibited. The maypole bowers are made of sticks woven around a sapling or a fern and surrounded by a circular raised court. Two species build a massive hutlike structure about 1.5 meters high around the maypole. The structure encloses a domed runway that opens onto a cleared exhibition area. The golden bowerbird places sticks on adjacent saplings joined by a cross branch, which is used as a display perch. Two other species clear and decorate display courts, but they do not build bowers. The males of one such species build a mat of ferns decorated with shells, and they drape lichen over nearby trees. The males of the other species clear a court on the forest floor decorated only with large leaves.

The decorations associated with the bowers vary greatly among species and include naturally found objects: snail shells, pebbles, feathers, insect parts and bits of bone. Near human settlements the decorations include manmade objects that match the color

of natural objects: coins, clothespins, plastic bottle tops, pieces of glass, jewelry, paper, teaspoons, nails, screws, thimbles and the like. The stealing habits of the great gray bowerbird are well known to the aboriginals of northern Australia. Fathers-in-law in that society are notorious for taking whatever they want, and the aboriginal word for father-in-law, *juwara*, is also applied to the bowerbird.

Darwin's fascination with bowerbirds went far deeper than mere appreciation of their coloring, playfulness and architectural skill. When bowers were first noticed by Western observers, they were thought to be nests. As early as 1865, however, Gould carefully observed that bowers were sites for sexual display and mating. Darwin, who was familiar with Gould's work, discussed bower building in his book *The Descent of Man and Selection in Relation to Sex*. Apart from its use as a stage, however, the function of the bower had remained obscure until the recent resurgence of interest in sexual selection. Bowerbirds and their bowers afford a unique opportunity to evaluate competing theories of sexual selection. With the new theoretical tools biologists are now beginning to understand the evolution of one of the most extraordinary behaviors in animals, and it is possible to give a much fuller answer to the question: Why do bowerbirds build bowers?

Darwin viewed sexual selection as a process separate from natural selection because the main selective forces in sexual selection are social rather than environmental. Indeed, exaggerated male display characteristics, such as the ornate plumes, calls and dances seen in a variety of avian groups, cannot be reasonably explained without considering the effects of social interactions. Darwin described two elements in sexual selection: male competition for females and

female choice of males. Male competition is evident in many species and its importance is generally accepted. The role of female choice, however, remains a hotly debated issue.

The codiscoverer of the process of natural selection, Alfred Russel Wallace, disputed the importance of female choice in animal courtship. He doubted that females of nonhuman species had the mental capacity to differentiate among males. The capacity of females to choose is no longer at issue, but the criteria on which the choice might be based and its relation to male competition must still be resolved. In a wide variety of animals as different as scorpionflies and mockingbirds male contributions of food or other materials appear to be the basis of female choice. The males of most bird species take an active role in parental care, and the likelihood of male assistance as perceived by the female seems to be critical in determining the pairing patterns. Male contributions are generally labor-intensive, and in such species the females benefit by choosing unpaired males as mates. The result is that among birds most pairings are monogamous.

For a few avian species, however, such as the prairie chicken, the cock-of-the-rock, the peafowl and the bowerbirds, the males offer no direct assistance to the females and provide them only with sperm. In such species the males have evolved extreme characteristics of sexual display, and their effectiveness in attracting mates varies widely among individuals. Yet in spite of the lack of tangible inducement, the females of such species show a strong preference for particular males. There is much discussion about why such preferences exist and how they might be related to the evolution of elaborate displays in males.

There are several divergent views about how sexual selection functions when males contribute only sperm



SATIN BOWERBIRD (*Ptilonorhynchus violaceus*) of eastern Australia is shown standing on the platform at the north end of his bower. The deep, iridescent satiny blue coloration identifies the bird as a mature adult male; females and younger males of the species are dark green on the back and spotted yellow-white on the underside. The bower is built by the male on a court cleared on the ground. It is made of sticks woven into two vertical walls that enclose an avenue on the surface of the broad platform base. Bowerbirds also build nests in which the young are born, but the bower

and the nest are distinct in shape, building location and function. The decorated platform of the bower serves as a stage for the display of the male and as a mating site. The structural quality of the bower and its decorative embellishments are major factors in the female's choice of a mate, and so the bower is the focus of the competition among male bowerbirds for mates. The satin bowerbird, intensively studied by the author and his colleagues, is the only bowerbird species for which patterns of female choice are known in detail. The photograph was made by Hans and Judy Beste.



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to females. The two most widely discussed general hypotheses are known as the good-genes models and the runaway models. In both kinds of models the female actively chooses her mate, and both models give a plausible explanation for the evolution of bowers. Each of them, however, depends on unproved assumptions, and neither has been shown to have operated in a natural population. Two other models, the proximate-benefit model and the passive-choice model, have been much less discussed, but they may turn out to be important in understanding the evolution of male display.

The hypotheses collectively known as good-genes models stress that a female that discriminates among her potential mates can enhance the overall health and vigor of her offspring. Thus according to the model, male displays evolve because they provide females with information about the relative

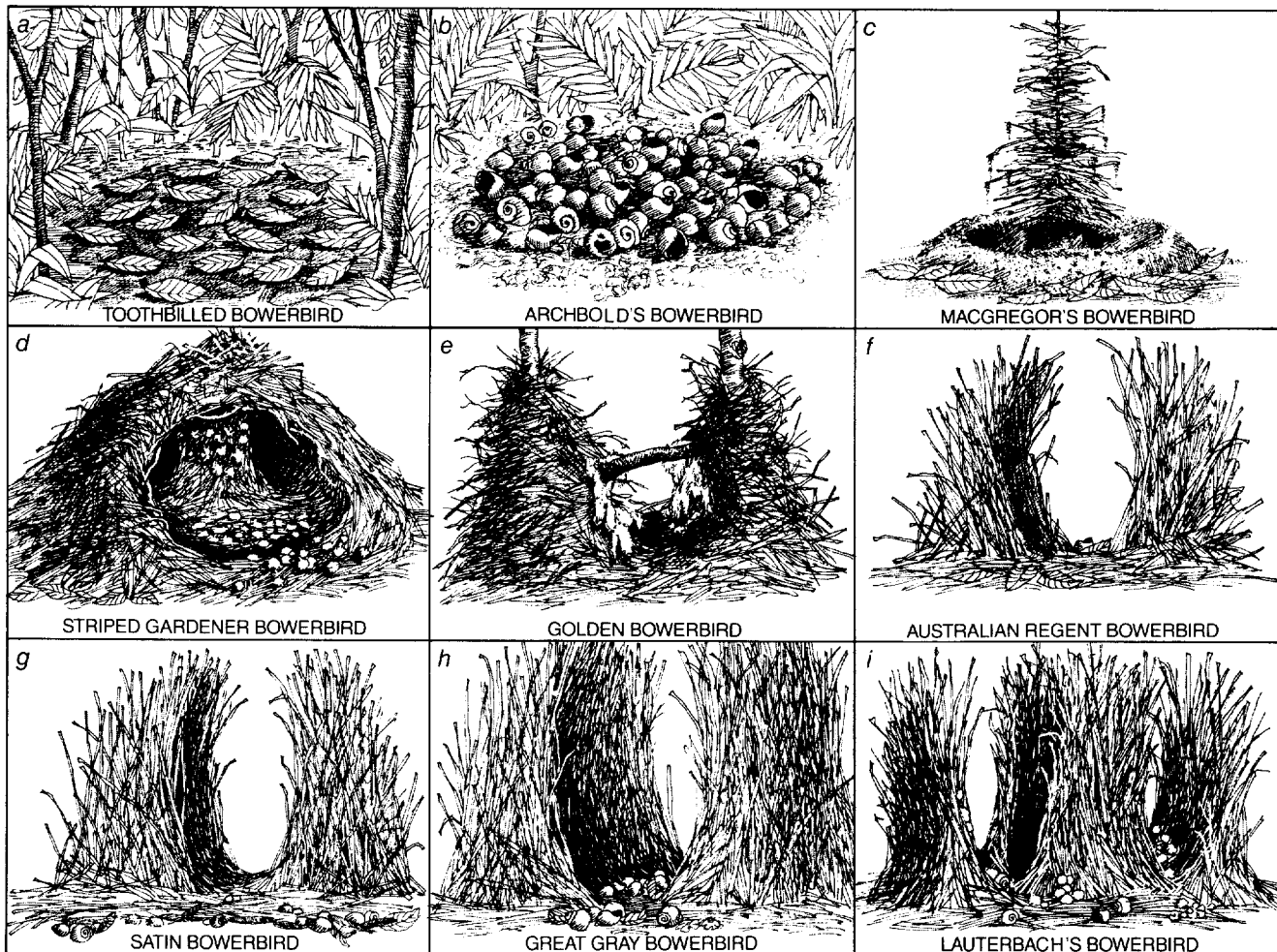
quality of a male as a sire. But to what aspects of the male should a discriminating female attend?

Richard D. Howard of Purdue University, Tim Halliday of the Open University and several other biologists have suggested females favor older males over younger ones. The older males have presumably demonstrated their hardiness simply by having lived to an advanced age. For example, suppose older males tend to carry heritable traits promoting survival, such as disease resistance or predator avoidance. Then all else being equal, if the good-genes hypotheses are correct, the female should prefer the older males as mates. How is she to make that choice? One plausible strategy might be to attend to the more elaborate display characteristics among her suitors on the assumption that the more practiced and elaborate the male's display, the older the male. Thus the female's

search for an older mate might explain the elaboration of male display characteristics.

Females might also seek the genetic enhancement of their offspring by favoring active males able to court vigorously or by favoring males with bright plumage, which could indicate male health and disease resistance. Hence the sexual-display patterns of the males, including their exaggerated plumage and decorated bowers, may have evolved to provide information to females about heritable, fitness-enhancing traits. Complex traits, such as the male's overall vigor, may summarize the effects of genes throughout the genome. Such traits could be quite useful to the female in choosing a genetically superior partner.

In many animal species males compete with one another for access to females. Displays that show the dominance of a male in aggressive encoun-



MALE BOWERBIRD CONSTRUCTIONS vary from simply ornamented clearings on the ground (a) to elaborately decorated bowers. The bowers are classified into three or four major kinds. The mat bower (b) is a mat of lichens on the forest floor. The mats are well decorated with piles of snail shells. The maypole bower (c-e) is built of sticks woven around a central pole, often a sapling or a fern, and the structure is surrounded by a circular raised court. In two species males build a large hut over the maypole and pile deco-

urations on a court near the entrance (d). One species (e) piles sticks on adjacent saplings joined with a cross branch that functions as a display perch. Some biologists classify this bower as a separate kind. The avenue bower (f-i) is built of walls of sticks that enclose the avenue, which opens onto a platform. The decorations may be exhibited on the platform, on the avenue or on both, depending on the species. Lauterbach's bowerbird (i) builds an avenue bower in which a second set of walls is perpendicular to the main avenue.

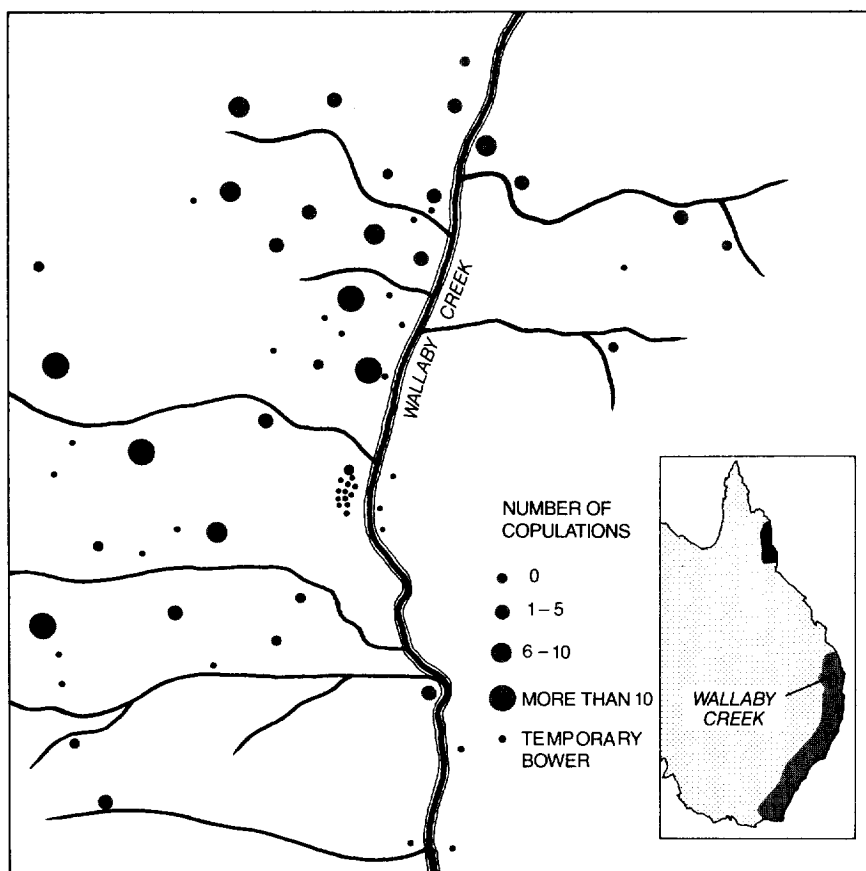
ters may reliably indicate his superior fitness relative to other nearby males. I have therefore suggested females may prefer to choose among males that give ostentatious displays because the females are seeking dominant males. Males giving such displays without harassment must be dominant because subordinate males attempting to give the same display would be challenged by higher-ranking males.

If mates are selected according to display patterns alone, one would expect that all mature males would have the plumage needed for a display but that only some of them would earn the opportunity to show it off. There is an analogue to this prediction for the decoration of bowers. Male bowerbirds continually attempt to destroy other bowers and steal their decorations, and that behavior is analogous to the competition for the opportunity to display plumage. Together with Stephen G. and Melinda A. Pruett-Jones of the University of California at San Diego, I have proposed that a male's ability to maintain a decorated bower of high quality may serve to indicate to the female his relative quality as a sire.

Amos Zahavi of the University of Tel Aviv has suggested the female might gain genetic benefits for her offspring if she favors a so-called handicapped male: a male displaying debilitating physical characteristics or behaviors. According to Zahavi, the elaborate sexual displays are genetically inherited handicaps. The female allegedly gains genetic benefits by choosing a male with a handicap because such a male has survived in spite of a highly disadvantageous trait.

The model has met with much criticism. The most significant flaw is its reliance on the environment to select only the fittest of the handicapped males. If the females are to find the best sires in the population, there must be a very high rate of male mortality attributable to the handicap. Otherwise the overall genetic superiority of the handicapped survivors in the population could not be guaranteed. The model's requirement of high mortality among the sons of handicapped males makes it unlikely that female preference for superior males could evolve according to such a scheme.

The runaway model for sexual selection was proposed by Ronald Fisher in 1930 to explain the evolution of exaggerated characteristics found only in males. He was the first to note that the pattern of female choice could be self-reinforcing: it could cause its own spread among females and the spread of the male-display characteristics on which it is based.



AUTHOR'S STUDY AREA is in a valley formed by Wallaby Creek in the Beauty State Forest of New South Wales. The inset map shows the location of the site as well as the range of two subspecies of satin bowerbird: *P. violaceus violaceus* (color) and *P. violaceus minor* (gray). Eucalyptus is a dominant canopy tree over much of the area; the understory varies and includes grassland and thick thorn scrub. Rain forest predominates in the low areas, along creeks and on the eastern side of the ridges west of Wallaby Creek. Sites of established male bowers of the study area are shown as colored circles; the diameter of the circles indicates the number of matings per season for the bower's owner. Sites of temporary bowers, built by younger males and destroyed soon after, are shown as black circles.

To illustrate the runaway process suppose there is a population in which there are two kinds of male and two kinds of female. The males differ in the presence or absence of a display characteristic, such as a red tail feather. The females differ in that some of them (the "choosers") mate only with males having a red tail feather, whereas others (the "nonchoosers") do not distinguish among males on the basis of tail-feather color.

In such a population the males having a red tail feather can mate with both chooser and nonchooser females. In contrast, males without a red tail feather can mate only with nonchooser females. Thus red-tailed males have more opportunities to mate and produce a greater proportion of progeny than males without a red tail feather; the proportion of red-tailed males in the population thereby increases. The sons of red-tailed males and chooser females carry a greater-than-random proportion of the genes that lead to

choosing behavior in females. As red-tailed males mate more often, the proportion of the traits specifying a female preference for red-tailed males also increases.

Once a pattern of female choice is established, there can be continued selection for more exaggerated male traits. The outcome of the runaway process depends strongly on the choice pattern. If females consistently prefer males having extreme characteristics, such male characteristics are expected to evolve. If, however, females prefer males with a less extreme trait, such as a single red tail feather, males in the population with one red tail feather will tend to predominate over males with an all-red tail. The survival costs of sexual display can affect the process. For example, as extreme characteristics develop in males, new female-choice patterns may arise that cause a reverse runaway toward less extreme male display characteristics.

Very little is known about how new

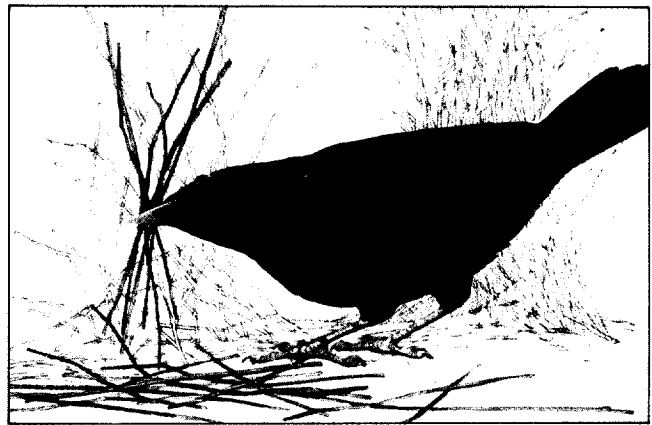
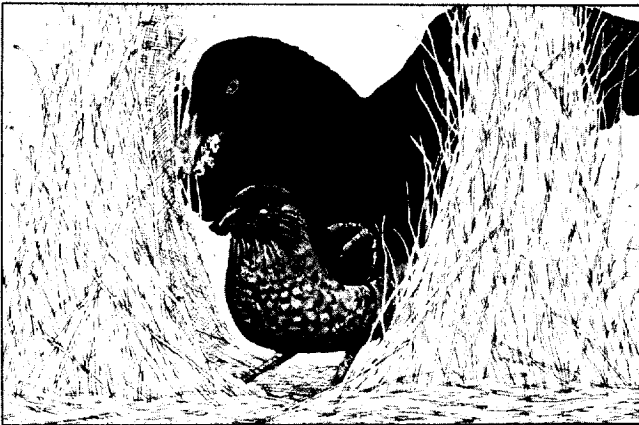
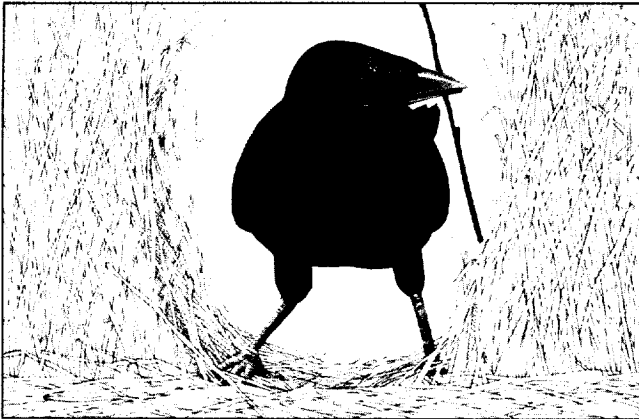
female-choice patterns arise. Moreover, when they do arise, it is not clear whether they favor only a slight enhancement of male characteristics or an extreme development. Several recent models of runaway selection conclude that female choice can be completely arbitrary and so can give rise to the evolution of arbitrary male characteristics.

The good-genes models and the runaway models thus make differing pre-

dictions about how extreme display traits are established. According to the good-genes model, natural selection should favor female preferences for traits that indicate differences in male qualities as sires. In the runaway models such an outcome is not necessarily expected. A runaway selection may not enhance the vigor of the offspring, and it might even promote traits that reduce their fitness.

The extent to which traits that re-

duce fitness might evolve is still a matter of debate. It would seem more likely that if different kinds of female preference were expressed in a population, the kinds tending to enhance fitness would have an evolutionary advantage over the ones that did not. The extent to which traits enhancing fitness win out over less advantageous ones must depend on at least two factors: the ease with which established traits can be replaced and the frequency



PATTERNS OF BREEDING BEHAVIOR of the satin bowerbird are depicted in the six-part diagram. The male builds his bower out of sticks (*top left*). When a female visits the bower, the male moves down to it from a perch in a nearby tree and begins his courtship (*top right*). After watching the display the female may crouch and tilt forward, and the male immediately mounts her (*middle left*).

Other males may compete with the owner of the bower for females by destroying the bower in the absence of the owner (*middle right*) or by stealing its decorations (not shown). A competing male may even try to interrupt or displace a male during copulation (*bottom left*). After successful copulation the female lays her eggs and rears her young in a nest that is separate from the bower (*bottom right*).

with which competing patterns of choice are found in a population.

Comparing the good-genes models with the runaway models is further complicated because the models need not be mutually exclusive. For example, if the initial female choice depended on the effects of good genes, it could lead to the selection of female-preference traits that are self-reinforcing. It is therefore unrealistic to expect the predictions of these models to be easily distinguishable in natural populations. Nevertheless, if the controversy is to be resolved, it will only be through studies of natural populations. One approach is to determine whether or not the patterns of male display are really arbitrary. Alternatively, one could show that they do indeed indicate the relative quality of the males as sires.

I noted above that there are at least two more possible explanations for the evolution of bower-building behavior. According to the proximate-benefit model, there may be immediate benefits for the female that chooses a male giving an extravagant display. For example, bright male plumage may better enable females to detect parasites and so avoid contact with males likely to transmit the parasites. Females that discriminate against infested males gain an obvious, immediate benefit over less choosy females. Other kinds of immediate gain might also arise for the discriminating female. A male giving a display without interference from other males might be able to offer superior protection from predators, and males with elaborate plumage are more likely to be mature and so carry viable sperm.

Finally, some biologists have suggested female choice has had little to do with the evolution of exaggerated male display. According to the passive-display model, put forward by Malte Andersson of the University of Göteborg and Geoffrey A. Parker of the University of Liverpool, elaborate male displays may have evolved as advertising devices. Males with the most ostentatious displays are more readily visible to females and so such males have more chances to mate. Gains from the additional matings repay the males for the extra cost of surviving while giving an extravagant display. The model does not require that females exhibit any active preference for males with larger displays. If a female simultaneously encounters two males that differ in the extent to which their displays are elaborated, the model predicts the size of the displays should not influence her mating decision. For bowerbirds this model implies that the bower is a device for advertising to fe-

males the presence of a courting male and that males with larger, better decorated bowers are sexually successful because they are more often found by females.

Although substantial efforts in constructing theoretical models have sharpened the questions one would like to answer about how elaborate displays have evolved, there have been few attempts to test the models in natural populations. In part the lack of testing is a result of the difficulty of finding observable subjects with appropriate characteristics. The special characteristics of the bowerbird's display make it possible to study female preferences in detail. I have already mentioned that male bowerbirds give no material assistance to females or to their young, and the females are free to choose among males from widely separated display sites. One can therefore assume that biases observed in female preferences for males are related to characteristics of the male's display, including his bower, plumage and behavior in the presence of the female.

Furthermore, there may be a functional equivalence between the decorations on the bower and brightly colored plumage that may make it possible to manipulate the general display patterns experimentally. More than two decades ago E. Thomas Gilliard [see "The Evolution of Bowerbirds," by E. Thomas Gilliard; SCIENTIFIC AMERICAN, August, 1963] suggested there is an inverse correlation between the degree of plumage elaboration in males and the size and degree of the decoration of the bowers. Thus, Gilliard noted, the decorated bowers may play the same role in courtship as showy displays of plumage; in fact, he suggested, bowers are a kind of displaced plumage that allow the animals building them to dispense with bright coloration. The development is called the transfer effect. If it is real, it suggests the same forces shaped both the evolution of bower building and decorating behavior and the displays of showy plumage.

Unlike plumage, the bower and its decorations can be easily manipulated and quantified with no direct effect on the bird. Matings take place at the bower, and so cameras monitoring the bowers can record the choice of a mate by the females and the mating success of the males. The observations can be compared with the quality of the bower and the elaborateness of its decoration. Finally, male behavior that can be observed near the bowers is an important indicator of how competition can distinguish among potential suitors. Males often steal bower decora-

tions and destroy the bowers of other males, and the patterns of such aggressive behavior can be compared with the quality of a male's display and his success in finding a mate.

In 1980 I began an intensive study of the satin bowerbird (*Ptilonorhynchus violaceus*) in eastern Australia. J. M. Marshall, Reta Vellenga and Richard Donaghey, who was then at Monash University, had done important early work, and their efforts made the life history of satins the best documented of any bowerbird species. Donaghey allowed me to take over a study population with which he had worked, so that the histories and identities of some males had already been known for four years. At that time the details of female choice were not known for any bowerbird species.

The satin bowerbird ranges along the southern and central east coast of Australia. My research site is in a valley formed by Wallaby Creek in Beaury State Forest of New South Wales [see illustration on page 95]. Vellenga had shown that the male is slightly larger than the female and gets his satiny blue plumage in his sixth year. The coloration of adult males differs markedly from the dark green back and spotted yellow-white underside of females and juveniles. The male builds bowers made of sticks on courts cleared on the ground.

The north end of the bower faces the sun at midday and opens onto a display platform, which the mature male covers with bright yellow straw and yellow leaves. A variety of decorations are laid on the platform, including blue parrot feathers, blue and yellow blossoms, insect parts, in particular the outer coverings of cicadas, and other natural objects. Large objects including the shells of land snails are arranged at the outer edge of the platform, and feathers are distributed evenly over the yellow platform between its outer edge and the avenue of the bower. Small objects held by the male in his mouth during courtship are found in a small pile near the bower.

The carpet of yellow straw and leaves on the bower platform creates a bright glow that is particularly noticeable at bowers in forests. The male prunes the leaves above the platform, apparently to allow sunlight to illuminate the platform. The display of shiny blue objects, which are relatively uncommon, and their placement on a yellow background suggests an attempt to give an unambiguous and highly visible signal.

In order to study the behavior of individuals we capture bowerbirds flocking in open pastures. Each bird is

fitted with a unique color-band combination, measured and assessed for plumage, the color of its beak and legs, scratches or other evidence of fighting and external parasites. We assign the bird to an age category according to the colors of its plumage and its beak.

My volunteer assistants, graduate students and I record the behavior of males at feeding sites, noting the number of times a male is attacked and how often he attacks others. At the bowers we observe the birds from hides, and we also continuously monitor activity at bowers with remote-control super-8 motion-picture cameras throughout the mating season. The cameras expose a frame every two seconds as long as there is a break in an invisible beam of infrared light passing through the bower. This record enabled us to identify individual visitors to the bowers and to note their activities, including the destruction of the bower, the stealing of its decorations, courtship and copulation. We also made daily records of the bower quality and the movement of marked decorations at more than 33 bowers in the course of the study.

At Wallaby Creek mating begins in early November and continues until late December. In mid-October males become active around the bowers: rebuilding of the bowers at permanent sites is completed, and intensive decorating is begun. Young males visit the bowers and the bower owners often display to them. By early November, however, the bower owners become less tolerant of male visitors; they spend more time near the bower and engage more actively in destroying nearby bowers and in stealing their decorations. Females overwintering at the southern end of the valley start moving north toward the highest concentration of male bowers. In mid-November the matings begin. The males then spend most of their time perched in trees near the bower, calling frequently and moving down to the bow-

er to display to females, to protect it from marauders, to build it or to "paint" it with the saliva generated in chewing bits of vegetation. Matings peak at the end of November and are mostly finished by mid-December.

When a female visits the bower, the male begins his display, often holding a decoration in his beak. He faces the female while he stands on the platform. He gives a whirring call while prancing, fluffing up his feathers and flapping his wings to the beat of the call. Calls are punctuated with periods of silence, quiet chortling, buzzing or mimicry of other birds. The female's initial response is to enter the bower and "taste," or nip, at a few sticks. Then she intently watches the courtship. If she is ready to copulate, she crouches and tilts forward. The male immediately mounts her. At any stage she may leave, thereby ending the courtship. Typically a female mates only once. She later lays two eggs in a nest that is usually outside the area defended by her mate. The hatching of the eggs coincides with the emergence of large numbers of cicadas.

Established males destroy bowers other males may try to build nearby, but during the mating season young males can establish temporary bowers at sites removed from the permanent ones. There is intense courtship at the temporary sites among males that appear to be practicing and learning the display. Such males also visit permanent bowers. If the owner is not present, the visitor may paint the bower, attempt a display or court a visiting female. During courtship by a bower owner other males may hide in the surrounding vegetation and then try to interrupt or displace a copulating male.

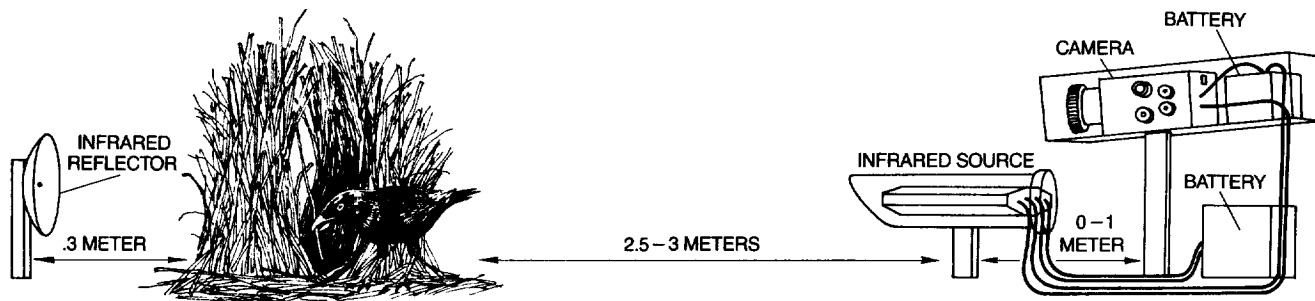
Most hypotheses about the evolution of elaborate displays assume the quality of the display affects the female's willingness to mate. For satin bowerbirds mating success varies widely among males: we observed one

male that mated with 33 females during the season, whereas many other males did not mate at all. When we ranked bowers for quality, we found a strong positive correlation with male mating success. Neat and well-built bowers with symmetrical walls, fine, densely packed sticks and a highly sculptured appearance were owned by particularly successful males.

To test the importance of bower decorations in the female's choice of a mate we removed the decorations from the bowers of a randomly selected group of males. We then compared their success in mating with the success of a control group we did not disturb. As we had predicted, the decorations do indeed influence mating: we found a significantly higher rate of mating in the control group than we did in the experimental group. Moreover, the number of decorations on the platforms of undisturbed bowers—particularly the number of feathers—was correlated with male mating success in each year of the study.

The discovery that decorations are important in male display led me to a study of decoration stealing. We found that blue feathers are stolen at a much higher rate than other decorations in proportion to their frequency on the bower platforms, and that (because they are rare in the habitat) stealing is the principal means of obtaining them. By monitoring the number of feathers on bower platforms throughout the mating season we discovered that the number on the platforms of successful males peaks at the height of the mating season. At the same time the number of feathers on the platforms of unsuccessful males is reduced.

In another experiment we introduced individually marked blue feathers to the bowers of a group of males, and we added no feathers to the bowers of a control group. We then reversed the treatments of the experimental and the control groups, and we recorded the movements of the feath-



EXPERIMENTAL MONITORING SYSTEM employed by the author in his study of the satin bowerbird is diagrammed schematically. An infrared beam, invisible to the bowerbird, is projected through the avenue of the bower to a reflector. When the beam is

interrupted, a super-8 motion-picture camera exposes one frame every two seconds. Birds were also observed from hides. The system enabled the author to monitor the behavior and identity of bower owners and visitors at 33 bowers for the 50-day mating season.

ers in each instance. Yet whatever the initial placement of the feathers, the same males, namely the most active thieves, tended to accumulate the feathers on their bower platforms. The result is strong evidence that stealing is the most important factor in the final number of feathers displayed on the platforms. Because the quality of the bower decoration affects the success of the male in mating, feather stealing appears to affect mating success. More dominant males tend to be more successful at feather stealing.

We also found that the average quality of a male's display depends on the frequency with which it is destroyed by marauding visitors. The more frequent the destruction, the lower the overall quality of the bower. The pattern of destruction can indicate male dominance to the female because females generally limit their bower visits to a small area. If a bower is maintained in relatively good condition, it can serve as a signal to the female that the owner can defend it from attack and destroy the bowers of his neighbors as well. The behavior patterns we found for bower decorating are consistent with the patterns of bower destruction: the bowers of older, dominant males are destroyed less often than those of younger, subordinate males.

How do such observations conform with the models for the evolution of selection patterns I have described above? There are several lines of evidence to suggest females favor dominant males. They choose mates that are able to keep bowers in good repair and well decorated. Such males tend to be the ones that are dominant at feeding sites; their decorative preferences are for objects scarce in the habitat and prized by other males. The age of the male also seems important. Older males maintain bowers of better quality and decorate them more elaborately, and they are more successful in protecting their bowers from destruction. Moreover, older males give more refined courtship calls.

It may be that both male dominance and age are important to the female's choice. Bower building appears to take some practice, but only the most aggressive young males are able to practice building and decorating bowers in the face of repeated destruction by other males. A female that chooses an older, established male with a well-built, well-decorated bower and a refined courtship call has evidence that her prospective mate not only has been able to survive to a relatively old age but also has been able to do it while learning to build and maintain a high-

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quality bower under the rigors of male competition.

The remaining good-genes model, the handicap, is not supported by the behavior of bowerbirds. The model predicts that large differences in male mortality are associated with differences in the quality of male displays. That is not what one finds. The mortality of displaying males is low, and it appears to be independent of the quality of male displays.

The runaway model can lead to a large number of possible outcomes. Versions of the model that suggest arbitrary outcomes yield no prediction about the kinds of traits that should evolve; hence they cannot easily be falsified. In some cases an arbitrary choice resulting from runaway selection might give rise to the same behavior as a choice made on the basis of male dominance. For example, if females had evolved a tendency to favor males with well-built, well-decorated bowers, males able to steal decorations and destroy bowers, or in other words the dominant males, would thereby be selected.

The existence of patterns consistent with other models weakens the case for the runaway models, particularly if the patterns can be shown to recur in various species. In satin bowerbirds we found that males favored scarce decorations. If a similar pattern in other

species were found, it would support the suggestion that the female assessment of male dominance is important in the choice of a mate.

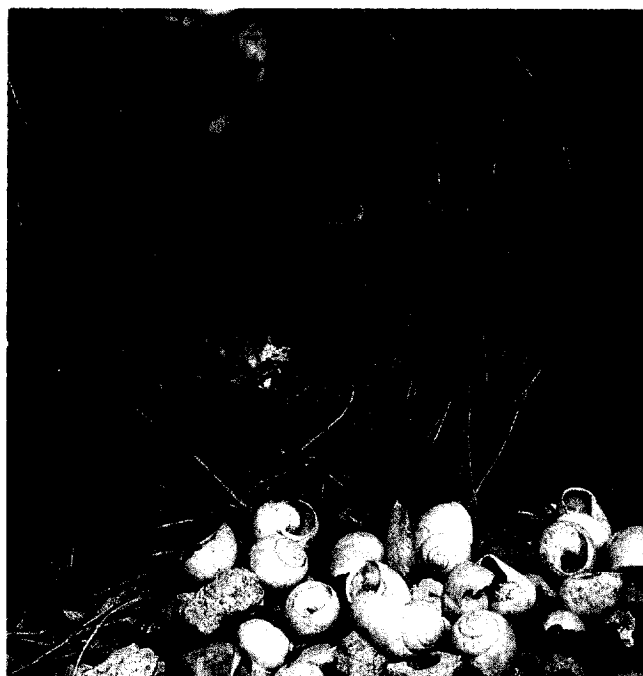
Can passive choice explain the patterns of mate selection we observed? Probably not. We found that sexually successful males tend to receive more female visitors to their bowers than less successful males, and they mate with a greater proportion of the females. Generally females visit several bowers before mating, and their choice is correlated with the overall mating success of the males. In contrast, passive choice seems unlikely. Bowlers are on the ground and often under cover; the call of the bower owner from his nearby perch is much more noticeable to a naive female than the bower itself. Furthermore, females are long-lived and therefore probably familiar with all the bower sites in the area they search; it seems unlikely that mere prominence would affect the choice of such females.

There may be some proximate benefit from the bower for the female as a protection from intruding males. We often saw males trying to interrupt matings by bower owners. Usually the owner chased the intruder away and the female remained in his bower, although occasionally copulation was interrupted. When females were on the ground outside a bower, however, they

seemed to be uneasy and commonly flew away if intruders came near.

To summarize, the evidence available suggests female satin bowerbirds actively differentiate among males according to the quality of their displays. The females may also choose sires according to the decorations associated with the bowers. The protection hypothesis offers an alternative explanation for the evolution of bower building, but it does not explain why the bowers are decorated. The runaway model cannot be excluded as a possible alternative explanation.

The work on satin bowerbirds is a first step in understanding the evolution of exaggerated characteristics, and we have established the plausibility of several models of that evolution. Nevertheless, studies of mating choice in other bowerbirds will be necessary if one is to explain why bowerbirds build bowers. To what extent do other species show a preference for rare decorations? Do they steal the decorations of other bowerbirds and destroy their bowers? How do males learn to give their displays? Will the findings suggest the same causal relations between male behavior and female choice? Why are bowers built by some species but not by others? Such questions will surely be resolved by further patient observation.



TRANSFER EFFECT, first proposed by E. Thomas Gilliard, is illustrated by the bowerbirds and their bowers in the photographs. The male Australian regent bowerbird (*Sericulus chrysocephalus*), which displays bright plumage, builds a bower of indifferent structural quality and makes little attempt to decorate it (*left*). In contrast, the male great gray bowerbird (*Chlamydera nuchalis*), a bird of dull color, builds an elaborate bower that is richly decorated with

shells, flower petals and a variety of manmade objects (*right*). Gilliard suggested the size and degree of decoration of the bower are inversely correlated with the elaborateness of the plumage color. Decorated bowers may therefore have the same function for the male as colorful plumage displays, and any hypotheses that explain the evolution of the bower may also explain the evolution of colorful plumage. The photographs were made by Hans and Judy Beste.

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The runaway model can lead to a large number of possible outcomes. Versions of the model that suggest arbitrary outcomes yield no prediction about the kinds of traits that should evolve; hence they cannot easily be falsified. In some cases an arbitrary choice resulting from runaway selection might give rise to the same behavior as a choice made on the basis of male dominance. For example, if females had evolved a tendency to favor males with well-built, well-decorated bowers, males able to steal decorations and destroy bowers, or in other words the dominant males, would thereby be selected.

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