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## The Evolution of Bower-building and the Assessment of Male Quality

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### Abstract and Summary

A hypothesis is proposed for explaining the evolution of display courts in birds. We suggest that males who show ownership of display courts are better able to inform females of their high dominance status, which is an indicator of their quality as a sire. The elaborate display structures of bowerbirds are viewed as an extreme example of selection to show ownership of these "markers". Specific problems with the evolution of bowers are considered.

Sexual display at specific sites is a critical aspect of social behaviour in a wide variety of avian species. In a small but diverse array of species males construct specialized courts for display to females. These males are polygynous and do not assist females in providing parental care. Included among court-building birds are species with quite distinct evolutionary histories, habitat preferences, and geographic locations. Manakins (*Manacus manacus*, *Pipra erythrocephala*) and cotingas (*Rupicola peruviana*, *Xipholena punicea*) display in groups on simple cleared courts in neotropical rainforests (SNOW 1976, 1982; LILL 1974 a and b, 1976); JACKSON's dancing whydah (*Drepanoplectes jacksoni*) tramps down a display ring in the high altitude grasslands of East Africa (VAN SOMEREN 1958). The lyrebirds (*Menura*) build and display from earthen mounds in the temperate forests of southeastern Australia (LILL 1979). Two genera of birds-of-paradise (*Parotia* and *Diphylodes*) clear courts in forests of New Guinea (GILLIARD 1969).

Building of display sites reaches its most complex and elaborate levels among bowerbirds. There are 18 bowerbird species. Males of 14 species clear

courts, and in 13 species, males build and decorate structures, called bowers, at these sites. GILLIARD (1969), who provided the most extensive review of bowerbird life history, recognized three types of bowers. The first, the *avenue bower*, consists of two vertical walls of sticks on top of a broad platform base. It is built by birds of 8 species in three genera (*Sericulus*, *Chlamydera*, and *Ptilonorhynchus*) that are found in habitats ranging from closed forest to open grasslands in New Guinea and Australia. In many species, the north end of the avenue opens onto a display area where decorations are concentrated (VELLENGA 1970). Each avenue-building species has specific preferences in the type and color of decorations it uses. Five species in two genera (*Amblyornis* and *Prionodura*) build a second type of bower called a *maypole bower*. These bowers are built around saplings or ferns and may reach up to 3 m high. Two bowerbird species, *A. inornatus* and *A. subalaris*, build a hut-like bower around the maypole that may be 1.5 m tall and enclose a domed runway which opens onto a cleared area where decorations are accumulated. *Prionodura newtonia* piles sticks on adjacent saplings which are joined by a cross branch that the male uses as a display perch. The third type of bower, the *mat bower*, is built by *Archboldia papuensis* and consists of a mat of ferns on the forest floor with nearby trees draped with lichen. *Scenopoeetes dentiostrois* is the only court clearer of the otherwise monogamous catbird group of bowerbirds. Males clear an area of forest floor and decorate it with numerous yellow leaves. No bower structure is built. MARSHALL (1954), GILLIARD (1969), and COOPER and FORSHAW (1977), provide detailed reviews of the literature on bowerbird breeding behaviour.

Although court-clearing behaviour has attracted much attention from naturalists (GILLIARD 1963; SNOW 1976, 1982), there exists no general theory to describe why court clearing has evolved. Specific hypotheses have been proposed for bowerbirds by SÖDERBERG (1929), MARSHALL (1954), GILLIARD (1963, 1969), and DIAMOND (1982a and b), but their hypotheses are neither general nor do they fit with recent models of sexual selection. Here we briefly critique previous ideas for the evolution of bower-building. We then propose the marker hypothesis to explain the evolution of bower building and related behaviours. According to this hypothesis females prefer males able to build and maintain well constructed, elaborately decorated bowers because the quality of the bower gives the female information about the male's physical superiority over other males and this is correlated with his quality as a mate. The marker hypothesis is then extended as a general explanation for site-specific sexual displays common in polygynous avian species in which males provide no material contribution to females.

### The Nest Hypothesis

Previous hypotheses for the evolution of bower-building suggest that females require a nest-like structure in association with the male display site in order to be sufficiently stimulated to reproduce (SÖDERBERG 1929; DAVIES

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in COOPER and FORSHAW 1977; DIAMOND 1982 a and b). According to the nest hypothesis, a history of selection on female birds has caused them to become dependent on the nest to be properly stimulated to reproduce. In polygynous bowerbird species, bower-building by males is hypothesized to have evolved as a replacement for the nest stimulus needed for female reproduction. MARSHALL (1954) and GILLIARD (1969) suggest that bower-building may be a result of displacement activity by males emancipated from parental duties. However, neither of these authors view this as a complete explanation. Moreover, it does not explain why, early in the evolution of bower-building behaviour, females favored males who built incipient bowers.

Bowers are the only structures other than nests built by birds, and because both are commonly made of sticks it is reasonable to consider a hypothesis that proposes a functional connection. However, the great majority of evidence weighs against the nest hypothesis as an explanation for why bowers are built. It portrays females as principally constrained by physiological problems associated with the control of the timing of mating. This is not consistent with much recent data that shows that females from a wide variety of taxa are capable of relatively sophisticated behaviour in mate selection (VERNER 1964; ORIANS 1969; THORNHILL 1976; PLESZCZYNSKA 1978; BORGIA 1980) and it discounts gains in fitness that accrue to females by careful choice of mates. The inability of the nest hypothesis to deal with other, more specific, problems provides the strongest evidence against that hypothesis.

*Why don't bowers resemble nests?* There are three very different types of bowers and none of them resemble a bowerbird's nest. Bowerbird females build uncovered nests of sticks placed in a circular pattern that is typical among most species of passerine birds. Mat bowers are flat, made of lichen, and have no stick structure. Maypole bowers are built around saplings and other vertical supports, and, although made of sticks, are not shaped to carry out the typical nest functions of holding eggs and young. Avenue bowers are made of vertically placed sticks arranged in two walls. This contrasts to the circular placement of sticks placed in a horizontal plane common among builders of open, uncovered nests. If bowers are thought to be the result of selection for a nest stimulus, then it would be expected that differences in the types of bowers should be correlated with difference in nest structure among bowerbird species. COOPER and FORSHAW's (1977) detailed description of bowerbird nests suggests no such correlation.

*Why are bowers on the ground?* The nest hypothesis provides no explanation of why bowers of all bowerbird species are on the ground. All bowerbird species nest in trees, presumably to avoid predators (DONAGHEY 1981), and individuals are reluctant to come to the ground except for specific needs. Both male satin (*Ptilonorhynchus violaceus*) and Macgregor's (*Amblyornis macgregoriae*) bowerbirds spend most of their time during the mating season on perches above their bowers. They come down to the bower only to carry out specific tasks such as bower building or courtship, and then return to their perch. They rarely stand inactive near their bower (DONAGHEY 1981; PRUETT-JONES and PRUETT-JONES 1982; BORGIA, pers. obs.). If bowers were built in trees, they

should provide a more realistic nest stimulus, and certainly small bowers such as avenue bowers could fit in trees. Those types of bowers that are large today must have been small in incipient stages so that selection for a nest stimulus should have kept them sufficiently small to be in trees.

*Why are bowers decorated?* No bowerbird species decorates its nest, so the nest hypothesis is not suited to explain this dominant feature of bowerbird behaviour. MARSHALL (1954) developed an additional explanation to deal with the problem of bower decoration: bower decorating behaviour evolved from courtship feeding. This idea was criticized by GILLIARD (1969) but supported by DIAMOND (1982 a and b). There is no evidence that courtship feeding is a regular part of the sexual display of any bowerbird species. In focal observations at bowers we have observed more than 300 complete courtship bouts of satin and Macgregor's bowerbirds at their bowers, and we have never seen a female take a display object either from the bower or the displaying male. Decorations are used by males in display, but the nature of such displays suggests that although decorations add to the male's attractiveness, they are not presented to the female as food.

Bower decorations are primarily inedible objects and include glass, feathers, stones, plastic, dried leaves, charcoal and snail shells, although fruits are also occasionally used (GILLIARD 1969).

A daily survey of bower decorations at bowers of 44 male satin bowerbirds through an entire mating season shows that edible objects make up less than .5% of decorations on bowers. Among the remaining species, *C. cerviniventris* is alone in using primarily edible objects, principally figs.

If courtship feeding were the underlying cause for the accumulation of decorations, why should objects that have no food value be so often favored as decorations, and why should such large numbers of these objects be accumulated? Moreover, decorations that are most preferred by male and female satin bowerbirds (snail shells and blue feathers) and accumulated in large numbers, are rarely held by males during sexual display (BORGIA 1985).

*Is male display at a nest required for stimulation of female reproduction?* In polygynous bowerbird species, nest-building typically occurs before males and females associate. A female's ability to build a nest before courtship suggests that male stimulation is not a necessary ingredient for this key aspect of reproductive behaviour. Is it then reasonable to assume that the absence of male stimulation at a nest will be critical in the evolution of bower-building behaviour?

The requirement for male display at a nest is a key assumption of the nest hypothesis. There is no evidence that females from any bowerbird species or their close relatives require male display at a nest to control the timing of reproduction, nor that such stimulation is commonly required among birds. In fact, no evidence is presented that courtship occurs at the nest. Contrary evidence is available from the numerous and phylogenetically diverse array of polygynous species in which males do not court females at nests. Ancestors of each of these species have made the transition from monogamy to polygyny similar to the one made by ancestors of bowerbirds without any evidence of a

need to display at a nest or nest model. Moreover, the frequent transitions from monogamous to polygynous mating systems which are consistently associated with changed ecological conditions (CROOK 1965; BROWN 1964; EMLEN and ORING 1977) imply that the evolution of polygyny has not been greatly limited by problems associated with the control of the timing of reproduction.

*Is court-clearing required for the transition to bower-building behaviour?* GILLIARD (1969) concluded that the court-clearing behaviour of *S. dentirostris* is the most primitive of all polygynous bowerbirds because it does not involve the construction of a bower. This view is supported by the commonness of court-clearing among non-bowerbirds relative to the building of bower-like structures. If the behaviour of *S. dentirostris* is indicative of ancestral polygynous bowerbirds and male display at cleared courts preceded the evolution of bower-building, then females must have solved problems with the control of timing of reproduction before bower-building evolved. It is unlikely that females would re-evolve a dependency on nest stimulation that is necessary, according to the nest hypothesis, to drive the evolution of bower-building.

#### Male Quality, Female Choice, and Sexual Display

In place of the nest hypothesis, we suggest an alternative explanation for the evolution of bower-building behaviour. In promiscuous vertebrate species, males who are the most successful reproducers are commonly those who are most aggressive or dominant in intra-sexual interactions (DAVIES 1978). In promiscuous species and especially lek species, males provide no material benefits to females or their offspring. Although direct evidence is lacking, circumstantial evidence suggests that females choose mates based on the quality of genetic benefits the male provides. On mating leks (1) dominant males typically occupy central positions, (2) females strongly favor males who occupy central positions, (3) females often pass over other sexually competent males, and (4) females are willing to wait to mate with a successful male already engaged with another female (see BORGIA 1979). The evolution of lek aggregations is probably related to female preference for grouped males, which arises so that males can be more directly compared (ALEXANDER 1975; BORGIA 1979). Dominant males at central positions on the lek show off their status through their ability to maintain their position even though challenged by other males on the lek. Outcomes of intense aggressive interactions may be the best overall indicator of a male's quality as a sire because this trait provides an effective summary of how genes throughout the male's genome act to affect his development.

In species where males display from dispersed sites, females may find it more difficult to directly compare males to determine their rank. However, if dispersed males have evolved — through the effects of female preference — to engage in ostentatious displays and/or exhibit loud calls, females would have additional cues of a given male's rank. This would be especially important when dispersed males defend only a display site, and do not provide females with any material benefits. BORGIA (1979) has suggested that males able to

exhibit elaborate displays that can be detected at great distances without interruption by other males are able to indicate that they are dominant, high quality males. Thus, the evolution of elaborate, showy plumages in many polygynous species with no male parental care may have occurred because these plumages assist females in finding the most dominant males.

### The Marker Hypothesis

If bower decorations and the bower itself function in place of showy plumage, then behaviour associated with bower construction may have arisen in the same context. Males able to show ownership of defended, decorated display sites give females evidence of their relative quality as a mate. As with the elaboration of plumage, females should favor males who can produce uninterrupted, ostentatious displays from their display sites. Once begun, such selection could lead to the accumulation of decorations for the display site and the construction of bowers. The decorated court and the bowers become, then, a marker of male status and quality. By comparing bowers of different males, a female can assess each male's relative status according to the quality of display at the bower site. This assessment would include evaluation of the degree of elaboration of the display site, and the male's ability to display at his bower without disruption.

The marker hypothesis is especially useful in understanding the complex behaviour of bowerbirds observed in the field. The immediate predictions of this hypothesis are: (1) male-male interactions would center on the bower and males should try to affect the quality of each other's bowers, (2) females should compare the bowers of different males, and (3) female choice should be based on display site characteristics. The first prediction is confirmed from field studies: in most species that have been observed in detail, males frequently raid other males' bowers to steal decorations and destroy bowers (MARSHALL 1954; CHISHOLM and CHAFFER 1956; GILLIARD 1969; BELL 1970; VELLENGA 1970; DONAGHEY 1981; PRUETT-JONES and PRUETT-JONES 1982; BORGIA 1985). In the satin bowerbird, dominant males steal decorations and destroy bowers of nearby subordinates (MARSHALL 1954; VELLENGA 1970; BORGIA 1985). In Macgregor's bowerbird, immature, uncrested males build bowers, but are readily displaced and dominated by adult males (M. A. PRUETT-JONES, unpubl.).

Female satin bowerbirds visit the bowers of several males before mating. 22 adjacent bowers were continuously monitored with cameras through the entire mating season in 1981. Female satin bowerbirds were individually marked, and those seen to copulate visited an average of 3.56 bowers (BORGIA, unpubl. data). This is a conservative estimate of female visitation because not all bowers known in the area could be monitored, and females may be able to assess the quality of some bowers without entering the bower where they would be detected by the monitoring equipment.

The third prediction, that of female choice, has been confirmed in satin bowerbirds (BORGIA 1985). The mating success of males is correlated with the

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number of decorations on bowers. Thus, males able to gather numerous decorations and protect them and their bowers from marauders, achieve the highest number of copulations. Male ability to accumulate bower decorations and maintain a high quality bower appears to serve as an important indicator of male status.

Additional support for the marker hypothesis comes from its ability to provide an explanation for patterns of decoration of bowers. GILLIARD (1956) noted an inverse correlation between the level of bower decoration and the elaborateness of male plumage in species of the genus *Amblyornis*. He called this the "transfer effect" and argued that bowers and bower decorations had become secondary sexual characteristics, and that decorations are a substitute for elaborate male plumage. This hypothesis has recently been supported by an analysis of male plumage and bower decorations for all bowerbirds (BORGIA ms). The existence of the inverse correlation between plumage and bower characteristics supports the hypothesis that these characteristics have been shaped by similar selection pressures. The nest hypothesis provides no explanation for the transfer effect. Other criticisms of the nest hypothesis are not applicable when directed at the marker hypothesis. The marker hypothesis makes no prediction about the shape or location of bowers. Bird behaviour in the decoration and construction of bowers is suggested to have evolved for the same reason, so bower decoration requires no special explanation. The marker hypothesis is consistent with the prevailing view of sexual selection theory and assumes that the same processes that have operated in the evolution of other polygynous species have operated in bowerbirds.

### Other Models for Bower-building

A large number of other hypotheses have been developed to explain exaggerated plumages in birds (see BATESON 1983), and some of these also apply to the evolution of bowers. Among these, the runaway (FISHER 1930), male age (WILBUR et al. 1978; HALLIDAY 1978; HOWARD 1978) and handicap (ZAHAVI 1975, 1977) hypotheses have received most attention and might account for the evolution of bower-building behaviour, however each has important limitations.

Recent models of the runaway process have shown that it might produce a wide variety of outcomes (LANDE 1981; ARNOLD 1983) and there is no a priori reason to expect that bowers or anything like them might be produced by this process. Perhaps most difficult for this model to explain are recurrent patterns such as court clearing and complex displays used in courtship in groups with different evolutionary histories (BORGIA, ms). Given that female selection for male dominance might initiate an episode of runaway, it is possible that patterns of display that recur in different groups exist because these two processes operate together.

The male age model suggests that females may be choosing for the same type of benefits as discussed in the male dominance model, but are using age

instead of dominance as a selective agent. Male age in satin bowerbirds is strongly correlated with the quality of male bowers and male mating success (BORGIA, unpubl.), therefore it is not unreasonable to expect that some female selection for age might be occurring. However, the male age model cannot explain the high levels of bower destruction and it seems most likely that if selection for older males is occurring, it is operating in conjunction with female choice for male dominance.

According to ZAHAVI's hypothesis females favor males with handicaps because males who are able to survive with handicaps indicate their overall fitness to females. ZAHAVI argues (1977) that handicaps should be relatively expensive so that they may be reliable indicators of male quality. However, expensive handicaps should outweigh gains females can expect to receive from such a choice pattern (MAYNARD SMITH 1976; DAVIS and O'DONALD 1976; BELL 1978), so there is little theoretical support for this model. The bower might be viewed as a handicap, but evidence from patterns of male mortality in satin bowerbirds (BORGIA, unpubl.) suggests that bower construction and defense are not as risky an enterprise as would be implied by ZAHAVI's hypothesis.

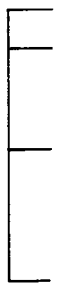
### Cleared Courts as Markers

In considering the evolution of bower building we have followed GILLIARD's suggestion that cleared, undecorated courts were an intermediate stage in the evolution of complex bower-building behaviour. We propose that cleared courts were the original markers, and these were elaborated to form decorated bowers. Courts are common in other species, and these and other types of displays may serve as markers in those species. For instance, a male's display at a recognizable display site, such as a cleared court, gives females information about that male's status. Dominant males might prevent the clearing of courts by other males near their own court, and limit access of other males to courts he has cleared. Courts of the bowerbird *S. dentirostris* or the bird-of-paradise *Diphyllodes* may be examples, however, there have been few observations of these species.

### The Evolution of Bower Structure

The evolution of specific bower types represents an additional problem. Although the bower may function as part of a marker system, the marker hypothesis does not explain the diversity of bower structure seen among the various species. Avenue bowers of all Australian species are typically built at the southern edge of the male's display platform (SERVENTY 1955; PECKOVER 1970; VELLENGA 1970). One possible current function is to orient females toward the male displaying on the brightly illuminated platform. However, this is not a likely function for maypole bowers and probably was not important during the early evolution of avenue bowers.

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The additional complexity of bowers may have evolved because of the protection they provide to females as they are courted by males. The loud displays of males are not only important in sexual competition with conspecific males, but coincidentally alert predators to the bird's presence on the ground. The availability of protected sites might reduce the risk to females during display. The avenue bower offers two exits and the narrow opening at the top allows for overhead viewing by females. The hut-like bowers also offer protection to the female. A predator cannot see or attack the female from above. These bowers have rear exits that allow escape from frontal attack and the central pole would provide a barrier to prevent direct movement of the predator toward the female.

One prediction from the protection hypothesis is that the complex bower structures that provide protection for females should be more common in open unprotected habitats than in situations where natural cover provides protection. Significantly, bowerbirds typically build display sites in more open habitats than those of birds-of-paradise, which clear courts but do not build bower structures. The hypothesis can also be tested by comparisons among bowerbird species. Specifically, the simple maypole bowers of *A. macgregoriae* and *A. flavifrons* and the bower of *Prionodura* that offer no cover for females may represent cases where protection from surrounding vegetation allowed the bower to take on solely a marker function. Within the genus *Amblyornis*, *A. macgregoriae* build open bowers in closed montane forests whereas *A. subularis* builds an enclosed hut-like bower in more open second-growth habitats in lower elevations of the same mountain ranges (H. BELL, pers. comm.). *P. violaceus* and four species of the genus *Chlamydera* build protective bowers in open habitats. *A. papuensis* and *S. dentiostriis*, however, build no stick structures but instead clear and decorate courts in closed forests. *A. inornatus* is an exception to our prediction, whereas the three *Sericulus* species are difficult to categorize. Male *S. chrysocephalis* are most active in dense rainforest, yet their bowers appear to be built in adjacent second-growth areas (BORGIA, pers. obs.). *Sericulus* bowers are similar in form to those of other avenue bower-builders, and should therefore offer some protection against predators. However, it is unclear where and to what extent bowers are built (GILLIARD 1969). We summarize the results of these comparisons in Table 1. In our analysis we

Table 1: Bower structure related to forest type

	Open bower	Closed bower
Open forest		<i>Chlamydera</i> <i>Ptilonorhynchus</i> <i>A. inornatus</i>
Closed forest	<i>Archboldia</i> <i>Prionodura</i> <i>Scenopoeetes</i> <i>A. macgregoriae</i> and <i>A. flavifrons</i> *	<i>A. subularis</i>

\* These species are considered together because it is likely that many characters they share are due to their close relationship.

excluded *Sericulus* and grouped species of a genus that shows the same bower-building and habitat preferences. There is a tendency for protective bowers to be in open habitats and this is supported by a chi square test ( $\chi^2 = 4.08$ ,  $p < .05$ ), but not a Fisher's exact test ( $p > 0.1$ ).

Protection is, however, an unlikely explanation for the evolution of early bower-building tendencies. Incipient bowers must have involved only a few sticks; it is unlikely that these structures could have offered any significant protection. By contrast, court-clearing probably preceded bower-building, so it is likely that generalized selection for markers operated even before bowers occurred.

### Conclusions

We propose that bowers and bower-building behaviour evolved as part of a general mechanism to allow females to accurately assess relative status and quality of males and, therefore, their quality as mates. The bower and its decorations may thus represent a "marker" of the resident male's aggressive abilities. Males displaying at high quality markers are likely to be dominant in local populations, and we assume that dominant males are most often the best choice of mates for females when males offer no material contribution to females or their offspring. The use of markers may be especially important when males are dispersed and females cannot directly compare males. The marker hypothesis suggests possible avenues by which multiple-male displays and terrestrial display courts evolved. Whereas evolution of bower-building behaviour is viewed as being initiated by selection operating through the marker hypothesis, bower architecture is suggested to have evolved as a means of protecting females from predators during male display.

### Zusammenfassung

Nach unserer Ansicht entwickelten sich die Lauben und das Laubenverhalten der Vögel im Rahmen allgemeiner Mechanismen, die dem Weibchen eine genaue Schätzung des relativen Status und der Qualität des Männchens ermöglichen. So mögen die Laube und ihr Schmuck Anzeiger der aggressiven Fähigkeit des ansässigen Männchens sein. Männchen, die sich neben einem Anzeiger für hohe Qualität zur Schau stellen, werden wahrscheinlich in der Nachbarschaft dominierend sein, und wir nehmen an, daß dominierende Männchen auch die beste Wahl für das Weibchen sind, wenn diese ihm oder seinen Jungen materiell nichts anbieten können. Der Gebrauch von anzeigenden Zeichen mag höchst wichtig sein, wenn Männchen weit zerstreut leben und die Weibchen keine Möglichkeit haben, die Männchen direkt zu vergleichen. Die Anzeiger-Hypothese schlägt Wege vor, auf denen sich männliche Schaustellung und terrestrische Balzarenen entwickelten. Die Variation in der Laubenstruktur wird als ein Mittel angesehen, während der männlichen Schaustellung das Weibchen vor Räubern zu schützen.

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