Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis

GERALD BORGIA

Department of Zoology, University of Maryland, College Park, MD 20742, U.S.A.

Abstract. Bowerbirds build large bowers of twigs decorated with brightly coloured objects at display sites where males court females. The bower and its decorations are hypothesized to influence female choice in these birds. However, there have been no empirical tests of this hypothesis. Data from two years of field research on the satin bowerbird (*Ptilonorhynchus violaceus*) show: (1) an extremely skewed distribution of matings among males, and (2) a consistent pattern of female preference for particular males, especially those with well-constructed, highly-decorated bowers. These results support the hypothesis that bower quality is important in influencing female mating preferences. In particular, they support the 'marker' hypothesis, which suggests that the construction of bowers evolved to provide females with information about the relative quality of males.

The causes of female mate preference in species in which males contribute no material benefits (e.g. food, nest sites) to females or their offspring have become an issue of great interest to evolutionary biologists (Fisher 1930; Alexander 1975; Emlen & Oring 1977; Halliday 1978; Borgia 1979; West-Eberhard 1979; Thornhill 1980; Bradbury 1981; Andersson 1982; Hamilton & Zuk 1982; Searcy 1982). In many species with such mating systems, males aggregate to perform sexual displays in groups called leks. Often there is a decided skew in mating success among males, and a small number of males account for the vast majority of matings, at least over a single season (Davies 1978). Distinct female preference for some males has been related to male position on leks where females commonly choose males in central positions (Buechner & Roth 1974; Davies 1978; Borgia 1979). In numerous species, however, males make no material contribution to females, yet are dispersed while displaying. Gilliard (1969) has called these 'exploded arenas'. Little is known about how matings are distributed on exploded arenas and why males in some species display alone rather than in groups.

The unique behaviour associated with bower-building in male satin bowerbirds, *Ptilonorhynchus violaceus*, is well suited for testing hypotheses about the evolution of male display and related patterns of female choice. The male satin bowerbird's bower consists of two parallel walls made of fine twigs that stand on a court cleared on the ground. The walls are 10 cm apart and form a 30-cm central avenue. Males decorate a stick platform on the north end of their bowers with a variety of objects including feathers, flowers and snake skins. Bowers are used as sites for courting females, and mating takes place inside the bower; males steal decorations and destroy the bowers of other males (Marshall 1954; Gilliard 1969; Bell 1970; Vellenga 1970, 1980; Donaghey 1981). Bowers are typically spaced more than 100 m apart in forested areas, and males actively defend the immediate area around the bower from other intruding males. This behaviour makes this species especially valuable for testing hypotheses about the evolution of female choice, because the bower and its decorations can be easily quantified, decorations on bowers can be experimentally manipulated without directly affecting the bird, and the bower provides a site where matings will occur and can be monitored. Although it has been frequently suggested that the quality of the bower and its decorations may influence female mating decisions (Marshall 1954; Gilliard 1969; Vellenga 1970; Wilson 1975), this hypothesis has not been tested with quantitative data on the mating behaviour of bowerbirds. Here I describe a study designed (1) to determine the distribution of matings among males in an expanded lek mating system, and (2) to relate patterns of male mating success to the quality of the bower and bower decorations. These results are then used to evaluate models for the evolution of bower-building behaviour.

ıale
ıalysis

.A.

ıt display sites
nale choice in
ı years of field
listribution of
les, especially
ıis that bower
t the 'marker'
ı information

ıntral avenue.
e north end of
ıcts including
wers are used
ng takes place
orations and
Iarshall 1954;
1970, 1980;
ı spaced more
s, and males
ı around the
his behaviour
le for testing
ımale choice,
ı can be easily
an be experi-
y affecting the
ıhere matings
though it has
ıuality of the
uence female
Iilliard 1969;
ypothesis has
data on the
e I describe a
istribution of
ıd lek mating
male mating
r and bower
ıd to evaluate
uilding beha-

METHODS

This research was carried out in 1980 and 1981 in open-canopy eucalyptus forest at Wallaby Creek, Beaury State Forest, New South Wales, Australia. In 1980 an experiment was performed in which decorations were removed from some bowers and others were left intact. In 1981 bowers were monitored with no experimental manipulation. In each year daily records were kept on the number and type of decorations on bowers, and on the quality of bowers. Twenty-two bowers were monitored by super-8 movie cameras controlled by interval timers, and observed by a team of five field observers. The camera monitoring system was improved in 1981, with detectors that started cameras when an invisible infrared beam passing through the bower avenue was broken.

In each year 22 of the most active bowers of adult-plumage males were selected for continuous monitoring. In 1980, 22 bowers were assigned to pairs on the basis of numbers of bower decorations. One member of each pair was randomly assigned to the control group and the other to the experimental group. Bowers of the experimental group had all decorations except three yellow leaves removed daily. Yellow objects are commonly held in the male's beak during active displays to females. Three yellow leaves were left on each removal bower so as not to hamper the male's ability to display. Leaves are the most commonly used display object, and they occurred on all bowers. No decorations were removed from bowers in the control group. In both years the numbers of each of nine types of bower decorations, and estimates of four characteristics of bower quality, were recorded daily for each group. The classes of decorations counted and recorded were: blue feathers, snail shells, yellow blossoms, blue blossoms, yellow leaves, yellow straw, cicada skins, other natural objects (mostly insect parts), and man-made objects. Bower characteristics were ranked by observers with no prior knowledge of male mating success into four categories, from excellent to poor. Bowers were similarly evaluated for symmetry of structure, stick size, stick density, and overall quality of construction. Bowers receiving the highest overall rank were symmetrical, had fine straight sticks, sticks packed close together, and thick curved walls.

Spearman (r_s) and Kendall (r_k) rank correlations are used because of small sample sizes and an irregular pattern of variance in the 1980 data set. These tests were also used in 1981 to allow direct comparisons between years.

Observer presence at the bower appeared to be the major disruptive factor resulting from experimental manipulations in 1981. However, because of time spent by observers counting decorations and marking feathers for other experiments, this effect was equivalent between experimental and control groups.

RESULTS

In 1980 a total of 15 copulations were recorded among bowers that were monitored, and in 1981, with the improved camera system, 212 copulations were recorded. The distribution of matings among males is shown in Table I and Fig. 1. Data for both

Table I. Numbers of copulations by male bower owners in 1980 and 1981

Bower no.	No. of 1980 copulations by owner	No. of 1981 copulations by owner
1	0	—
2	0	—
3	0	3
4	0	5
5a*	0	—
5b	—	8
6	2	20
7	0	4
9	4	33
10	0	1
11	0	0
12	3	25
13	3	21
14	0	—
15	1	21
16	2	13
17	0	3
18	0	12
19	0	14
22	0	6
23	0	—
28	0	—
29	0	3
30	—	1
31	—	9
32	—	3
36	—	1
37	—	1

* A new male (5b) took over bower 5 in 1981.
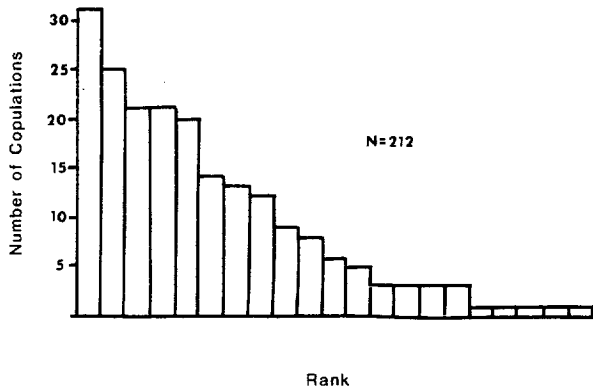
Animal Behaviour, 33, 1

Figure 1. The distribution of copulations among males of the study population in 1981. Males are ranked by decreasing numbers of copulations observed. $\bar{X}=8.9$; $\text{SD}=9.2$.

years, but especially 1981, show a strong skew in the distribution of matings among males. In 1981 the top five males accounted for 56% of all matings. This pattern is similar to that observed for true lek species (Davies 1978). These results probably underestimate the variation in male reproductive success, because I biased the bowers that were monitored in favour of well-decorated bowers, which are more attractive to females (see below), and because many young but reproductively competent males do not own bowers. There is also a significant correlation between years in the relative success of males ($r_k = 0.666$, $P < 0.05$). These results suggest that relatively high variation in male mating success occurred in both years, and that the females showed a consistent bias in favour of some males.

For the 1980 removal experiment I predicted that if bower decorations and quality had important effects on male mating success, then: (1) males in the group that retained its decorations should mate more often than males in the group from which decorations were removed, and (2) the number of decorations present on bowers should be positively correlated with male mating success. Moreover, by examining the relationship between various characteristics of the bower (including decorations), the relative importance of each characteristic in affecting female mating decisions could be estimated. Of the 15 observed copulations, 12 occurred in the control group and three in the experimental group (binomial $P = 0.018$). This result supports the prediction of a higher level of mating success in the control group.

I attempted to determine if males from whose bowers decorations had been removed might be deterred in their attempts to court and display to females. However, my data suggest that experimental manipulations had no important direct effect on attempts by males to mate. There were no differences between treatment groups in the time owners spent near bowers ($t_{21} = 0.13$; $P = 0.90$), the frequency of display by owners ($t_{21} = 0.53$; $P = 0.60$), and in visitation rates by green (juvenile male and female) birds ($t_{21} = 0.45$; $P = 0.66$).

The hypothesis that a male's bower decorations significantly influence his mating opportunities is also supported by positive correlations between the mean number of each type of bower decoration and mating success for males of the control group. Comparisons are restricted to the 11 bowers in the control group, because the number of decorations on these bowers was not directly affected by experimental manipulations. Spearman rank correlations of male mating success and the mean number of each of the nine types of bower decorations show that the number of blue feathers and number of snail shells (Table II) are significantly correlated with male mating success.

In 1981, comparisons were based on correlative relationships between decoration and bower variables and male mating success from all 22 bowers. Significant rank correlations occurred between

Table II. Spearman rank correlation between mean numbers of the nine decoration types and male mating success

Decoration type	1980 ($N=11$)	1981 ($N=22$)
Yellow leaves	0.514	0.365
	(0.064)*	(0.043)
Yellow straw	0.3496	0.175
	(0.161)	(0.213)
Blue feathers	0.784	0.461
	(0.004)	(0.013)
Snail shells	0.665	0.536
	(0.018)	(0.004)
Blue blossoms	0.225	0.334
	(0.266)	(0.059)
Yellow blossoms	0.438	0.187
	(0.102)	(0.197)
Cicada skins	0.124	0.219
	(0.367)	(0.158)
Man-made objects	0.092	0.332
	(0.400)	(0.060)
Natural objects	0.075	0.286
	(0.418)	(0.093)

* Parentheses indicate P values.

ed might be
nd display to
at experimen-
irect effect on
ere no differ-
e time owners
·90), the fre-
53; $P=0·60$),
nile male and

r decorations
portunities is
s between the
:coration and
ntrol group.
bowers in the
f decorations
affected by
an rank cor-
nd the mean
bower deco-
feathers and
significantly

n correlative
l bower vari-
ill 22 bowers.
red between

between mean
d male mating

1981 ($N=22$)

0·365
(0·043)
0·175
(0·213)
0·461
(0·013)
0·536
(0·004)
0·334
(0·059)
0·187
(0·197)
0·219
(0·158)
0·332
(0·060)
0·286
(0·093)

---

male mating success and the following decoration types: number of blue feathers, number of snail shells, and number of yellow leaves. In Table II, comparisons of the 1980 and 1981 data show that the same two variables had the highest correlations with male mating success in each year. The occurrence of highly significant correlations ($P < 0·02$) in successive years involving the same variables makes it unlikely that the correlation of either of these two variables with male mating success is caused by chance.

The large number of copulations observed in 1981 allowed me to analyse the relative contribution of specific decoration types toward explaining the variation in male mating success. A stepwise regression procedure showed that the number of snail shells explained the greatest amount of variation associated with male mating success ($F_{1,21} = 5·48$, $r^2 = 0·21$); no other decoration variable provided a significant increase in the level of variance explained. This result is largely due to the high correlation among the decoration variables, especially those which have been shown to be significantly correlated with male mating success. For example, the number of snail shells and blue feathers were highly correlated ($r_s = 0·68$, $P = 0·001$).

Indices of bower quality also showed significant correlations with male mating success in the 1981 data. All four measures of bower quality were significantly correlated with male reproductive success: symmetry of structure ($r_s = 0·587$, $P = 0·002$), stick size ($r_s = 0·532$, $P = 0·01$), stick density ($r_s = 0·42$, $P = 0·024$), and quality of construction ($r_s = 0·54$, $P = 0·004$). Inclusion of these variables in a stepwise regression analysis with decoration variables significantly increased the level of explained variation. Three variables, symmetry of structure, number of snail shells, and number of yellow leaves, contributed significantly toward explaining the variation in male mating success ($F_{3,19} = 3·69$, $r^2 = 0·368$, $P < 0·05$).

DISCUSSION

Marshall (1954), Gilliard (1969) and Diamond (1982a,b) have argued that bower-building behaviour arose because females and males need a courtship nest to synchronize mating. This hypothesis is weak because it fails to explain the absence of similarity between bowers and nests, the occur-

rence of bowers on the ground (whereas nests of all 18 bowerbird species are in trees), and the lack of any evidence from either court-clearing bowerbirds that do not build bowers, or other species, that females require a bower to stimulate ovulation (Borgia et al., in press, provide a more detailed discussion of the evolution of bowers and courts).

Alternative hypotheses based on more generally accepted models of sexual selection seem to provide more likely explanations of bower evolution. It has been frequently suggested that females prefer aggressively dominant males because these males are able to demonstrate their vigour relative to other males and thus indicate their quality as sires (Trivers 1972; Alexander 1975; Halliday 1978; Borgia 1979; Searcy 1982). In species in which males contribute no material benefits to females, male dominance status on leks is often associated with the ownership of a central territory. Thus, it is possible for females to judge a male's status by his position on a lek (Davies 1978; Borgia 1979). Displaying male bowerbirds do not aggregate, and because a male's status might otherwise be difficult to judge, bowers may function as markers that convey information to females about the relative quality of males. By their ability to build, maintain, and display at high-quality bowers, despite the attempts of other males to destroy bowers and steal decorations, males give females a means of assessing their dominance status and, ultimately, their quality as mates (Borgia et al., in press). The marker hypothesis is attractive because it explains the use of a cleared and sometimes decorated display site, which is common among species like bowerbirds with exploded leks. In addition, it suggests that the ultimate basis for female choice may be the same in all species where males make no material contribution to females. Female bowerbirds may be different only in how they assess male quality. Gilliard (1956) noted that bowerbird species with the most highly decorated bowers tend to be those with males that have the dullest plumage. Through what he called the transfer effect, Gilliard argued that bright plumage has been replaced by bower decorations. This equivalence suggests that bowers, bower decorations and plumage may have similar functions in sexual selection. Thus the test of this hypothesis can be seen as a test of a more general model.

If the marker hypothesis is correct, then aggressively dominant males should have high-quality bowers and these males should be most successful

in attracting females. The data presented here show a relationship between bower quality and male mating success. I assessed dominance from male interactions at feeding sites and the relative ability of males to prevent destruction of their own bowers. Success in agonistic encounters at feeding sites was positively correlated with mating success (Borgia, unpublished data). Bowers that are destroyed are often bowers of lower-than-average quality. Significant correlations in the predicted direction were found between the number of times a bower was destroyed and three of four measures of bower quality (stick density, quality of construction and stick size; Borgia, unpublished data). In addition, male mating success was inversely correlated with both the frequency at which a male's bower was destroyed and the rate at which decorations were stolen from a male's bower (Borgia, unpublished data). Thus the available data support the relationship between male dominance, bower quality and male mating success that was predicted by the marker hypothesis.

These results are also consistent with a second hypothesis, which proposes that females have evolved to prefer males with well-decorated bowers independently of the effects of male dominance. It is possible that female preference for elaborate displays may have evolved through Fisher's (1930) runaway process. The correlations between male dominance and bower quality may have evolved secondarily as a result of selection on males to compete for decorations necessary to produce well-decorated bowers. Additional experiments on the mating behaviour of satin bowerbirds should help clarify which of these models is correct. For example, the consistent pattern of female preference for males who are able to accumulate feathers and snail shells as decorations on their bowers suggests that these objects, which seem rare compared to the other decorations used (Borgia, unpublished data), may be preferred because only the most dominant males can accumulate these decorations on their bowers in large numbers. A model in which female preferences were established independently of the advantages to females of choosing dominant males would not predict this result.

ACKNOWLEDGMENTS

REFERENCES

Alexander, R. D. 1975. Natural selection and specialized chorusing behavior in acoustical insects. In: *Insects, Science, and Society* (Ed. by D. Pimentel), pp. 37–77. New York: Academic Press.

Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature, Lond.*, **299**, 818–820.

Bell, H. 1970. Brown 'painting' by Lauterbach's bowerbird. *Emu*, **66**, 353.

Borgia, G. 1979. Sexual selection and the evolution of mating systems. In: *Sexual Selection and Reproductive Competition* (Ed. by M. & A. Blum), pp. 19–80. New York: Academic Press.

Borgia, G., Pruett-Jones, S. & Pruett-Jones, M. In press. The evolution of bowers as markers of male quality. *Z. Tierpsychol.*

Bradbury, J. 1981. The evolution of leks. In: *The Evolution of Social Behavior* (Ed. by R. Alexander & D. Tinkle), pp. 138–169. Concord, Massachusetts: Chiron Press.

Buechner, H. K. & Roth, A. H. 1974. The lek system in the Uganda kob antelope. *Am. Zool.*, **14**, 145–162.

Davies, N. B. 1978. Ecological questions about territorial behavior. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 317–350. Sunderland, Massachusetts: Sinauer.

Diamond, J. 1982a. Rediscovery of the yellow-fronted gardener bowerbird. *Science, N.Y.*, **216**, 952.

Diamond, J. 1982b. Evolution of bowerbirds' bowers: animal origins of aesthetic sense. *Nature, Lond.*, **297**, 99–102.

Donaghey, R. 1981. Parental strategies in the green catbird (*Ailuroedus crassirostris*) and the satin bowerbird (*Ptilonorhynchus violaceus*). Ph.D. thesis, Monash University, Melbourne, Victoria.

Emlen, S. & Oring, L. 1977. Ecology, sexual selection,

and specialized
cts. In: *Insects,*
tel), pp. 37–77.

cts for extreme
., **299,** 818–820.
rbach's bower-

ne evolution of
d Reproductive
pp. 19–80. New

es, M. In press.
nale quality. *Z.*

leks. In: *The*
Alexander & D.
husetts: Chiron

ne lek system in
14, 145–162.
bout territorial
n Evolutionary
B. Davies), pp.
Sinauer.
yellow-fronted
5, 952.
rbirds' bowers:
re, Lond., **297,**

s in the green
he satin bower-
thesis, Monash

exual selection,

and the evolution of mating systems. *Science, N.Y.,* **197,** 215–223.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection.* Oxford: Clarendon Press.

Gilliard, E. T. 1956. Bower ornamentation versus plumage characters in bowerbirds. *Auk,* **73,** 450–451.

Gilliard, E. T. 1969. *Birds of Paradise and Bowerbirds.* London: Weidenfeld & Nicholson.

Halliday, T. 1978. Sexual selection and mate choice. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 180–213. Sunderland, Massachusetts: Sinauer.

Hamilton, W. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science, N.Y.,* **218,** 384–387.

Marshall, A. J. 1954. *Bower-birds: Their Displays and Breeding Cycles.* Oxford: Clarendon Press.

Searcy, W. 1982. The evolutionary effects of mate selection. *Ann. Rev. Ecol. Syst.,* **13,** 57–85.

Thornhill, R. 1980. Competitive, charming males and choosy females: was Darwin correct? *Fla Entomol.,* **63,** 5–30.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. G. Campbell), pp. 136–179. Chicago: Aldine Press.

Vellenga, R. 1970. Behavior of the male satin bower-bird at the bower. *Austral. Bird Bander,* **1,** 3–11.

Vellenga, R. 1980. Distribution of bowers of the satin bowerbird *Ptilonorhynchus violaceus. Emu,* **81,** 27–33.

West-Eberhard, M. J. 1979. Sexual selection, social competition, and evolution. *Proc. Am. Phil. Soc.,* **123,** 222–234.

Wilson, E. O. 1975. *Sociobiology.* Cambridge, Massachusetts: Belknap Harvard.