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THE COST OF DISPLAY IN THE NON-RESOURCE-BASED MATING SYSTEM OF THE SATIN BOWERBIRD

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Abstract.—Cost of display has emerged as a prominent theme in some recent discussions of models that attempt to explain the evolution of exaggerated sexual display traits in males. Here I use comparative and experimental information from an 8-yr field study of the satin bowerbird (*Ptilonorhynchus violaceus*) to test predictions from sexual selection models that focus on the cost of male display. Two of these models predict a high absolute cost of male display when extended to the satin bowerbird. Eight different tests showed no evidence of the predicted high cost of display, and four produced significant results in the opposite direction. These results are consistent with the claim that truthful advertising need not be costly and Gilliard's suggestion that there has been selection for reduced cost of male display among bowerbirds. Evidence showing that exaggerated male display traits do not have a high absolute cost may help resolve the long-standing question of how these displays evolve.

Darwin (1871) proposed that female choice causes the evolution of extreme male display traits. Recent studies of species that have evolved some of the most elaborate of these male displays appear to support Darwin's claim. In these species, a small proportion of males commonly achieve a high fraction of copulations (see, e.g., Gibson and Bradbury 1986, table 17.1), and males with the most elaborate displays are favored by females (Andersson 1982a, 1989; Borgia 1985a; Gibson and Bradbury 1986; Höglund and Lundberg 1987; McDonald 1989).

A multisided argument persists over the mechanisms by which female choice could promote the evolution of extreme male display traits (see Bradbury and Andersson 1988). A critical and still unresolved issue in this discussion involves the cost of these traits. At least two of the many sexual selection models developed to explain extreme male display attribute a significant role to display costs. Lande's (1981) quantitative genetic model of female choice holds that a stable line of equilibrium results from the conflicting forces of female choice for the elaborated male trait and costs arising from expressing them. A prediction of this model is that at equilibrium these two forces should balance. Thus, for cases in which there is a steep selection gradient associated with the female preference (where males who express the most extreme form of the trait gain high mating success), a high cost of male display is expected.

In Zahavi's (1975) discussion of his handicap model, costly male display traits may evolve because they provide females with reliable information about male

ability to sire high-viability offspring. Zahavi says, "A mature, colorful male has already proved itself to be of better quality (than one with cryptic plumage) since it has already withstood the extra predation risk involved in its plumage" (p. 210). In this scenario, exceedingly high levels of predation would be necessary to provide females with information about even a small improvement in male quality (Borgia 1986). High costs might also be necessary to produce effective display in some other versions of the handicap model (see, e.g., Andersson 1982b; Kodrick-Brown and Brown 1984; Nur and Hasson 1984; Grafen 1991), in which females assess male ability to produce expensive traits such as deer antlers. The effectiveness of such cost-dependent mechanisms for advertising male vigor has been questioned by Davis and O'Donald (1976) and Maynard Smith (1976), who pointed out that the cost of display must be subtracted from benefits females receive from the overall increase in offspring viability.

An alternative view is that displays with a high absolute cost may not be necessary for producing truthful advertising of male quality. Other good-genes models suggest that inexpensive displays may accurately reveal a male's overall condition. For example, elaborate male dominance signals may become reliable, inexpensive indicators of male quality (Borgia 1979). Bright male plumage, which may indicate disease resistance (Hamilton and Zuk 1982), may not be expensive for disease-free males. Recently, Michod and Hasson (1990) have developed mathematical models consistent with the possibility of low-cost male display traits that are reliable indicators of male fitness. Models of sensory exploitation (Burley 1985; Ryan et al. 1990) have no requirement for costly displays.

Attempts to measure reproductive costs for females have often been unsuccessful (see, e.g., Bell and Koufopanou 1986). By contrast, costs to males in highly polygynous species have been frequently demonstrated. These include high costs associated with advertising displays that result in increased predation (Bell 1979; Ryan et al. 1982), increased parasitization (Cade 1975), and decreased growth rate (Given 1988). In elephant seals (LeBoeuf 1974) and red deer (Clutton-Brock et al. 1982), it is common for males to be highly successful harem masters for only a single season. This short opportunity of reproduction is attributed to very high reproductive costs.

There have been few attempts to measure display costs in species with exaggerated male traits. Møller (1989) found that, in the swallow *Hirunda rustica,* males with experimentally lengthened tails were preferred by females but that these males were less efficient foragers (Møller 1988) and had decreased fledgling success the following year. However, because males have an important role in caring for offspring, it is not clear how these findings may be generalized to cases in which males have extreme display characters but contribute only sperm. Vehrencamp et al. (1989) found high energy expenditures associated with male display in sage grouse but did not determine if these expenditures translated into significant reductions in future ability to reproduce.

Here I test the general hypothesis that there is a formidable cost of display in the satin bowerbird, *Ptilonorhynchus violaceus*. Gilliard (1956, 1969) has argued that bowerbirds have replaced bright plumage displays with building and decorating elaborate bower structures. Because these displays are not carried by the

bird, bower displays can be easily quantified and are amenable to experimental manipulation. Satin bowerbirds mate in the bower, and monitoring bowers with cameras allows the opportunity to score male mating success. Both bower decorations and bower quality appear to influence female mating decisions (Borgia 1985a). Because satin bowerbird bowers are on the ground and hidden by vegetation, it is unlikely that they function in male signaling of aggression or as long-distance mate attraction signals for females.

Although the issue of costs of display has received considerable attention in discussions of sexual selection (see, e.g., Maynard Smith 1991), there has been little effort to define display costs explicitly. For species like satin bowerbirds, in which males have no role in parental care, the costs of display result from two major causes: mortality that disqualifies males from additional reproduction or reductions in vigor or energy reserves that affect the quality of future display. Thus, the costs of display must be measured by the effect behaviors and associated morphological traits have on the future ability of males to produce attractive displays.

Both the cost-dependent version of the handicap model (the pure epistasis model; Maynard Smith 1991) and Lande's (1981) quantitative genetic model for runaway sexual selection, when applied to the satin bowerbird, predict a high cost of display. In the original handicap model (Zahavi 1975), high costs are part of the mechanism allowing females to choose vigorous males effectively. In satin bowerbirds, there is a strong female preference for males with well-built and well-decorated bowers (Borgia 1985a), which indicates a steep selection gradient for these male display traits. Under these conditions, Lande's (1981) quantitative genetic model predicts that steep selection gradients are balanced by a high cost of male display.

Here I use information derived from an 8-yr field study of the satin bowerbird to test the claim that successful male displays require costly effort that severely diminishes a male's prospects for future reproduction. I develop eight subhypotheses designed to evaluate the general hypothesis of a high absolute cost for male display. I include all relevant comparisons from my work on satin bowerbirds that bear on the issue of costs associated with male display. Tests of these hypotheses use independent data sets and address different aspects of the problem of the cost of display. The hypotheses overlap to the extent that they address the same general question. Multiple tests of related independent hypotheses reduce the possibility that important large costs of display will go undetected.

METHODS

Data used in this study were collected from August 1980 through September 1988 at Wallaby Creek, in the Beaury State Forest, 120 km northwest of Lismore, New South Wales, Australia. An area 1.5 km in each direction from capture sites was thoroughly surveyed for bowers, and the identity of the owner was determined for each bower. Birds were captured in baited traps and removed immediately. The birds were color banded, scored for plumage characters and number of ectoparasites, weighed, measured for wing length, and then immediately re-

leased. In 1986 there was a drought associated with extremely low temperatures late into the typical mating season. Some males uncharacteristically failed to maintain bowers during the mating season, and nearly all showed atypical weight loss and loss of muscle mass.

Plumage and beak color and measurements of wing length can be used to determine the age and sex of satin bowerbirds (see, e.g., Vellenga 1979). I estimated males' ages from my records of the dates when they obtained adult plumage (Borgia 1986).

Each permanent bower site was monitored by a camera controlled by an infrared device that triggered the camera when birds entered the bower (Borgia 1985a, 1986). Matings occurred in the bower, and the camera system provided continuous monitoring at bowers throughout the entire mating season. Male mating success (Borgia 1985a) was tabulated from film taken at each male's bower.

Decorations were counted, and bower quality estimates were made on daily visits to bowers (Borgia 1985a). Counts of all decoration types except yellow straw represent the total number of that type of decoration on the display court and on the bower. Yellow straw count represents the number of pieces of straw crossing a diagonal running from northeast to southwest across the display court. The data were reduced by taking seasonal means of decorations to represent values for individual decoration variables.

Male survival rate was assessed by observations of returns by bower owners to bower sites in successive years, observations and film records of males stealing decorations or destroying bowers of other bower holders, and censuses of males at trapping sites and at bowers adjacent to the study area (see, e.g., Borgia 1986; Collis and Borgia 1992). These diverse methods of censusing make it very unlikely that surviving birds were undetected. Males at permanent bower sites were extremely faithful to their bower territories; fewer than 3% of males moved to a different territory once becoming established at a site. Moreover, food at trapping sites was very attractive to birds and drew in bower holders from a much wider area than the study site so that, if a missing male had moved, it is likely that he would have been detected at trapping sites. None of the known bower holders that were missing at bowers and trapping sites in 1 yr reappeared in any context in a later year.

For comparisons of within- and between-season mortality rates, an expected proportion of deaths in and out of the mating season was generated by multiplying the proportion of "in-season" months (3/12) and "out-season" months (9/12) by the total number of deaths.

Estimates of male longevity on bowers were complicated by the long tenure of males at their bower sites and the problem of interpreting incomplete records of male presence on bowers. Several males were present on bowers through the 8 yr of the study. Other males started on bowers and disappeared or started on bowers and were still present at the end of the study. Males were rank ordered by the length of time they were known to be bower holders, and ranks for males were adjusted upward for those who were residing at bowers at either the beginning or end of the study. Males were given a one-rank increase for being present at the beginning or still on bowers at the end of the study and a two-rank increase

TABLE 1

Seasonal Male Mortality at Permanent Bower Sites

Year	Deaths outside Mating Season	Deaths during Mating Season	Total Deaths
1980	. . .	1	1
1981	0	0	0
1982	3	0	3
1983	3	1	4
1984	4	1	5
1985	4	1	5
1986	4	1	5
1987	4	0	4
1988	0	. . .	0
Observed	22	5	27
Expected	21.3	5.7	27

if present at both the beginning and end. These ranked data were then used in Spearman correlations with decoration numbers to evaluate effects of length of tenure on the degree of bower decoration.

Blue plastic squares (2.5 cm^2) were used in an experiment to assess the effect of decoration numbers on male use of bower decorations. Males were divided into two groups in 1984. Twenty plastic chips were placed on the display courts of one group, and the other group received none. My research assistants and I made these chips resistant to stealing by gluing them to the heads of 10-cm nails and then inserting the nails into the ground. Five days after the initial placement of chips, piles of five chips without attached nails were placed at the edge of the display courts of males in both treatment groups. Movement of chips onto courts was recorded twice daily over the next 3 d. Here I report the total number of chips moved onto bowers over this period.

Males improve the quality of their bowers as they age (Borgia 1986a; Collis and Borgia 1992). I adjusted for male age with a residuals analysis. Additional statistical methods included Student's t-test (t), Spearman rank correlation (r_s), and χ^2 analysis.

Tests of Hypotheses

Hypothesis 1. If there is a high cost to bower building and associated displays, then mortality should be higher for bower holders during the mating season than outside the season when bowers are not maintained.

If bower building, decoration, and display increase male risk from predators, as suggested in the quotation from Zahavi (1975) above, then comparisons of mortality inside and outside the mating season should indicate these costs. This test does not evaluate display costs that might occur after the mating season (e.g., increased mortality related to spent energy reserves).

Result. There was no difference between the expected and observed proportion of deaths inside and outside the mating season (table 1). The absence of a

TABLE 2

CORRELATION OF THE NUMBER OF YEARS A MALE CONTROLS A
BOWER SITE AND BOWER CHARACTERS ADJUSTED
FOR AGE-RELATED IMPROVEMENT

Character	Partial Correlation	P Value
Quality of construction	.42	.01
No. of yellow leaves	.05	NS
Yellow straw count	− .02	NS
No. of blue feathers	.24	.10
No. of snail shells	.19	.19
No. of yellow blossoms	.14	.36
No. of blue blossoms	.04	NS
No. of cicada skins	− .14	.36
No. of natural objects	.15	.32
No. of man-made objects	.24	.09
Total no. of decorations	.26	.07

NOTE.—$N = 49$; NS $= P > .40$.

difference in mortality rates supports the null hypothesis that males are no more susceptible to dying inside than outside the mating season. The overall mortality among male satin bowerbirds holding permanent bowers was 7.42% per year.

HYPOTHESIS 2. If the evolution of elaborate bower displays is limited by the risks taken in building and decorating bowers, then male longevity on bowers should be inversely correlated with bower quality and degree of decoration.

This test is designed to measure the effects of high costs of display that may take place both inside and outside the mating season. It was noted earlier that, in species with a high degree of polygyny, it is not common for males to repeat as dominant reproducers. The cost of maintaining high status through a mating season significantly lowers their residual reproductive value. Hence, for species with costly, highly elaborate displays, a similar boom-and-bust pattern of reproductive behavior should exist. This should be reflected in the patterns of male mortality (hypothesis 2), quality of bower displays (hypothesis 3), and the overall patterns of reproduction (hypothesis 4). These tests are best suited for evaluating predictions of high-cost models that assume no association between the magnitude of a male's display and his overall quality (see, e.g., Lande 1981).

Result. Table 2 shows the correlation of male longevity on bowers compared with the degree of bower decoration and the quality of bower construction, both corrected for age-related improvement of bowers. Four variables, including quality of construction and total number of decorations, showed significant or near-significant positive correlations, but these were all in an opposite direction to what was predicted by the high cost of display hypothesis. This result suggests that long-lived males tend to have better-constructed bowers with more decorations.

HYPOTHESIS 3. If bower characters attractive to females require extreme expenditures of male effort, then there should be reversals in bower quality and degree of decoration between years.

TABLE 3

CORRELATION OF BOWER CHARACTERS BETWEEN 1981 AND 1982

Character	Spearman Correlation	P Value
Quality of construction	.57	.001
No. of yellow leaves	.53	.004
Yellow straw count	.62	.001
No. of blue feathers	.38	.06
No. of snail shells	.63	.001
No. of yellow blossoms	.10	.33
No. of blue blossoms	.53	.004
No. of cicada skins	.56	.002
No. of natural objects	.02	.31
No. of man-made objects	.71	.001
Total no. of decorations	.54	.004

NOTE.—$N = 28$.

Like the red deer discussed previously, males who expend a great deal of time and energy in 1 yr should be weakened by costly bower building and so should be unable to mount the same high level of effort the next year.

Result. Bower quality and the number of decorations used by individual males in 1981 and 1982 (table 3) all showed positive correlations. The summary variables bower quality and total number of decorations were both highly significant. Six of nine variables describing the number of individual decoration types were also significant, and another was marginally significant. Experimental manipulation of decorations precluded meaningful comparisons of decorations with 1983 and later years. Bower quality comparisons could be made between 1982 and 1983, and these were highly significant ($r_s = 0.74$, $N = 24$, $P < .001$). The strong positive correlation between years in bower quality and decoration traits fails to support the hypothesis that the production of a high-quality display in 1 yr severely reduces male ability to produce a high-quality display in the next year.

HYPOTHESIS 4. If there are especially high costs associated with obtaining matings, then male mating success should be negatively correlated in successive years.

Males who expend a high level of effort to obtain matings in 1 yr should be sufficiently exhausted from these activities so that they are unable to expend the same level of effort and attract as many mates the next year.

Result. Correlations in reproductive success for males between years are significant and positive except for 1986 (table 4). The differing results in correlations involving 1986 are probably because of unusual conditions that year. A drought and unusually cold weather may have caused some males to desert their bowers. That season was atypical because numerous birds from other species were found dead, and the peak in mating activity for satin bowerbirds was 1 mo later than in previous years.

HYPOTHESIS 5. If holding a bower is costly, then there should be greater loss of condition among males who attempt to hold bowers than those who do not.

As discussed above, 1986 was a year when males were stressed by extreme

TABLE 4

BETWEEN-YEAR CORRELATIONS OF MALE MATING SUCCESS

	1981	1982	1983	1984	1985
1982	.829	. . .	. . .	. . .	. . .
	(18)				
1983	.756	.721	. . .	. . .	. . .
	(14)	(22)			
1984	.653	.759	.779	. . .	. . .
	(14)	(20)	(24)		
1985	.255	.449	.509	.734	. . .
	(12)	(17)	(20)	(20)	
1986	.550	.178	.145	− .286	− .047
	(10)	(14)	(17)	(17)	(22)

NOTE.—Sample size indicated in parentheses.

TABLE 5

WEIGHT LOSS (g) BY MALE SATIN BOWERBIRDS IN 1986

	Bower Holders ($N = 15$)	Non–Bower Holders ($N = 11$)
Early-season weight	234.9 ± 4.6	237.0 ± 6.4
Late-season weight	207.3 ± 2.7	208.7 ± 3.6
Weight loss (%)	11.5 ± 1.3	11.8 ± 1.7

drought and low temperatures. It would seem that bower holding would be most costly under conditions in which males are stressed. Costly bower holding and court decoration under the extreme conditions in 1986 should have caused males who held bowers that year to show a high level of weight loss relative to their body size.

   Result. I compared weight loss of bower holders and non-bower-holders in 1986. There was no difference in initial weight of males or in the percentage of weight loss in these two groups (table 5).

   HYPOTHESIS 6. If the elaboration of display is limited by its physical cost to males, then the loss of condition among males should be correlated with the quality of their displays.

   The hypothesis that displays are costly leads to the prediction that when males are stressed, effort directed at producing displays should be correlated with a loss in condition of the male.

   Result. Table 6 shows results from the Spearman correlation between weight loss in 1986 and scores for bower quality and decoration characters. None of these results are significant.

   HYPOTHESIS 7. If cost is the only factor limiting decoration use, then males provided with decorations at no cost should use all available decorations.

   This experiment seeks to remove decoration availability and cost of decoration gathering as factors affecting male decoration use. By removing these costs,

TABLE 6

SPEARMAN CORRELATIONS FOR PERCENTAGE WEIGHT LOSS BY BOWER
HOLDERS VERSUS BOWER CHARACTERS IN 1986

Character	Spearman Correlation	P Value
Quality of construction	−.20	NS
No. of yellow leaves	−.07	NS
Yellow straw count	.37	.18
No. of blue feathers	−.11	NS
No. of snail shells	−.13	NS
No. of yellow blossoms	.07	NS
No. of blue blossoms	.23	NS
No. of cicada skins	−.13	NS
No. of natural objects	−.35	.20
No. of man-made objects	−.09	NS

NOTE.—N = 15; NS = P > .40.

TABLE 7

USE OF BLUE PLASTIC CHIPS ON COURTS BY MALE SATIN BOWERBIRDS ON
DECORATION-ENHANCED AND -NONENHANCED BOWERS

	DECORATION POSITION ON COURT AFTER EXPERIMENT*				PERCENTAGE MALES USING ALL CHIPS
	Off	On	Missing	Gained†	
Replicate 1:					
Chip	23	43	4	3	40 (6/15)
Nonchip	4	64	19	7	67 (12/18)
Replicate 2:					
Chip	28	41	1	2	43 (6/14)
Nonchip	7	74	2	3	88 (15/17)

* Decorations moved onto a court and then lost are not subtracted from the "On" total.
† Decorations gained from other males' bowers.

constraints on male decoration use are eliminated, and males should react by using all available decorations.

Result. Results in table 7 show that males who already had chips on their bowers used fewer additional blue plastic chips when these were supplied in piles near their bowers.

HYPOTHESIS 8. If bower displays are costly, then males who have had decorations removed or bowers destroyed and then repair the damage should suffer increased mortality.

Elsewhere (Borgia 1985a) I reported the results of an experiment in which I removed decorations from the bowers of randomly selected males to study the effect of decoration loss on male mating success. Information from this experiment can be used to evaluate the effect of imposing on males the cost of obtaining new decorations for their bowers. If this is expensive, then lower overall survival rate in the removal group is expected. In another experiment (G. Borgia, unpublished manuscript), bowers of males in an experimental group were destroyed at

4-d intervals. If these bowers are costly to rebuild, then male mortality should be higher in the experimental than the control group.

Result. Two males from the control group and none from the removal group died during the 1980 mating season, when decorations were removed. This pattern was opposite to the predicted direction but was not significant ($\chi^2 = 0.8$, df = 1, $P = .4$). All of the remaining males were sighted the following year. There was no mortality among males from either group during the 1984 mating season when bowers were destroyed. Two males from the experimental group and one from the control group were not sighted the following year, but this difference was not significant ($\chi^2 = 0.436$, df = 1, $P = .48$).

<div align="center">DISCUSSION</div>

Several sexual selection models have assumed that costs of display might be critical in defining the extent of male trait elaboration. I tested this general hypothesis in satin bowerbirds with eight different comparisons designed to uncover different modes by which costs might be expressed. None of these comparisons showed patterns that are consistent with the hypothesis that there are high costs. Several of these tests (2, 3, 4, and 7) produced results that are significant and in the opposite direction of predictions based on the expectation of a high cost of display.

Of particular interest is the finding of strong positive between-year correlations in male mating success. These results indicate that males are able to maintain their attractiveness to females over successive years and fail to support the hypothesis that costs of display induce between-year reversals in male reproductive success. Because positive correlations persist over multiple years, it appears that display costs do not cause reversals in male mating success even after several years.

Results of the blue chip addition experiment indicate that males limit their use of decorations even when the cost of bower decoration is negligible. Thus, the proximate cost of obtaining decorations is not the primary factor limiting the addition of decorations onto display courts.

The result showing a positive correlation of male longevity on bowers and display quality is of special interest for additional reasons. First, it indicates that the lifetime reproductive success of males with well-decorated bowers is greater than expected from single-season estimates and that the selection gradient for male display traits is even steeper than would be suggested by single-season estimates (Borgia 1985*a*). This finding enhances the expectation from the Lande (1981) runaway sexual selection model that there should be high overall costs from male display in satin bowerbirds and decreases the likelihood that this model explains satin bowerbird displays.

Second, the results support the general prediction of good-genes (including handicap) models, that successful males are able to develop high-quality displays more easily than other males. More recent versions of handicap models (see, e.g., Zahavi 1977; Andersson 1982*a;* Kodrick-Brown and Brown 1984; Grafen 1991) suggest that male genetic quality is inversely related to the marginal cost

of enhancing display quality. The result showing greater survival by males with the highest-quality displays is generally consistent with this claim. Handicap models have commonly been used to explain the evolution of costly characters such as deer antlers, and it is often argued that the costliness of display characters is essential for truthful advertising. In general, handicap models have not been explicit in defining the level of cost necessary to produce their claimed effects. The above results may conflict with handicap models to the extent that those models require the production of expensive male display by all males.

Truthful advertising may not require displays with a high absolute cost. A useful analogy is humans competing in a 100-m race. Results of a race among individuals nearing reproductive age may give prospective mates reliable information about the potential for individual contestants to pass on genes that would produce vigorous offspring. Success in such races occurs with no or very small negative effects on participant survival but may pay large dividends in mate attraction. Thus, displays of vigor can lead to truthful advertising without being costly. Similar kinds of tests may occur in natural populations.

If mate choice is based on characters for which increased expenditure of effort (e.g., risk taking) causes little or no improvement, then the costliness of displays may not be critical in allowing females to find quality mates. For instance, if males know their status in a social group, low-cost displays may provide truthful information to visiting females. Males need only offer a signal that reflects their status and that is effectively advertised to surrounding males. Under these circumstances, males that produce untruthful signals will be suppressed by more dominant individuals. The absolute cost of the male display can be unrelated to its value to females.

The overall costs from displaying might then be dependent on differences between males (e.g., experience or genetic quality) that affect the predictability of male encounters. There can be little gain from conflict if the outcome is predetermined (Parker 1974). In an established hierarchy, males could then use inexpensive displays to reliably signal their status or related characters important for female mating decisions and avoid the costs of display.

Gilliard's (1956, 1969) observations on patterns of bower evolution suggest that producing low-cost displays may be a general evolutionary trend among bowerbirds. He proposed that bower displays of bowerbirds may have evolved as replacements for more costly male plumage display characters. He noted an inverse relationship among species in male plumage brightness and the degree of decoration and elaboration of bowers. Gilliard (1969, p. 397) claimed that the transfer of display functions from the male to the bower led to an overall decrease in the cost of display. If true, this indicates that inexpensive versions of exaggerated displays have been favored by selection to replace more costly displays (see, e.g., Borgia 1979, 1987; Seger and Trivers 1986).

Important elements in satin bowerbird behavior suggest that outcomes of male interactions are predictable and, to a large extent, dependent on learning. Bower site ownership is typically stable over multiple years (Borgia 1986), and those attempts to place new bowers near the sites of established males are nearly always resolved in favor of permanent bower holders. High between-year correlations

in the percentage of male "wins" in aggressive encounters at feeding sites (G. Borgia and C. Loffredo, unpublished manuscript), involvement in bower destruction (Borgia 1985b), decoration stealing (Borgia and Gore 1986), and mating success (reported above) further support the claim of predictable social interactions.

Much of this predictability may arise because of the important effects of experience. Male satin bowerbirds have delayed maturity, not reaching adult plumage until they are 7 yr old (Vellenga 1979). Males engage in frequent displays that are directed at empty bowers or at males visiting the bower (Marshall 1954; Loffredo and Borgia 1985; Borgia 1986) that are best explained as practice displays. There is age-related improvement in juvenile and adult males in the quality of male display components (Loffredo and Borgia 1985), male aggressive ability (Collis and Borgia 1992), and male mating success (Borgia 1986). Testosterone implants in juvenile males have shown that these males, when raised to adult levels of testosterone, remain subordinate and unable to produce adult-quality displays (Collis and Borgia 1992). These data suggest that, in satin bowerbirds, experience plays a large role in determining the outcome of social interactions. The high predictability of these relationships may limit the frequency of tests and their resultant costs and allow the operation of inexpensive and effective displays of male status.

If the cost of the trait is not a necessary part of female assessment of males and inexpensive versions of traits are no less attractive, then inexpensive alternative versions of display traits should evolve. Moreover, females that evolve to identify and choose males with inexpensive displays will have sons with increased survival rates. These effects should cause both the novel display trait and the associated female preference to spread in the population. The costs of display traits might be lowered by retaining the parts of traits that are effective in stimulating females (thus retaining the mating advantage for males with a modified trait) but reducing parts of traits that add expense but are not important in mate choice. For example, in birds of paradise, the evolution of distinctive tail wires of *Seleucidis*, *Paradisaea rudolphi*, and *Cicinnurus* and the head wires of *Parotia* are feathers modified by the loss of vanes. These reduced structures may be less costly to carry than full feathers of a similar length, but they may still be entirely effective in display.

The above results measure only costs to males after they begin to hold bowers. It is possible that important costs associated with differences in male display quality arise before males mature. There are, however, several features in the development of satin bowerbird display that indicate that this is not true. If, for example, the development of male displays were dependent on heavy preadult cost, then much of the range in variation in bower decoration and quality should occur among young males. Bowers of young males are, however, uniformly of poor construction, and much of the variation in bower quality occurs as a result of postjuvenile age-related improvement (G. Borgia, personal observation). Thus, much of the variation in display quality arises after males are sexually mature bower holders and are then accessible to the tests discussed earlier.

Some sexually selected traits are unambiguously expensive, and it is not my intention here to suggest otherwise. The antlers of deer and the advertising calls

of anurans are two examples. However, the evolution of these traits can be best explained as products of direct selection on males. For example, it seems very likely that deer antlers evolved as weapons for sexual combat and that frog calls function in passive attraction (see, e.g., Parker 1983). Any role these traits may now have in female choice could have resulted as a secondary adaptation that occurred after the major costs associated with these traits were in place. Thus, costly displays may be widespread, but the results discussed here suggest that exaggerated displays may sometimes evolve even if they do not produce high costs in displaying males.

Much of the interest in the evolution of exaggerated male displays arises from the question of how costly male displays evolve in the absence of correspondingly large benefits to females. The results here suggest that, at least for some cases, male displays are not as expensive as has been commonly assumed.

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