

Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus violaceus*)

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Summary. Male satin bowerbirds often destroy the bowers of other males. Bowders are a key element in male sexual display and their destruction represents a unique pattern of sexual competition. For two mating seasons bowders of displaying males were continuously monitored to produce a complete record of bower destructions. The number of destructions at bowders and the amount of destruction of bowders were inversely correlated with bower quality. The best predictor of male bower destroying behavior is male aggressiveness at feeding sites. Males directed most destructions at adjacent bower sites. These results show that male interactions are important in determining differences in the quality of display among male satin bowerbirds, and are consistent with the view that females use bowders as indicators of male quality in mate choice.

Introduction

Bowerbirds (Ptilonorhynchidae) are unique among animals in that males build and decorate elaborate structures called bowders that are used exclusively for courting and mating females. Males provide no assistance to females in rearing young, nor do they associate with females after mating. Fourteen species of bowerbirds build bowders, and the shape of bowders and the type of decorations used differ among species (Marshall 1954; Gilliard 1969; Cooper and Forshaw 1977). Bower destruction by conspecific males is widespread among bower-building species (Marshall 1954; Peckover 1970; Vellenga 1970; Pruett-Jones and Pruett-Jones 1983), but has never been studied in detail. Male susceptibility to bower destruction may strongly affect fitness of individual males because the quality of bowders

and the mating success of bower owners are highly correlated (Borgia 1985). Identification of the factors that influence bower destructions may provide clues to why bower building evolved.

When bowders were first found they were thought to be nests (Gilliard 1969). However, John Gould (1848) noted that they were sites for sexual display and mating. Soderberg (1929) suggested that bowders evolved as a "nest stimulus" necessary to induce female ovulation. This "nest hypothesis" remains the most common explanation for bower-building (c.f., Cooper and Forshaw 1977; Diamond 1982). However, Borgia et al. (1985) noted that this hypothesis fails to explain important features of bower construction including why bowders are built on the ground (all species nest in trees), and why males decorate their bowders (nests are not decorated).

There have been numerous recent attempts to use sexual selection theory to explain the relationship between male display and female choice in polygynous species, like bowerbirds, in which males provide no material assistance to females or their offspring (e.g., Fisher 1930; Trivers 1972; Zahavi 1975; Borgia 1979; LeCroy et al. 1980; Halliday 1983; Hamilton and Zuk 1982; Davis and O'Donald 1976; Bell 1978; Thornhill 1980; Andersson 1982; Arnold 1983). However, male bower-building behavior as a form of display has received very little attention.

Recent versions of Fisher's (1930) runaway model have been put forth as explanations for the evolution of male display characters (e.g., Arnold 1983). These models suggest that female preferences that do not enhance the viability of their offspring might evolve (Lande 1981; Kirkpatrick 1982). Display characters, such as bowders, are viewed as arbitrary results of the runaway sexual selection process. As such, these models are diffi-

cult to falsify because they make no clear predictions about one of the key phenotypic results of sexual selection: male sexual display.

Borgia et al. (1985) suggest that females may use bowers as "indicators" to assess the quality of prospective mates. Bower destroyers reduce the attractiveness of bowers of competing males. Males able to maintain their bowers in good condition despite attempted destructions by other males give females evidence that they can repel intrusions by competing males at their display site. This ability to repel destroyers may, through its effect on bower quality, serve as an indicator of a male's quality as a sire, and preference for males with high quality bowers should yield offspring of high relative fitness. The indicator hypothesis makes specific falsifiable predictions about male bower-destroying behavior: (1) bower destructions must be important in lowering the quality of bower displays, (2) males should direct bower-destroying behavior toward their most likely sexual competitors, and (3) aggressive dominance in males is related to their ability to destroy bowers and resist destruction of their own bower. The inability to demonstrate behaviors consistent with these predictions would falsify the indicator model.

It has also been suggested that females may prefer old males (Halliday 1983; Howard 1979; Wilbur et al. 1978). By choosing old males females may gain from the opportunity to mate with a male who has been able to survive the rigors of selection and will presumably be more likely to have offspring with these same attributes. We can test this model to determine if bower destroying behavior or resistance to destruction is correlated with male age. Especially vigorous males might also be preferred by females because this vigor may be a signal of overall well being (Trivers 1972). Females might use bower quality as a means to test overall well-being.

There are several other sexual selection models that might be considered in the context of bower evolution. Borgia et al. (1985) suggest that the bower might provide protection for females during courtship. This hypothesis may only apply to enclosed bowers; the maypole bowers of *Amblyornis macgregoriae* and *Prionodura newtonia* seem to offer little protection. Le Croy et al. (1980) propose that sex-limited male displays may function primarily as signals in male aggression. Parker's (1983) passive choice models suggest that bowers could be used by females as a mechanism for locating males. The relative hidden position of bowers implies that neither of these models is applicable to explaining the evolution of bowers.

Here I describe patterns of destruction over two years at the bowers of satin bowerbirds. The results show that bower destructions reduce the quality of male bowers, males typically destroy between bowers of near neighbors, and males who are most aggressive in destroying bowers tend to be aggressively dominant at feeding sites. The number of destructions at a bower site is not correlated with male age. These results indicate an important role for male interactions in influencing the quality of male display and are consistent with predictions from the indicator hypothesis.

Methods

The study area is situated at Wallaby Creek, which is 140 km SW of Brisbane in Beaurie State Forest, N.S.W., Australia. This site is located in a valley formed by Wallaby Creek, which constitutes the 2-km eastern border of the rectangular study area that extends 1.5 km into a system of ridges formed by the creek's tributaries. Several distinct forest associations cover the area. *Eucalyptus* is the dominant canopy tree over much of the area. The understory varies and includes grassland, thick thorn scrub, and rain-forest species. Rain-forest predominates in low areas, along creeks, and on the eastern side of higher ridges.

The behavior of male satin bowerbirds was monitored at bowers at Wallaby Creek through the peak of the mating season (5 November to 24 December). Satin bowerbirds on the study site, including all bower owners, were banded with unique color patterns and these marks were used to establish the identity of bower destroyers. In 1981 and 1982, 26 and 33 bowers, respectively, were monitored using a specially designed camera system that recorded behavior at the bower (including destructions) and the identity of all birds visiting the bower (see Borgia 1985). In addition, a crew of field observers made daily observations from hides near bowers. They recorded the identity of destroyers, the duration and extent of destructions, stealing that might have occurred in conjunction with destruction, and the presence or absence of the bower owner near the bower. The location of each bower was mapped and we measured the distances to neighboring bowers.

Male interactions at feeding sites were used to assess relative male dominance at sites away from borders. Males were observed at three trapping sites with bread used as bait. Observers focused on one trap for each recording period and noted all interactions at that trap. Aggressive interactions involve attacks by one male on another, with the victim either hopping away from the attacker or returning the attack. Males were scored for the number of times they were attacked and attacked other males.

Feathers were individually marked when they appeared on bower platforms, and their daily movement between bowers was followed. Data on feather stealing are taken from Borgia and Gore (1986). Bower quality was assessed daily using a subjective scale by observers naive about the bower holder's past record of destruction, bower quality, and mating success (see Borgia 1985). Two of these subjective measures of bower quality (stick size and stick density) are highly correlated with actual measurements.

Spearman rank-correlations (r_s), Pearson product-moment correlation (r), Student's t -test, partial correlations, and Wilcoxon matched-pairs signed-rank test (W) were used for statisti-

cal comparisons (Conover 1971). Means are expressed as $\bar{X} \pm 95\%$ C.I. Sokal and Rohlf's (1969 p. 612) test for combined probabilities was used to test for statistical significance in multiple-year comparisons.

Results

Destruction rates

Each bower was destroyed an average of 4.0 ± 1.9 (1981 - Table 1a) and 8.2 ± 2.4 (1982 - Table 1b) times through the monitoring period each year. The daily destruction rate was 0.08 and 0.16 destructions per bower per day. This rate of destruction is much lower than the 0.10 destructions/h found by Pruett-Jones and Pruett-Jones (1983) for the bowerbird *Amblyornis macgregoriae*.

The difference in the number of destructions at bowers between years appears to be real. Comparisons based only on bowers observed in both

years show a significant increase ($P < 0.05$) in the average number of destructions between seasons. This parallels a lower rate of feather stealing in 1981 than 1982 (Borgia and Gore 1986). Although the cause of this difference is unknown, it may be related to the lower number of feathers at bowers in 1981 than in 1982.

1. Bower destruction and bower quality

Victims of destruction. Males may destroy the bowers of other males to reduce the quality of bowers of sexual competitors. This hypothesis requires that bower destructions have a significant effect on bower quality. The demonstration of an inverse relationship between bower quality and the amount of destruction at a male's bower would support this hypothesis.

The results show that four measures of bower quality are negatively correlated with the frequency

Table 1. Victims and destroyers for each bower destruction in 1981 (1a) and 1982 (1b). XX represents destructions where the identity of the destroyer is unknown

Table 1a

	Victim																				Total				
	3	4	5	6	7	9	10	11	12	13	14	15	16	17	18	19	22	29	30	31		32	37	38	
3		1																		1					2
4																				7					7
5		3		1																1					5
6					3																				3
7				1										1	4										6
9																									0
10																									0
11								1															3		4
12																									0
13														2											2
14													1							1					2
15										1										1			5		6
16																									0
17								1																	1
18					3																				3
19																									0
22									1					1								2			4
29																									0
30																									0
31	3	2	2																						7
32													2												2
37																									0
38									1					1						2					4
44													1												1
47																								2	2
48									3																3
54		5																							5
60								1																	1
XX	1	2	1						3	2				3						1			8		21
Total	4	13	3	2	6	0	3	9	2	0	0	5	6	1	4	0	0	2	2	9	10	10	0		91

Table 2. The correlation of bower quality with the frequency with which a bower is destroyed

Bower characteristics		Symmetry of bower walls	Stick size	Stick density	Quality of construction
1981	r_s	-0.299	-0.371	-0.396	-0.441
$n=23$	P	0.083	0.041	0.031	0.018
1982	r_s	-0.259	-0.236	-0.298	-0.336
$n=30$	P	0.084	0.104	0.055	0.036
Combined	P	0.040	0.032	0.019	0.006

Table 3. The correlation of bower quality with the total amount of destruction at bowers (the number of destructions at a bower X the mean level of destruction at the bower)

Bower characteristics		Symmetry of bower walls	Stick size	Stick density	Quality of construction
1981	r_s	-0.406	-0.389	-0.491	-0.520
$n=22$	P	0.030	0.037	0.010	0.007
1982	r_s	-0.434	-0.311	-0.579	-0.526
$n=29$	P	0.024	0.084	0.003	0.006
Combined	P	0.005	0.035	0.004	0.001

Table 4. The correlation of the quality of a male's bower and the number of bowers he destroys

Bower characteristics		Symmetry of bower walls	Stick size	Stick density	Quality of construction
1981	r_s	-0.234	0.053	0.039	-0.002
$n=28$	P	0.453	0.393	0.422	0.496
1982	r_s	0.238	0.317	0.115	0.149
$n=31$	P	0.098	0.041	0.268	0.213
Combined	P	0.194	0.081	0.372	0.334

same factors tended to cause males to be victims in each year. The total amount of destruction at a bower was not significantly correlated with the number of feathers on bowers.

Bower destroyers. The number of times a male destroyed a bower is not significantly correlated with any of the four bower quality variables (Table 4). The number of decorations on males' bowers in 1981 was not significantly correlated with how often those males were destroyers. However, in 1982, the number of each of 5 types of decorations on bowers was positively correlated with the frequency with which the bower owner destroyed

other bowers (yellow straw, $P=0.023$; blue feathers, $P=0.034$; yellow blossoms, $P=0.002$; cicadas, $P=0.024$; man-made objects, $P=0.047$). The number of destructions by a male is correlated with the number of feathers he steals ($r_s=0.328$, $P=0.036$) and loses to other males ($r_s=0.326$, $P=0.037$).

There was a significant correlation between the number of times a male destroyed other bowers compared to the number of times he was a victim (1981: $r_s=0.376$, $n=23$, $P=0.038$; 1982: $r_s=0.118$, $n=30$, $P=0.268$; combined $P=0.045$). The frequency that a male was a destroyer was strongly correlated between years ($r_s=0.474$, $n=28$, $P=0.005$).

Destruction patterns. The high proportion of incomplete destructions suggests that bower destruction may be costly to intruding males. Males appear to minimize time they spend destroying target bowers, typically making only brief visits ($\bar{X}=96.6 \pm 23.4$ s), and focusing their efforts on destruction. The duration of the destroyer's visit to the bower is highly correlated with the percentage of destruction ($r_s=0.649$, $n=66$, $P=0.001$).

Destructions at established bowers generally occurred when the owner was not near the bower (82 of 87 cases, 94.3%). In the five remaining instances, the bower owner was perched in a nearby tree when the intruder approached the target bower and began destroying. Three times the intruder was discovered and chased by the owner. In two other cases the intruder destroyed the bower in the presence of the owner. Bower destroyers were interrupted by the owner in 15 of 87 cases.

We could not systematically observe male interactions more than 20 feet away from the bower because they were obscured by the surrounding vegetation. Therefore, we do not know how often males visited each bower with the intention of destroying and were chased by the owner, or how often intruding males chased the owner and were then able to destroy. Males visiting a bower to destroy typically approach with stealth, flying in quietly and perching motionless in trees as they approach the target bower. On several occasions we have seen destroying males land on the ground more than 15 m from the bower and approach it walking quietly and with hesitation. Thus, bower destructions can occur while the owner is not visible but still is in the immediate area.

In the great majority of cases destructions appeared to occur when the owner was not in the immediate vicinity of the bower. In most cases when the owner arrived during a destruction he

usually drove away the destroyer. Destroyers discovered by owners were usually unable to steal decorations (14 of 15 cases). This contrasts with a stealing rate of 72% (52 of 72 cases) for uninterrupted visits. Males may inflict only partial destruction on bowers because the gains from continued destruction are outweighed by possible losses from being caught in the act of stealing. Losses might include the risk of a fight and a lost opportunity to steal.

2. Determinants of destruction rates

Destruction and near neighbor distance. The distance between bowers may affect a male's opportunity to destroy and his susceptibility to having his own bower destroyed. Two variables were used to measure the effect of the actual distance to neighbors on destruction rate: (1) distance to nearest neighbor, and (2) mean distance to the 5 nearest neighbors. The second variable was chosen to provide an estimate of the distance between neighbors likely to be involved in destructions (see above). A low value for this variable indicates a high concentration of bowers in the vicinity of the bower under consideration. The effect of near or nearest neighbors on the number of bower destructions was evaluated by comparing the frequency with which males destroy bowers, or are the victims of destructions, with these variables.

There was no significant rank correlation between nearest neighbor distance and the frequency with which a male destroys bowers (1981: $P=0.19$; 1982: $P=0.23$). However, there was a tendency for bowers with close nearest neighbors to be destroyed often (1981: $r_s = -0.344$, $n=26$, $P=0.059$; 1982: $r_s = -0.242$, $n=26$, $P=0.098$; combined $P=0.037$). The average distance to the 5 nearest bowers showed a marginally significant correlation with a tendency to destroy (1981: $r_s = -0.339$, $n=26$, $P=0.039$; 1982: $r_s = -0.057$, $n=33$, $P=0.380$; combined $P=0.07$), and the average distance was significantly correlated with how often a male was a victim of destruction (1981: $r_s = -0.146$, $n=26$, $P=0.256$; 1982: $r_s = -0.358$, $n=33$, $P=0.026$; combined probability $P=0.04$). Distance to neighbors is important in determining how often a male is a victim of destruction, and may affect how often he is a perpetrator.

Destruction and relative position of neighbors. If bower-destroying behavior evolved as a mechanism to lower the quality of bowers of sexual competitors, then we expect that males gain most from destructions directed at neighbors' bowers. The

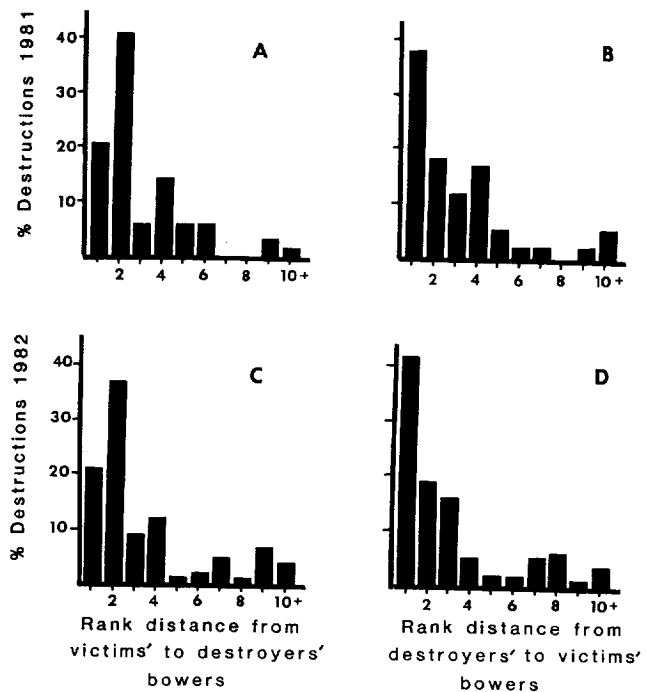


Fig. 1. Rank distance to neighbors and number of destructions

tendency for males to destroy neighbors' bowers, independent of the effects of absolute distance, was evaluated by comparing neighbors ranked by distance. Males focused the majority of their destructions on near neighbors (rank 5 or closer), which were victims of 91% (1981) and 83% (1982) of all destructions. In each year nearly half of the destructions were directed at the nearest neighbor (Fig. 1B, D). These data support the prediction that destroyers focus their destructions on adjacent bowers belonging to males who are likely to be their most important sexual competitors.

Among males who were victims of destruction, the nearest neighbor was not the most common destroyer (Fig. 1A, C), but even for these males the majority of destructions came from near neighbors (1981: 87%, 1982: 81%). This difference in patterns between perpetrators and victims suggests that males who are frequent victims often have a nearest neighbor who is not an active destroyer.

Also to be considered is the effect of rank distance on male tendency to destroy or be destroyed. The rate at which males destroy bowers might be correlated with the relative distance males travel to destroy bowers. There is, however, no significant correlation between the mean rank distance of bowers males destroy and how often he destroys (1981: $r_s = -0.373$, $n=15$, $P=0.086$; 1982: $r_s = 0.226$, $n=25$, $P=0.139$), or the frequency with which a male's bower is destroyed and the rank distance from which males come to destroy (1981:

$r_s = -0.117$, $n=15$, $P=0.346$; 1982: $r_s = -0.135$, $n=26$, $P=0.256$).

Male age and bower destruction. The age of bower-holding males is correlated with mating success and male aggression at feeding sites (Borgia 1986), so it is possible that bower destroying behavior is influenced by male age, and that females use bower quality to assess male age. There was no significant correlation between the age of males and the number of bowers that they destroyed (1981: $r_s = -0.062$, $n=27$, $P=0.379$; 1982: $r_s = 0.199$, $n=30$, $P=0.145$), or the frequency with which their own bowers were destroyed (1981: $r_s = 0.039$, $n=21$, $P=0.432$; 1982: $r_s = 0.061$, $n=29$, $P=0.376$). No significant correlation was found between male age and the amount of destruction at a male's bower (1981: $r_s = -0.004$, $n=21$, $P=0.494$; 1982: $r_s = 0.029$, $n=28$, $P=0.442$). However, male age appears to affect the distance males travel to destroy bowers. There is a significant correlation between male age and the rank distance to bowers males destroy (1981: $r_s = 0.469$, $n=13$, $P=0.053$; 1982: $r_s = 0.642$, $n=24$, $P=0.001$). This result might be due to age-related differences in the distance to neighbors. However, there is no significant correlation between male age and distance to near neighbors (1981: $r_s = 0.049$, $n=13$, $P=0.430$; 1982: $r_s = 0.068$, $n=31$, $P=0.358$). There is a significant correlation between nearest neighbor distance and male age (1981: $r_s = 0.317$, $n=13$, $P=0.020$; 1982: $r_s = 0.317$, $n=31$, $P=0.041$), however, this correlation is in the opposite direction of what is expected, if having close neighbors is to cause an increase in the likelihood of destruction. In summary, there is no correlation of male age with the tendency to destroy, but older males tend to destroy bowers at a greater rank distance than younger males.

Male aggression and patterns of destruction. The indicator hypothesis suggests that bower destroying behavior is an aggressive act that reflects the dominance relationships among males. Male success in aggressive encounters was measured at feeding sites away from bowers and is used here as a measure of male dominance. If bower destroying behavior is influenced by the dominance status of a male, then this behavior should be positively correlated with male aggression at feeding sites. The number of times a male destroys bowers was positively correlated with the total number of his attacks on other males at feeding sites (1981: $r_s = 0.588$, $n=17$, $P<0.001$; 1982: $r_s = 0.403$, $n=21$, $P=0.012$; combined probability $P=0.001$), and

the proportion of total encounters (times attacked+attacks) in which he was the attacker (1981: $r_s = 0.495$, $n=17$, $P=0.003$; 1982: $r_s = 0.259$, $n=21$, $P=0.080$; combined probability $P=0.022$). These results support the hypothesis that male bower destroying behavior is related to male aggressive dominance.

The indicator hypothesis also predicts that destruction at bowers is inversely correlated with male dominance. This prediction assumes that males are not commonly forced to leave the immediate vicinity of their bower (e.g., to feed). There was no significant correlation between the number of destructions at a male's bower and his aggressiveness at feeding sites (1981: $r_s = -0.057$, $n=13$, $P=0.397$; 1982: $r_s = 0.209$, $n=30$, $P=0.133$). However, the aggressiveness of a bower owner at feeding sites was negatively correlated with the amount of destruction at his bower (1981: $r_s = 0.320$, $n=18$, $P=0.060$; 1982: $r_s = 0.209$, $n=31$, $P=0.139$; combined probability $P=0.05$). These results do not show the expected inverse correlation between the number of destructions at a bower and male dominance. However, the results suggest that the threat posed by more aggressive males may cause destroyers to avoid long visits at their bowers, thereby reducing the possibility of the destroyer being caught in the act of destruction. This also should lead to less destruction at bowers of aggressively dominant males.

Correlations among variables. The above analysis shows that distance to near neighbors and male aggression at feeding sites are significantly correlated with the male tendency to destroy bowers. These variables have been treated as if they were independent, however, so it appears possible that intercorrelation among variables might account for the observed results. Partial correlations were used so that the contribution of each of these variables could be measured independent of the effects of the other. Near neighbor distance caused almost no change in the correlation between male aggressiveness and the number of bowers a male destroys ($P<0.01$). Controlling for male aggressiveness has only a small effect on the correlation between distance to near neighbors and the number of bowers a male destroys ($P<0.05$).

The correlation of feather-stealing with the number of destructions at a bower indicates the possibility that bower destruction may be so strongly associated with feather-stealing that the observed relationship between bower quality and male mating success might be due to a correlation between feather-stealing and bower destruction.

There is a significant correlation between the number of destructions at a bower and bower quality ($P < 0.05$) using a partial correlation to control for the effects of feather-stealing. This result suggests that destructions occurring without stealing are sufficient to explain significant reductions in the quality of males' bowers.

Discussion

The above results agree with the requirements for the indicator model. Data showing that bower destructions lower the quality of bowers establish destructions as an important factor affecting male display. Evidence that males focus destructions on near neighbors, taken together with the observation that females tend to restrict visits to males in a small area (Borgia, in preparation), supports the hypothesis that males focus destructions on their most likely sexual competitors. The highly significant correlation between male dominance at feeding sites and the number of destructions by a male provides evidence that destroying behavior is an aggressive act, and a mechanism by which aggressively dominant males can affect the quality of the bower of other nearby males. The expected inverse correlation between male dominance at feeding sites and the number of times a male's bower was destroyed did not occur. This result combined with observations of male bower destroying behavior suggests that many destructions occur when the bower owner is not in the immediate vicinity of the bower, and may not be able to defend the bower. However, the absence of data on attempted destructions limits my opportunity to assess the importance of male dominance in preventing destructions at bowers. Nonetheless, other data indicate that differences in male aggressiveness may affect the amount of destruction at bowers. The inverse correlation between male dominance and the duration of destruction at males' bowers implies that destroyers may limit the length of visits at bowers and, consequently, the amount of destruction they inflict at bowers of more aggressive males where they may suffer higher costs if caught destroying. In addition, observations at bowers of young males attempting to establish bowers show that owners of nearby established bowers frequently chase these young males out of the area and then destroy their bowers (Borgia, in preparation). Thus, in order to hold a bower, a male must be sufficiently aggressive to fend off males at neighboring sites who repeatedly attempt destructions.

The focus of this analysis has been on the effect

of destructions on bower quality with emphasis on how destructions might somehow indicate male quality as a sire. Variance in the quality of bowers is not only a product of male ability to defend bowers, but also to build bowers. The analysis of male bower building ability has been handicapped by difficulty in measuring bower building ability independent of the effects of destruction. Of interest is the strong correlation of bower quality with male age (Borgia 1986). This suggests that male ability to build bowers is a function of male age. This is supported by the generally poor quality of young males' newly built bowers, the large amount of "practice" bower building by young males, and the failure of young males to bend sticks to produce a bower with rounded walls (Borgia, in preparation). However, I was unable to demonstrate a significant age-related effect on destruction. This pattern suggests that females who choose males with high quality bowers might gain information about male age and male aggressiveness, the former from male ability to build bowers and the latter from male ability to defend bowers.

The occurrence of high levels of male interactions, which is a necessary condition for the operation of the "indicator" model, is also consistent with several of the other models. Although models such as 'runaway' and 'female protection' make no explicit predictions about the importance of male interactions, bower destroying behavior might still evolve. If females favor males with well-built bowers for reasons unrelated to their quality as sires, then males might evolve to destroy their neighbors' bowers, benefiting from their neighbors' reduced ability to successfully court females. Dominant males would be expected to maintain high quality bowers through their greater ability to destroy the bowers of other males and protect their own. However, male interactions are not necessary for the operation of the runaway model and would not occur if females evolve choice patterns that favored male displays that are not influenced by threats from other males. Hence, these hypotheses might be distinguished by comparing a number of species to determine if male interactions affect male display. If female choice in a number of 'exploded arena' species operates so as to allow females to evaluate male dominance, as was found here for bowerbirds, then there would be strong support for the indicator hypothesis.

Male raids at bowers of other males may result in theft of decorations, bower destruction or both. There was a significant correlation between the number of decorations stolen and the number of destructions at a bower; however only a small pro-

portion of the total variation in bower destructions is accounted for by stealing. Unlike stealing behavior (Borgia and Gore 1986), the distance to near neighbors is a poor predictor of the number of times a male destroys. The correlation between the number of times a male destroys and the number of times he is a victim of destruction is weaker than the correlation between the number of times he is a perpetrator and a victim of feather theft. This suggests a much lower degree of reciprocity in destroying behavior than in feather-stealing. The total number of stealing bouts at a bower is much greater than the number of destructions, and stealing without destruction is much more common than stealing with destruction, or destruction without stealing (Borgia in preparation). Thus different factors appear to motivate feather-stealing and bower-destroying behavior.

Polygynous species in which males display individually commonly have extreme plumage or other displays, and it is frequently assumed that female choice in these species operates uninfluenced by male interactions (e.g., Darwin 1871; Arnold 1983; Parker 1983). This contrasts with the generally acknowledged importance of male interactions in lekking species (e.g., ruffs: Hogan-Warberg 1966, buff-breasted sandpipers: Meyers 1979; prairie chickens: Ballard and Robel 1974; sage grouse: Wiley 1973; but see Bradbury and Gibson 1983). There are few detailed studies of exploded arena species, and the continuous monitoring of the satin bowerbird bowers has provided a rare opportunity to assess the importance of male interactions in one of them.

Gilliard's (1956) observation of an inverse degree of development between the bowers and male plumage among bowerbirds led him to propose that bower displays may have similar functions to exaggerated plumage displays. The limited information available on other species in which males have extravagant, solitary displays makes it difficult to determine if the important effect of male interactions on display observed in satin bowerbirds is characteristic of other species with 'exploded arenas', or if it is unique to bowerbirds and results from their peculiar bower-building behavior.

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