

Feather stealing in the satin bowerbird (*Ptilonorhynchus violaceus*): male competition and the quality of display

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Abstract. Male satin bowerbirds use feathers to decorate their bowers and often steal feathers and other decorations from the bowers of other males. Decorations are a key element in sexual display and tracking their movement between bowers provides the first detailed information about this unique pattern of sexual competition. For two field seasons the movement of marked feathers was followed. Males varied greatly in stealing activity. The most active feather thieves were often from areas where bowers were close together and they were involved in reciprocal stealing with males at adjacent bowers. The rate of stealing by males was significantly correlated with the number of feathers on their bowers. This suggests that stealing is important in determining the level of bower decoration and mating success. Patterns of stealing behaviour support models of sexual selection which suggest that male interactions are important in influencing female choice through their effect on the quality of male display.

Bowerbirds (Ptilonorhynchidae) are unique among animals in that males build and decorate elaborate structures called bowers. These structures are used only for courting females, as females do not associate with males after mating. Fourteen of 18 species of bowerbirds build bowers, but the shape of bowers and the types of decorations used differ among species (Marshall 1954; Gilliard 1969; Cooper & Forshaw 1977). Male satin bowerbirds (*Ptilonorhynchus violaceus*) place decorations including snail shells, yellow flowers, blue blossoms, cicada exuviae, yellow straw, yellow leaves and blue feathers on a cleared area adjacent to the bower and steal decorations from other bower holders (Marshall 1954; Vellenga 1970).

Theft of decorations by bowerbirds is a unique form of sexual competition. The number of decorations on a bower is an important determinant of male mating success in the satin bowerbird (Borgia 1985a), yet the decorations appear to have no intrinsic value to either sex outside the context of sexual display. Almost all decorations used by bowerbirds are inedible (Cooper & Forshaw 1977) and female satin bowerbirds never take them or use them at nests.

There has been no intensive study of decoration stealing in any species. Marshall (1954) marked pieces of blue glass and noted that they moved long distances as they passed between bowers. Vellenga

(1970) described the collecting of blue toys by a male satin bowerbird, and the movement of these decorations to other bowers after his disappearance and presumed death. Anecdotal accounts of stealing in species of the genus *Chlamydera* were reviewed by Marshall (1954), and Diamond (1984) described stealing of blue poker chips between two bowers of *Amblyornis inornatus*. Male *Prionodura newtoniana* steal flowers of *Melalope broadbentiana* from the bowers of other males (C. Frith, personal communication). Stealing is unknown in the bowerbird *Amblyornis macgregoriae* which uses only very small decorations (M. & S. Pruett-Jones, personal communication).

A major objective of this paper is to provide basic information on the pattern and significance of feather stealing in the mating system of the satin bowerbird. The feathers used as decorations are almost exclusively those of two parrot species, the crimson rosella (*Platycercus elegans*) and the eastern rosella (*P. eximius*). Blue feathers are the most preferred of all objects stolen (Borgia, in preparation) and are one of only two types of decorations (the other being snail shells) the number of which on bowers is consistently correlated with male mating success (Borgia 1985a). Blue feathers are easy to mark and can be followed for an entire mating season. Moreover, they are extremely rare on the study area and can typically be found in abundance only on bowers (Borgia, in preparation). We consider factors that determine when and from which bird individual males steal

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feathers. These results can then be used to evaluate models for the evolution of sexual display.

There has been much recent interest in the relationship between exaggerated sexual display and female choice in polygynous species (e.g. Trivers 1972; Zahavi 1975; Davis & O'Donald 1976; Bell 1978; Borgia 1979; Thornhill 1980; Andersson 1982; Hamilton & Zuk 1982; Bateson 1983; Halliday 1983). Numerous models have been suggested to explain how exaggerated display might evolve (Fisher 1930; Zahavi 1975; Borgia 1979; LeCroy et al. 1980), yet there have been few tests of these hypotheses. One issue on which these models differ is the role of male competition in affecting male display and female choice. For example, the male dominance model (Borgia 1979; Borgia et al. 1985) predicts that aggressively dominant males should be favoured by females; Parker (1983) and Andersson's (1982) passive choice model and Fisher's (1930) runaway model make no predictions about the effect of male interactions on mate choice decisions.

Male competition for decorations in satin bowerbirds provides a useful model for studying the importance of male competition in shaping sexual display. Gilliard (1956) observed that the number of decorations on bowers and the degree of male plumage elaboration are inversely correlated among bower-building species. This led him to propose the 'transfer effect', which suggests that bower decorations function in place of the exaggerated plumage displays. The lack of information on the importance of male interactions in shaping exaggerated displays may be due to the solitary nature of display among males of these species and the consequent difficulty in making detailed observations. The study of feather stealing in bowerbirds allows us to identify the males involved in interactions, determine which factors influence the rate of interaction, and quantify the effects of stealing on the quality of display by competing males.

METHODS

The study area is situated at Wallaby Creek, 140 km south-west of Brisbane in Beaury State Forest, New South Wales, Australia. Wallaby Creek constitutes the 2-km eastern border of the rectangular study area which extends 1.5 km into a system of ridges formed by the creek's tributaries. Several distinct forest associations cover the area. *Eucalypt-*

tus is the dominant canopy tree. The understory varies and includes grassland, thick thorn scrub and rain-forest species. Rain forest predominates in low areas, along creeks, and on the east side of higher ridges. Wallaby Creek is isolated, so human disturbance at bowers is unlikely, and natural objects are the only commonly available decorations.

The stealing behaviour of male satin bowerbirds was monitored through the peak of the mating season from 15 November to 20 December by which time bowers had reached the peak level of decoration. In 1981 and 1982, 26 and 33 bowers respectively, were monitored. We mapped the location of each bower and measured the distances to neighbouring bowers. Bower owners were individually banded with unique colour patterns. Feathers found at the study bowers were marked with unique identification codes. On daily visits to bowers, observers recorded the number and identity of blue feathers. It has been established that thefts by other bowerbirds is the only likely mechanism for feather movement between bowers, and that the majority of stealing is done by adult males that own bowers (Borgia, in preparation).

We assumed that each feather that moved between a pair of bowers on one day was the result of one stealing event. This method introduces two sources of error: (1) it underestimates the frequency of stealing events by not taking into account reciprocal thefts of the same feathers between bowers between visits by observers, and (2) it overestimates the distance feathers are moved per theft because multiple thefts of a feather in one day were recorded as single thefts. Reciprocal and multiple thefts have been observed within a recording period. However, the resulting error is low because of the low probability of a theft between two bowers on the same day (see below), and because it is unlikely that all feathers will be returned to their original bower in a reciprocal theft if multiple feathers are stolen.

Unmarked feathers that appeared at bowers were assumed to have been found away from a bower and were not considered to be the result of a theft. Similarly, feathers disappearing from one bower and not appearing on another were assumed to have been lost (juvenile males sometimes take feathers to their temporary display sites).

The Spearman rank correlation, Pearson product-moment correlation, Student's *t*-test, and Wilcoxon matched-pairs signed-rank test were

used for statistical comparisons (Conover 1971). Means are expressed as $\bar{X} \pm \text{SD}$. Sokal & Rohlf (1969) significance test for combined proportions was used for multiple year comparisons.

RESULTS

Stealing Rates

A summary of the thefts between bowers and the total number of thefts at each bower for 1981 and 1982 are shown in Tables I and II respectively. During 1981, there was an average of $4.4 \pm 7.49 \pm 8.28$ thefts per bower, respectively per season. The daily stealing rate was 0.012 thefts per bower per day, with an average of 1.49 feathers taken per theft (Fig. 1). There is a strong correlation between the number of thefts by a male and the number of feathers stolen by him (1981: $r_s = 0.95$, $P < 0.001$; 1982: $r_s = 0.95$, $P < 0.001$). This result is due to the low number of feathers taken per theft. An average of 4.19 ± 7.09 (1981) and 6.13 ± 10.14 (1982) feathers were displayed at a bower during the season.

The mean number of feathers stolen per bower was nearly equal to the mean number of feathers on a bower through the season. It appears that feather stealing occurs at a sufficiently high rate to cause significant changes in the distribution of feathers among bowers.

In the following sections we consider factors which may influence stealing rates by males.

Stealing rates and bower decoration

If stealing is important in determining the number of feathers on bowers and thus influences mate choice patterns, then feather stealing should be correlated with the number of feathers on a male's bower. There is a strong relationship between the number of feathers on a male's bower and both the number of successful thefts (1981: $r_s = 0.458$, $P = 0.014$; 1982: $r_s = 0.458$, $P = 0.001$) and the number of successful attempts (1981: $r_s = 0.378$, $P = 0.038$; 1982: $r_s = 0.378$, $P = 0.001$). However, this result is confounded because the number of times a male steals is correlated with the number of times he is stolen from (1981: $r_s = 0.855$, $N = 26$, $P < 0.001$; 1982: $r_s = 0.836$, $N = 33$, $P < 0.001$), and the

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used for statistical comparisons (Conover 1971). Means are expressed as $\bar{X} \pm \text{SD}$. Sokal & Rohlf (1969) significance test for combined periods was used for multiple year comparisons.

RESULTS

Stealing Rates

A summary of the thefts between bowers and the total number of thefts at each bower and the total number of feathers stolen from each bower for 1981 and 1982 are shown in Tables I and II respectively. During 1981 and 1982, there was an average of 4.4 and 7.49 \pm 8.28 thefts per bower, respectively, per season. The daily stealing rate was 0.012 thefts per bower per day, with an average of 1.49 feathers taken per theft (Fig. 1). There is a strong correlation between the number of thefts by a male and the number of feathers stolen by him (1981: $r_s = 0.95$, $P < 0.001$; 1982: $r_s = 0.95$, $P < 0.001$). This result is due to the large number of feathers taken per theft. An average of 4.19 \pm 7.09 (1981) and 6.13 \pm 10.14 (1982) feathers were displayed at a bower during a season.

The mean number of feathers stolen from a bower was nearly equal to the mean number of feathers on a bower through the season. It appears that feather stealing occurs at a sufficiently high rate to cause significant changes in the distribution of feathers among bowers.

In the following sections we consider factors which may influence stealing rates by males.

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RESULTS

Stealing Rates

A summary of the thefts between any pair of bowers and the total number of thefts and feathers stolen from each bower for 1981 and 1982 are shown in Tables I and II respectively. During these years, there was an average of 4.46 ± 3.5 and 7.49 ± 8.28 thefts per bower, respectively, for each season. The daily stealing rate was 0.08 and 0.14 thefts per bower per day, with an average of 1.15 and 1.49 feathers taken per theft (Fig. 1). There is a strong correlation between the number of stealing bouts by a male and the number of feathers stolen by him (1981: $r_s = 0.95$, $P < 0.001$; 1982: $r_s = 0.93$, $P < 0.001$). This result is due to the low average number of feathers taken per theft. An average of 4.19 ± 7.09 (1981) and 6.13 ± 10.14 (1982) feathers were displayed at a bower during the mating season.

The mean number of feathers stolen from each bower was nearly equal to the mean number of feathers on a bower through the season. Therefore, it appears that feather stealing occurs at a sufficiently high rate to cause significant changes in the distribution of feathers among bowers.

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If stealing is important in determining the number of feathers on bowers and thereby influences mate choice patterns, then feather stealing should be correlated with the number of feathers on a male's bower. There is a significant relationship between the number of feathers on a male's bower and both the number of feathers he steals (1981: $r_s = 0.458$, $P = 0.014$; 1982: $r_s = 0.615$, $P = 0.001$) and the number of successful stealing bouts (1981: $r_s = 0.378$, $P = 0.038$; 1982: $r_s = 0.573$, $P = 0.001$). However, this result is complicated because the number of times a male steals is highly correlated with the number of times he is a victim of theft (1981: $r_s = 0.855$, $N = 26$, $P < 0.001$; 1982: $r_s = 0.836$, $N = 33$, $P < 0.001$), and the number of

feathers he gained is significantly correlated with the number that he lost (1981: $r_s = 0.873$, $N = 26$, $P < 0.001$; 1982: $r_s = 0.859$, $N = 33$, $P < 0.001$; Fig. 2).

We compared the net gain in feathers (number of feathers gained - number of feathers lost) and the proportion of successful bouts with feathers gained (number of bouts with feathers gained/number of bouts with feathers gained + number of bouts with feathers lost) with the mean number of feathers on the bower for each year. There was a significant correlation between the number of feathers on bowers and the net gain in feathers (1981: $r_s = 0.352$, $N = 29$, $P < 0.031$; 1982: $r_s = 0.221$, $N = 33$, $P < 0.109$; combined $P = 0.023$) and the proportion of bouts with feathers gained (1981: $r_s = 0.317$, $N = 29$, $P < 0.047$; 1982: $r_s = 0.285$, $N = 33$, $P < 0.054$; combined $P = 0.019$). These results show that males with more feathers on their bowers tend to steal more often than they are stolen from, and thereby support the argument that stealing is important in determining differences in the number of feathers on bowers.

The number of feathers stolen

The mean number of feathers taken by males is far less than the mean number of feathers present on bowers (see above) or the mean number which males can carry. We have observed males carry eight feathers in theft, and feather movement data suggest that as many as 10 feathers can be carried. Figure 1 shows that thefts involving four or more feathers are extremely rare. Thus males do not always maximize the number of feathers that they take.

There is, however, some evidence that the number of feathers males take is determined by the number of feathers on their bowers. The number of feathers on males' bowers at the time of a theft was compared with the mean number of feathers on their bowers for the entire season. There is a weak negative regression between the deviation in number of feathers from the seasonal mean and the number of feathers taken per theft for the 1982 season (1981: $r^2 = 0.003$, $P = 0.276$; 1982: $r^2 = -0.011$, $P = 0.046$). This result suggests that a male may steal more when it has a below-average number of feathers on its bower.

Males might adjust the number of feathers they steal according to the number on the victim's bower. There is a positive regression in one of two years between the number of feathers on a victim's

Victim						Thief's gains															
7	18	19	22	30	31	35	36	37	38	39	41	43	44	45	47	48	54	59	60	Feathers	Bouts
					23/7						1/1						11/7			17	12
1	1/1										1/1						40/10			69	22
3	1/1						1/1				3/3						3/2			13	12
	2/1				1/1	1/1														9	8
	1/1								2/2	1/1										4	4
									6/4	1/1									28/14	46	29
									1/1							2/1			8/4	37	19
		1/1							3/1						1/1					4	3
					3/2															7	4
				1/1																21	9
	2/1																			3	3
																				8	3
																				4	3
																				0	0
																				5	4
																				1	1
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																				40	30
	5/2						3/2	1/1		3/2							3/3			9	5
																				25	8
																				2	2
															12/7					12	7
																				12	7
																				1	1
					5/2															29	8
																				0	0
																				0	0
																				0	0
																				3	2
																				7	3
																				66	23
																				1	1
																				30	16
7	6	0	1	38		28	3	3	15	2	27	0	0	1	12	3	57	1	36	485	
5	3	0	1	17		9	2	2	10	2	12	0	0	1	7	2	22	1	18		249

7 with a total of 11 (e I). In 1982 the males thefts between them one member of a pair thefts was not active male as the inactive established male at two non-reciprocal bower was a frequent he made few success- ly, in 1982, the one ciation involved an lished male at bower

47. Stealing associations accounted for 58% and 63% of the total thefts by active males in 1981 and 1982 respectively, even though these males represent less than one-third of all males whose bowers were monitored.

The above definition of reciprocal stealing is based on the relative equality of total thefts throughout the mating season. Reciprocity implies that there is an alternation of gains and losses through the season, and that a male's decision to steal is based on losses due to stealing. An analysis of the pattern of thefts between stealing partners shows that thefts occur in a predominantly alternating pattern. The sequence of gains and losses

from a bower is scored so that the number of consecutive gains or losses (*c*) could be compared against the number of times that gains followed losses or vice versa (*x*). If *x* is greater than *c* we assume reciprocal exchanges to be common; if *c* equals *x*, gains and losses occur randomly; and if *c* is greater than *x*, gains and losses of feathers are grouped in time. Among the 13 bowers with active stealing in 1981 and 1982 (corrected for the effects of an unequal number of gains and losses) there were 10 where *x* was greater than *c*, two with ties, and one where *c* was greater than *x*. This result implies that males react by stealing when they are stolen from.



Figure 2. The number of feathers lost from a bower versus the number of feathers gained by the owner.

Stealing and the erection of new bowers

The establishment of males at new bower sites may be related to the occurrence of active stealing associations. In 1981 there were two new bowers established (31, 38) and one bower (11) still in the process of being established after several failed attempts in the previous year. Males from bowers 11 and 31 were involved in two of the six most active stealing associations.

In 1982 males were newly established at bowers 47, 54 and 60, and the male at bower 31 was again active. These males were involved in five of the six most active stealing associations. Males replaced established males at adjacent bowers 6 and 7, but were relatively inactive. The inactivity of the new

male at the bower-7 site may have occurred because he positioned the bower 70 m NNW in a direction away from bower 18, the owner of which actively stole from bower 7 in the previous year. The neighbours of the male at bower 6 were relatively young males. Adjacent males along the same ridge included the male at bower 7 who moved his bower to the west, and the male to the east (5), who was established late in 1980. The behaviour of the male at bower 60 is especially interesting because he had attempted to set up his bower in 1981 but it stood for only 3 days and was repeatedly destroyed by males from bowers to the east (9) and west (29). The male from bower 29 disappeared in 1982 and bower 60 was established 60 m WNW of where it was built

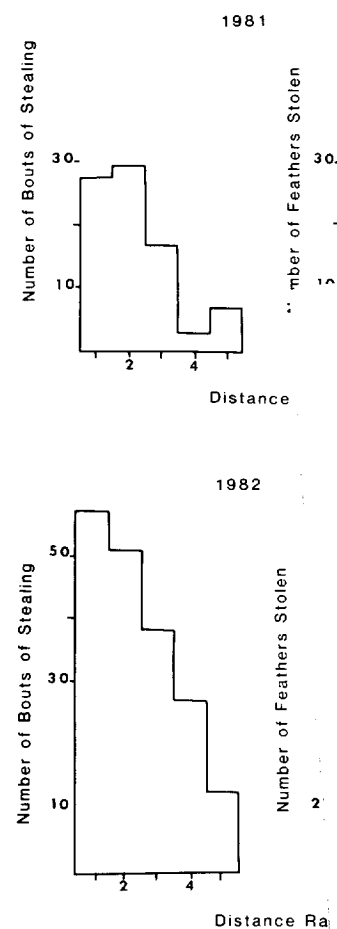


Figure 3. The number of thefts by distances from the victim's bower.

in 1981. The male at bower 54 set up his bower at a previously unoccupied site late in 1981 but it was repeatedly destroyed by the male at bower 4. Overall, among the males at new sites, six of seven bowers were involved in an active stealing association. Males at other males at established bowers were also often become involved in active stealing associations. Thus there is evidence that high rates of stealing may be related to attempts by new males to establish new bowers in the matrix of existing bowers. This often results in reciprocal stealing between adjacent bowers where stealing is not reciprocal and the 'partner' is the new bower owner.

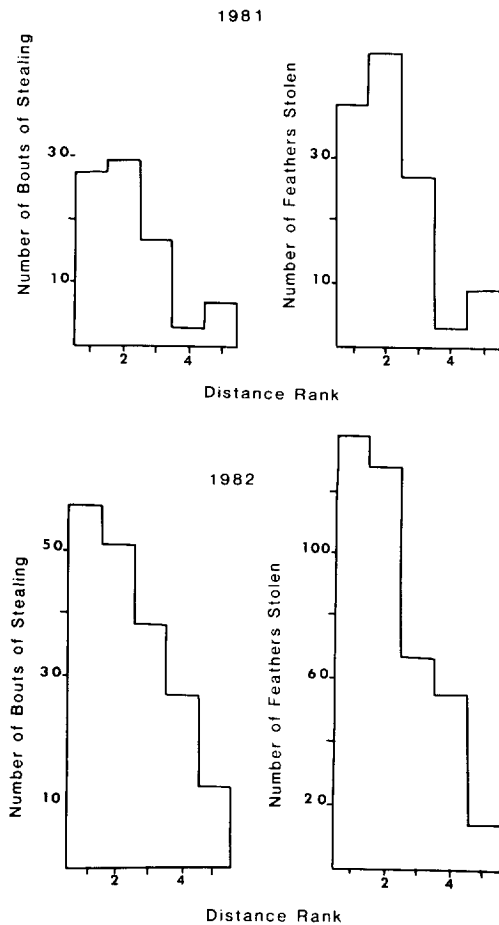


Figure 3. The number of thefts by males at different distances from the victim's bower.

DISCUSSION

Stealing feathers provides dual benefits to thieves: their decoration displays are augmented to the same extent as those of their victims are diminished. However, it is difficult to determine the relative importance of each of these effects in shaping stealing behaviour. The strong correlation of male mating success with the number of feathers on bowers (Borgia 1985a), taken together with the observation that theft from other bowers is the main source of feathers (Borgia, in preparation), suggests important benefits from stealing. The highly directed nature of feather theft, especially toward new males, implies that negative effects of stealing on neighbours is important. Males compete for a limited pool of females which seek mates over a relatively small area (Borgia, in preparation). By evicting other males that are attempting to establish new bower sites near their own, males may increase their own probability of mating. Males programmed primarily to maximize feather gain should steal wherever there are available feathers, and unless there are important advantages to stealing from a particular bower, it is unlikely that they would choose one bower as the focus for their stealing. The highly directed nature of stealing associations, the frequent involvement of new bower holders and the short term of these associations suggest that indirect gains from losses to neighbours have an important effect on determining male stealing patterns.

The comparison of patterns of feather theft and bower destruction give another indication of the importance to victims of feather losses due to feather theft. Borgia (1985b) has analysed bower destruction patterns in satin bowerbirds. He found that bower destructions were common and, like feather thieves, bower destroyers tended to interact most with near neighbours. Bower destructions were less frequent than the theft of feathers, and occurred in conjunction with stealing in most cases (61%). It was more common for feather thefts to occur without bower destruction than vice versa. The commonness of bower destruction suggests that harm to the bower display of other males is important, but the more frequent occurrence of stealing implies that stealing, which directly aids the thief in addition to harming the victim, carries a greater overall advantage.

The above data suggest that a male's tendency to steal is strongly influenced by the distance between

in 1981. The male at bower 54 set up his bower at a previously unoccupied site late in 1981. His bower was repeatedly destroyed by the male at nearby bower 4. Overall, among the males who set up bowers at new sites, six of seven became involved in an active stealing association. Males who replaced other males at established bower sites did not become involved in active stealing associations. Thus there is evidence that high rates of theft may be related to attempts by new males to establish new bowers in the matrix of existing bowers. This often results in reciprocal stealing associations, but where stealing is not reciprocal, the inactive 'partner' is the new bower owner.

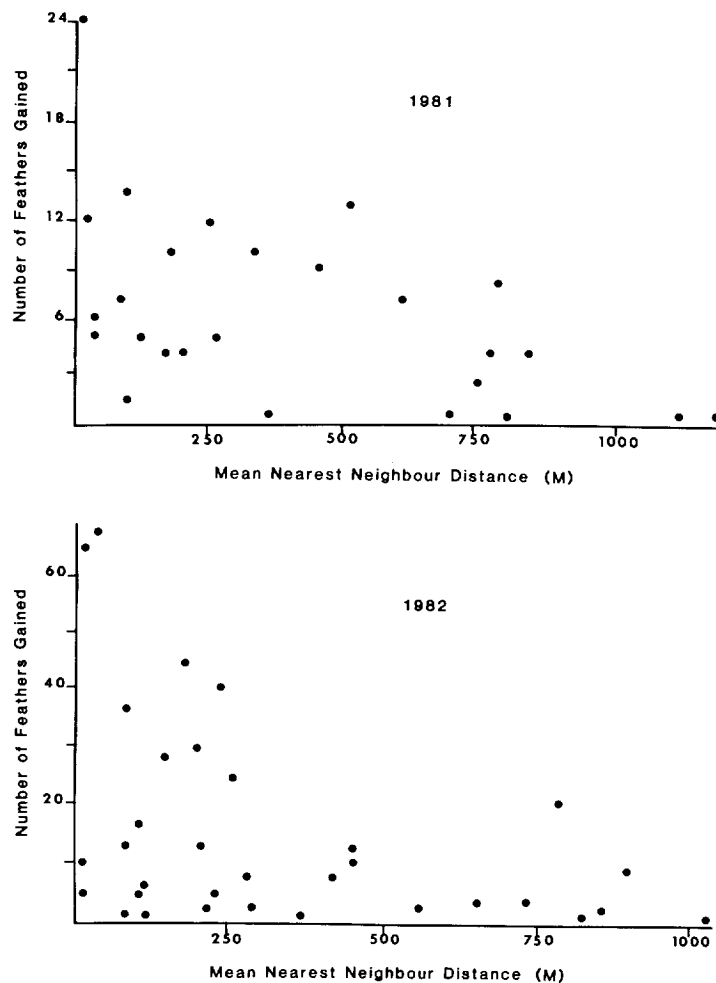


Figure 4. Mean distance to the five nearest bowers versus the number of feathers gained by the bower owner.

adjacent bowers and the level of decoration on those bowers. When bowers are farther apart, established males appear to find theft less rewarding. Inactive bower decorators often have neighbours with few decorations on their bower and are inactive as decoration thieves. Their failure to actively decorate and participate in stealing suggests that they may be subordinates attempting to control display sites near the bowers of established males. If these males attempted to decorate elaborately, nearby established males might be more likely to steal decorations and destroy their bower. Less ornate bowers would provide these males with an opportunity to produce a display, albeit of lower attractiveness to females.

Several lines of evidence demonstrate that some males may avoid high levels of decoration on their bowers in order to reduce the threat of interference by nearby males. The above data show that males with few feathers on their bowers are inactive in stealing. In addition, most decorations other than feathers, such as yellow straw, yellow leaves, and blue and yellow flowers, are abundant in the vicinity of bowers, but are not used in large numbers by inactive males. The total number of all types of decorations on a male's bower is positively correlated with the number of feathers on his bower (Borgia 1985a) and how often he steals (1981: $r_s = 0.327$, $N = 27$, $P = 0.032$; 1982: $r_s = 0.330$, $N = 33$, $P = 0.030$). Males in juvenile plumage may

steal decorations and decorate forms (Vellenga 1970, personal observation). The inability of juvenile males to steal decorations cannot be the sole explanation for poorly decorated bowers.

Feather stealing appears to be an important element in shaping the sexual display of satin bowerbirds. The generally high level of theft and the significant correlation between net gain from stealing and the number of feathers on each bower show that stealing has a strong influence on the number of feathers on a bower. Taken together with evidence that the number of decorations (particularly feathers) is highly correlated with male mating success (Borgia 1985a), these results suggest that males may enhance their own fitness at the expense of competing males through stealing. The above results are consistent with a model of mate selection in which females assess a male's quality on his success in conflict with other males.

The important role of competition in the quality of display among male satin bowerbirds may serve as a model for sexual selection in other species with extravagant displays. These results provide a focus for the study of the evolution of display would be much more difficult to study in species in which male interactions are limited to ritual contests or combat that is restricted to a specific site. Our investigation of the role of competition in satin bowerbirds raises the question of whether high levels of male interaction in the vicinity and quality of male display are characteristic of arena species.

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steal decorations and decorate temporary platforms (Vellenga 1970, personal observation). Thus, the inability of juvenile males to steal or collect decorations cannot be the sole explanation for their poorly decorated bowers.

Feather stealing appears to be an important element in shaping the sexual display of male satin bowerbirds. The generally high rates of feather theft and the significant correlations between the net gain from stealing and the number of feathers on each bower show that stealing has a direct influence on the number of feathers on a male's bower. Taken together with evidence that the number of decorations (particularly feathers) is highly correlated with male mating success (Borgia 1985a), these results suggest that males can enhance their own fitness at the expense of nearby competing males through stealing. Moreover, the results are consistent with models of sexual selection in which females assess a male's quality based on his success in conflict with other males.

The important role of competition in shaping the quality of display among male satin bowerbirds may serve as a model for sexual competition in other species with extravagant display. Bowlers provide a focus for the study of interactions that would be much more difficult to evaluate among species in which male interactions involve acoustical contests or combat that is not focused at a specific site. Our investigation of sexual competition in satin bowerbirds raises the possibility that high levels of male interaction influence the intensity and quality of male display in other exploded arena species.

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The influence of kinship on rhesus monkey aggression

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Abstract. Among the 100 rhesus monkey group members showed disproportionate aggression, particularly likely to show aggression towards kin. Contact aggression were most often directed towards kin, and aggression towards non-kin declined as animals matured. Males no longer received disproportionate aggression from kin significantly less aggression from non-kin. Males include mobbing a defeated victim. Females of all ages directed their aggression towards non-kin. The relative frequency of male aggression towards non-kin supports the hypothesis that aggression is used primarily for socialization, particularly active in the socialization of young.

There has been considerable discussion about the function of aggression in socially living animals and most authors recognize that aggression serves multiple functions in primate societies (Stein & Gordon 1974). Whereas most authors emphasize the disruptive effects of damaging aggression, we have argued that aggression serves a positive role in socialization in rhesus monkeys, *Macaca mulatta* (Ehardt 1985a). These animals have been known to inflict severe and even fatal wounds during agonistic encounters and, even if agonistic encounters are controlled by social mechanisms and tend to result in the less damaging forms of expression (Stein & Ehardt 1985b,c), the recipient of aggression may suffer severe injuries. The fact that monkeys of several taxa selectively direct aggression towards kin during agonistic encounters suggests that this function is best served by the defence of kin against aggressive attack (Kaplan 1977; Massey 1977; Bernstein & Ehardt 1985). It therefore seems counter-intuitive to argue that non-kin will receive more aggression as a consequence of socialization and that this too will serve inclusive fitness interests.

Hall (1964) believed that the single most proximal cause of aggression was