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Bower Destruction, Decoration Stealing and Female Choice in the Spotted Bowerbird *Chlamydera maculata*

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Summary: Male bowerbirds build and decorate bowers to attract females as copulation partners. Here we report the first information on the relationship between the bower and mating patterns in the Spotted Bowerbird *Chlamydera maculata*. The mating success of male Spotted Bowerbirds is correlated with the quality of male bowers and several measures of bower decoration. Bower destruction and decoration stealing are rare. The low rate of interaction among bower holders appears to result from the large distances between bowers. Studies of the Satin Bowerbird *Ptilonorhynchus violaceus* have shown a much higher level of stealing and destruction and support the view that male interactions are critical in determining the level of bower decoration and bower quality (Borgia 1985b; Borgia & Gore 1986). The low levels of stealing and destruction in Spotted Bowerbirds, coupled with the correlation of bower quality and mating success, suggest that high levels of male interaction are not a necessary prerequisite for females to use bowers as a factor influencing mate choice. We consider the implications of this finding in regard to the evolution of bower building and the evolution of sexual display.

Introduction

The functional significance of bower-building behaviour has long been of interest to biologists. In recent years much has been learned about the behaviour of some species, especially the Satin Bowerbird *Ptilonorhynchus violaceus* (Vellenga 1970, 1979, 1980; Donaghey 1981; Borgia 1985a,b, 1986; Loffredo & Borgia 1985; Borgia & Gore 1986; Borgia *et al.* 1987). On the other hand, the details of behaviour, especially factors affecting male reproductive success, remain largely unknown for other species (but see Pruett-Jones & Pruett-Jones 1982).

In studies of the Satin Bowerbird we found that male displays at bowers are important in affecting mate choice by females. Mate choice by females is influenced by the quality of bowers and bower decorations (Borgia 1985a), the quality of male acoustical displays at the bower (Loffredo & Borgia 1985) and the level of parasitic infection of males (Borgia 1986; Borgia & Collis 1989). We also found that the quality of some of these male display traits is affected by male interactions, in particular, that bower destructions by conspecific males significantly lower a male's bower quality and that decoration stealing significantly affects the distribution of decorations among bowers (Borgia & Gore 1986). This set of relationships suggests that females may be able to assess male value as a sire by inspecting bowers and their associated decorations (Borgia *et al.* 1985). The so-called good genes models claim that females prefer males that are vigorous (Trivers 1972; Andersson 1982), older (Halliday 1978; Howard 1979) and/or dominant (Borgia 1979; Borgia *et al.* 1985) because such males are more likely to sire vigorous offspring.

The Spotted Bowerbird *Chlamydera maculata* is a member of a genus made up of four species of avenue-building bowerbirds. The Spotted Bowerbird has been the subject of some general descriptive studies (Jackson 1912; Chaffer 1945; Serventy 1955; Warham 1962) but, like nearly all other bowerbird species, it has not been studied in sufficient detail so that factors affecting mating success are understood. The paucity of detailed studies of mate choice makes it difficult to assess if male interactions consistently affect the quality of male bower displays across bowerbird species. Here we assess the potential of male interactions to affect female choice through their effect on the quality of bowers and bower decoration.

Spotted Bowerbirds differ from Satin Bowerbirds in several interesting and important aspects of their display. Spotted Bowerbirds have monomorphic plumage and tend to decorate their bowers with a much greater number of display objects (Marshall 1954). Their bowers are farther apart (McGill 1960), have more widely dispersed decorations and exhibit a more equal distribution of decorations at the two bower entrances. The bower itself has a wider avenue and 'see-through' straw

walls (Borgia unpub. data). These differences suggest a high level of divergence between these species and this should provide an opportunity to test for functional similarity despite large differences in bower structure and associated characters.

Two objectives in studying the Spotted Bowerbird were to describe the patterns of interactions of males, especially in their effect on the quality of male displays, and to determine the importance of different components of male display on patterns of mate choice by females. This information should allow us to determine whether patterns of male display and interaction observed in Satin Bowerbirds are common across bowerbird species.

Study site

The study site was located in south-central Queensland, on a grazing property called 'Bullamon Plains' located 3 km N of the town of Thallon (28°30′S, 148°52′E). Bullamon Plains has been designated as a wildlife reserve by the Queensland National Parks and Wildlife Service. The habitat is semi-arid open woodland in which trees are widely spaced (>10 m) with grassland between. Wilga *Geijera parviflora*, *Eucalyptus* spp. and White Cypress Pine *Callitris columellaris* are the most common trees in undisturbed areas. The Moonie River runs through the property and water from the river is drained off into a series of canals that are used to occasionally flood large areas. Earthen 'tanks' (reservoirs made by digging and banking) dot the study site and on the western edge there is a bore drain (a canal fed by a bore). For several years before we started the project there had been a drought, the river flowed at a low rate and there had been no flooding. During our observation period the drought broke and in December one paddock with a bower under observation (bower 9) was flooded.

Methods

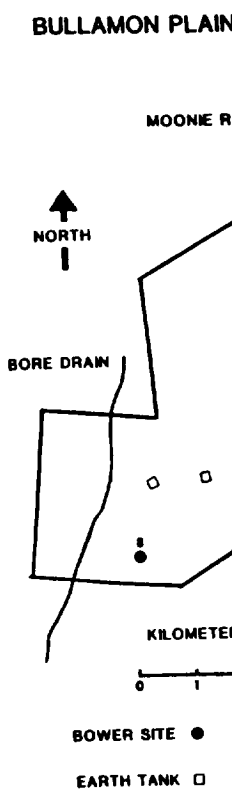
Twelve bowers were found on the study site. Most bowers were located with the assistance of workers on the Bullamon Plains property, keen naturalists who regularly traversed the study site mustering sheep. Additional bowers were located by us and by members of the Queensland Ornithological Society. This combined effort gave detailed coverage of the study site, so it is unlikely that many bower sites were missed.

Bower owners were captured and banded with distinctive colour band combinations, with the same two band sequence repeated on each leg. They also received a metal CSIRO band on the left leg above the plastic bands. Observations were made on a daily basis by two or three observers at different bowers from sunrise until 1200 h (Australian Eastern Standard Time) from 21 September until 15 December 1987; there was a total of 914 h of observation from hides. Observers rotated their visits among bower sites. Detailed notes were taken on individual behaviour around bowers. Behaviours during displays (displays given to an empty bower) and courtships (displays to a visiting bird) occurred with great rapidity. During these periods the birds' behaviours were either videotaped or verbally described into an audio tape recorder and later transcribed. Observations of the frequency of all behavioural variables, including copulations, were standardised for differences in the number of observation days at each bower. Each bower was observed for a minimum of six days.

Most female Spotted Bowerbirds were not banded, so we could not resolve if presumed females made multiple visits to mate at the same or different bowers. In one instance, a female mated twice in succession without leaving the bower (bower 2 on 17 November). Observations of marked Satin Bowerbird females indicated that multiple copulations at different bowers are rare and that it is not unusual for different females to revisit a male's bower to copulate on the same day (Borgia 1986). We developed rules for counting mating events based on these observations; a separate mating event was scored each time a female copulated and left the area. If the male and female copulated twice in the same visit, this was scored as a single mating event.

Bower dimensions

The dimensions of bowers were measured five times for each bower at intervals of 8-12 days. The direction of the bower avenue was measured by a compass and the more easterly bower entrance was designated as the east entrance and the other, the west entrance. Wall positions were defined in relation to this orientation. Other dimensions measured were bower avenue length and the lengths of the east and west platforms. Bowers typically had a cluster of decorations in the bower avenue near the bower centre. We measured the length along the main bower axis of this set of decorations and the distance from the edge of this pile to the east and west entrances. East and west entrance widths, north and south wall widths and total outside width were measured at 100 mm from ground height. The inside maxi-



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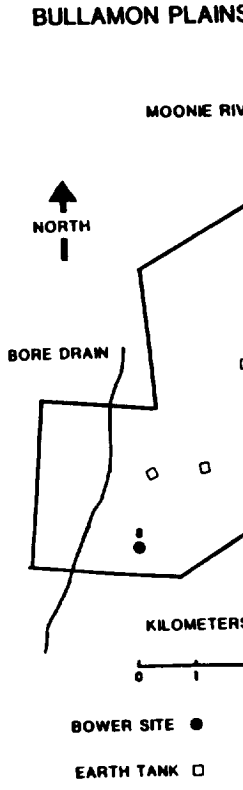

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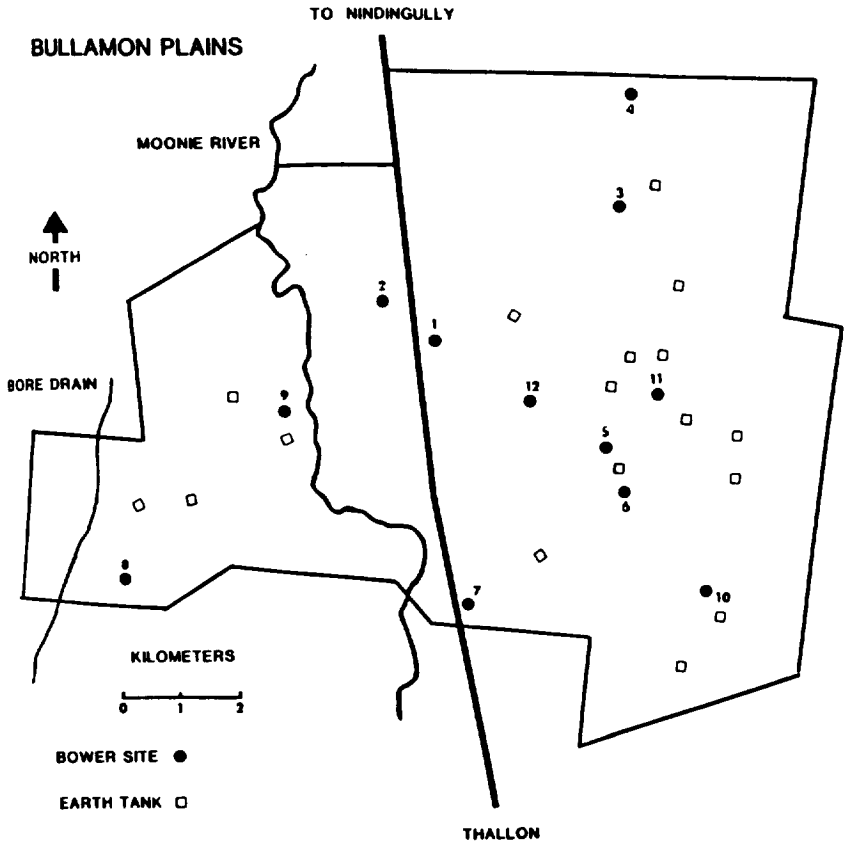


Figure 1 Map of the Bullamon Plains study area. Dots with numbers represent Spotted Bowerbird bower sites.

mum width was measured at the middle of the bower wall at 100 mm height (which typically was a point at which the bower wall bowed out compared with the opposite wall).

Bower quality

Bower walls were composed of straw placed in a stick base. Sticks were generally restricted to the lower parts of the bower walls, but the relative proportion of the wall made up by sticks and straw varied among bowers. Characteristics of bowers including quality of bower construction, symmetry of bower structure, the verticality of the walls and straw size were scored subjectively by field assistants on a scale of 1 to 7. Neither the authors nor observers had previous knowledge of the reproductive history of individual birds. Individuals scoring bowers were instructed to give the quality ratings of 1 to bowers with fine sculpturing and neat overall appearance and larger values for lower quality. Symmetrical bowers with vertical walls and thin straw were given ratings of 1 for these remaining variables. These measures and scoring procedures were chosen to allow direct comparisons with information on mate preferences of female Satin Bowerbirds (e.g. Borgia 1985a).

On the same days that bowers were measured, the number of decorations on bowers were counted. Decorations were noted by type and position. At the beginning of our study we marked the hard decorations (e.g. glass, bones and rocks) on each bower (except the small bits of clear glass in the centre of the bower) with a small dab of paint, the colour being unique to each bower. We did not notice birds reacting adversely to our marks on their decorations, and the marks stayed on the decorations through the entire observation period. For this analysis we scored numbers of decorations in different areas around the bowers. These areas include the bower floor, the inside of the bower wall (north and south), and the north, east, south and west platform areas. Decorations included both natural objects such as bones (especially sheep vertebrae), fruits or other plant

material, and man-made objects such as glass, metal or plastic objects. Items of the same type but of different colour (e.g. glass) were classed separately when they occurred at multiple bowers; otherwise, they were classed into several general categories. For analysis, decorations were also considered in general categories (e.g. metal, plant, fruit), and these were used in correlations with male mating success. For each class of decorations, a total count was recorded at bowers.

The use of landmarks allowed us to plot the bowers on an aerial photograph and to calculate interbower distances.

The Systat statistical package (Wilkinson 1986) was used for data analysis. Spearman rank correlations (r_s) were used for all bivariate comparisons. For tests of *a priori* hypotheses one-tailed P values were used. Stepwise regression was used to identify decoration variables in a model developed to explain variation in male mating success. The statistical results reported were then derived by using these variables in a multiple linear regression model.

Results

The distribution of bowers and interbower distances

Figure 1 shows the distribution of Spotted Bowerbird bowers on the Bullamon Plains property. Bowers were widely spaced. The closest bowers were numbers 5 and 6 approximately 860 m apart. The mean nearest neighbour distance was slightly less than 2 km ($\bar{X}$ = 1.83 ± 0.62 km). These nearest neighbour distances are much greater than those found for Satin Bowerbirds (Borgia 1985b; Donaghey 1981) or Macgregor's Bowerbirds (Pruett-Jones & Pruett-Jones 1982).

Bower destruction

Our monitoring of bowers showed that bower destruction was rare and through our entire observation period we saw only two instances, both by the same bird at the same bower on the same day. The owner of bower 9, a bower located nearly 5 km away, arrived and immediately began destroying bower 5 and continued for 8 min until the owner of bower 5 arrived and chased the destroyer away, by which time the bower was approximately 85% destroyed. The same bird reappeared 218 min later and began to destroy the mostly rebuilt bower. After tugging at the bower floor for 6 s he gave up and began 'inspecting' the bower. He then took two berries from the centre of the bower and left 100 s later.

On our visits to bowers we also noted when the bowers were in disrepair, presumably as a result of destruction by a marauding male. There were four cases (bowers 1, 4, 5, and 10) in which this occurred.

Decoration stealing

We observed only four instances of decoration stealing. Three thefts were by unbanded birds and we do not know if these birds owned bowers. Juvenile-plumage Satin Bowerbirds that do not control permanent bower sites often steal decorations (Borgia & Gore 1986). The fourth stealing event was associated with the destruction described above. Stealing occurred at a rate of 0.004 thefts per hour.

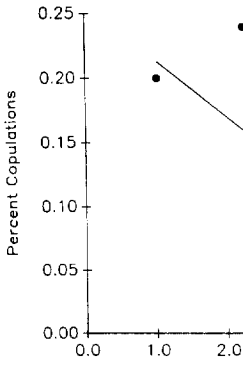
A low rate of stealing was also indicated from the marked decorations. Throughout the entire season only one marked decoration was found to have moved between bowers (from bower 6 to 12).

Displays and courtships

Male Spotted Bowerbirds displayed at unoccupied bowers (displays) and at bowers with another bird inside the bower (courtships). Details of these behaviours will be discussed elsewhere (Borgia unpubl. data). From 13 October to 15 December (the period of active mating, see below) we observed 57 displays and 190 courtships at a rate of 0.07 and 0.23 per hour, respectively.

Non-owner males sometimes used other males' bowers for courtship. In several cases non-owner males were banded and their prolonged attendance at the bower suggested that they did not own a bower elsewhere. We did not see one of our known bower owners using another male's bower for display. Some bowers appeared to be sites where numerous birds congregated, for example, 16 birds were in the vicinity of bower 11 at one time. The high rates of display by non-owners at these bowers to other known males and the scarcity of female-like behaviours, e.g. crouching in the bower, suggested that most of these visitors were males.

Distinctive behaviours allowed us to distinguish displays to male visitors from those to females. The displaying male and the bird in the bower showed patterns similar to those observed in male-male displays in Satin Bowerbirds in which the sex of visitors was known (Borgia 1986). That is, the courted bird would frequently and casually move in and out of the bower appearing uninterested in the male courting him and often actively placing sticks in the bower while being courted. Courtships that led to copulations showed that female Spotted Bowerbirds, like female Satin Bowerbirds, in-



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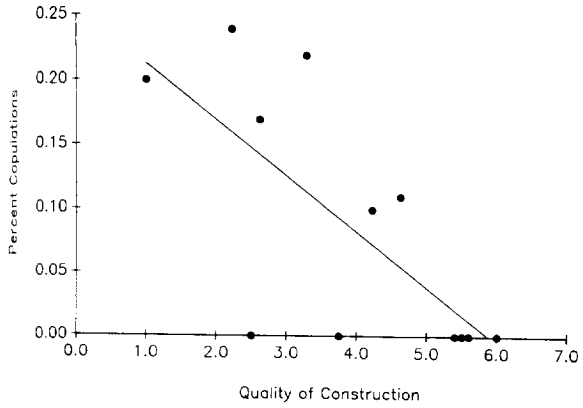

Figure 2 Corrected per cent copulations by male Spotted Bowerbird bower owners versus the quality of construction of individual bowers. Low numbers indicate high bower quality scores.

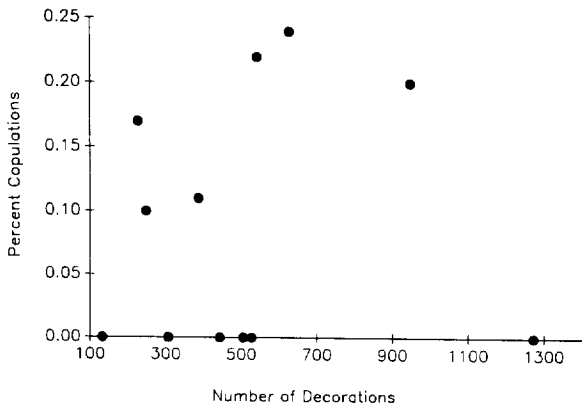

Figure 3 Corrected per cent copulations by male Spotted Bowerbird bower owners versus the number of decorations at individual bowers.

tently watch males and are very deliberate in moving in and out of the bower. Courted male Spotted Bowerbirds never crouched in the bower (as do females before copulation) and generally stood in line with the main axis of the bower during courtship. In several instances, when visiting males approached the courting male, the courting male reacted by attacking the visitor directly or by violently ramming his body into the end of the bower wall next to where the courted bird was standing. These attacks were never observed when visitors showed female-like behaviour.

Copulations

We observed 15 mating events (see Methods). Copulations lasted 2-4 s. Like Satin Bowerbirds (Borgia 1986), females shook violently after copulation. Of the 12 bower owners we observed, only six were seen to copulate. The owners of bowers 2, 7, 4, 11, 8 and 6 had 6, 4, 2, 1, 1 and 1 mating events respectively. Mating events were not clumped at any time through the period from 13 October to 15 December. On two days there were multiple copulations at a bower (three at bower 2 on 28 October, and two at bower 4 on 6 December).

Mating in Spotted Bowerbirds is somewhat different from that in other bowerbird species because of the orientation of the male's display relative to the bower. In Spotted Bowerbirds, females stand perpendicular to the main axis of the bower facing one of the walls (Borgia unpubl. data). In a few cases the females were not fully aligned with either major axis, and the male had to climb over the female in order to copulate with her.

Correlates of mating success

There was a significant positive correlation between our corrected measure of mating success (see methods) and the quality of construction of bowers ($r_s = 0.709$, $P < 0.001$; Fig. 2). The three other measures of bower quality also showed positive correlations with mating success, and two of these were also significant (Symmetry of structure: $r_s = 0.667$, $P < 0.01$; straw size: $r_s = 0.281$, $P > 0.05$; verticality of straw: $r_s = 0.547$, $P < 0.02$). Thus, overall, there appears to be a strong relationship between bower quality and mating success.

Corrected mating success showed a positive but nonsignificant correlation with the total number of decorations at bowers ($r_s = 0.392$, $P = 0.10$; Fig. 3). We found positive correlations between mating success and decoration counts in seven of eight specific areas (see methods) around the bower (binomial $P < 0.05$). Two of these were statistically significant (south platform: $r_s = 0.524$, $P < 0.05$; bower floor: $r_s = 0.557$, $P < 0.05$).

Successful males tended to have significant or near significant accumulations of reddish-pink glass at their bowers. We found large correlation coefficients between corrected male mating success and the presence of reddish-pink glass objects: pink ($r_s = 0.557$), red ($r_s = 0.733$) and purple glass ($r_s = 0.500$).

We developed a regression model to predict per cent mating success from decoration variables. A model that included red glass, total fruit and black glass was highly significant and could explain 96% of the variation in corrected male mating success.

Discussion

Our results strongly support the hypothesis that bower quality affects mate choice decisions by females. The connection between decorations and mating success is less clear. Spotted Bowerbirds may prefer decorations that match their reddish-pink nuchal crests. Various authors have suggested that bowerbird colour preferences are based on matching their plumage (see Morrison-Scott 1937; Marshall 1954). The predicted correlation between decoration number and male mating success approaches significance even with a small sample of bowers. Combined with the comparisons of decorations by area around the bower and the strong correlations of red-pink decorations with corrected male mating success, the hypothesis that decoration numbers affect male mating success should be considered as having received some limited support. In general, these results are consistent with findings from Satin Bowerbirds (Borgia 1985a).

In Spotted Bowerbirds decoration stealing and bower destruction is much less common than in Satin Bowerbirds. The observed rate of 0.002 destructions per hour for Spotted Bowerbirds is about 1/10 the frequency of destructions in Satin Bowerbirds (Borgia 1985b) and 1/100 of the destruction rate reported for Macgregor's Bowerbirds (Pruett-Jones & Pruett-Jones 1982). Stealing rates are also similarly low when compared with Satin Bowerbirds (Borgia & Gore 1986), the only species for which comparative data are available. Other behaviours around the bower, including courtship, display, and bower maintenance activities (e.g. building, painting, and decorating behaviour) do not show this dramatic difference; so it appears that the observed differences are not due to a lower overall level of activity around bowers or to an effect of observer disturbance on the tendency of non-owner birds to visit the bower.

The low rate of interference between bower holders suggests that, unlike Satin Bowerbirds, stealing and destruction did not have a major role in affecting bower and decoration quality. This raises the question of why Spotted Bowerbirds have low rates of interference between bower owners relative to other species. Interbower distance is critical in determining rates of bower destruction in Satin Bowerbirds (Borgia 1985b). In Spotted Bowerbirds, interbower distances are of the order of 10 times greater than they are for Satin Bowerbirds. This has two important effects that probably influence the likelihood of bower-related interactions among bower holders. First, the considerably larger distances between bowers greatly increase the cost of visits to other bowers both in terms of energetic costs and risk to the prospective marauder's bower, because males need to be absent for a long time in order to visit another bower. If, like Satin Bowerbirds, bowers are commonly destroyed when the owner is not present at his own bower, then multiple trips may be necessary before there is successful destruction. The cost of travelling over large interbower distances must be multiplied by the cost of multiple trips needed to gain an opportunity to destroy the bower with the owner not present.

In addition, Spotted Bowerbird males probably have greater difficulty in assessing opportunities to initiate raids on competitors' bowers. Satin Bowerbird males utter loud 'whistle' calls and advertising 'scratch' calls that may allow neighbouring males to assess their presence at the bower. By monitoring these calls, male Satin Bowerbirds may avoid trips to other males' bowers when the owner is present and they are not likely to accomplish a successful raid (Borgia unpubl. data). Spotted Bowerbird calls cannot be heard from adjacent bowers. Thus, an important cue available to Satin Bowerbird males that may reduce the costs associated with unsuccessful visitation to adjacent bowers is not available to Spotted Bowerbirds.

Evidence that females use the bower and its decorations in mate choice supports the view that bowers are display traits that have an evolved function in sexual display. This result provides a necessary element of support for Gilliard's (1956) conjecture that bower characters function in place of plumage characters in mate choice. This has now been shown for two species that differ greatly in their degree of plumage dimorphism. A second part of Gilliard's model is that the degree of bower elaboration is inversely related to plumage brightness. Spotted males are dull grey and brown and except for a small lilac nuchal crest are decidedly less brightly plumed than the strikingly dimorphic Satin Bowerbirds. Following from Gilliard's hypothesis, Satin Bowerbirds have smaller and less decorated bowers even though they are larger birds. What remains unclear is why these differences exist and to what extent they are the result of transference as suggested by Gilliard (1956).

Runaway selection has been proposed as an explanation for female preferences for exaggerated traits (Fisher 1930; Lande 1981; Kirkpatrick 1982, 1986) and this type of model may account for the female preference for owners of bowers with large numbers of bower decorations and well-decorated bowers as seen in Satin

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appear to be many s

crease the cost of visits
energetic costs and risk
bower, because males
in order to visit anoth-
rds, bowers are com-
r is not present at his
ay be necessary before
The cost of travelling
must be multiplied by
to gain an opportunity
er not present.
d males probably have
portunities to initiate
atin Bowerbird males
ertising 'scratch' calls
s to assess their pres-
these calls, male Satin
other males' bowers
hey are not likely to
Borgia unpubl. data).
e heard from adjacent
e available to Satin
the costs associated
jacent bowers is not

bower and its decora-
view that bowers are
d function in sexual
ecessary element of
njecture that bower
lumage characters in
nown for two species
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model is that the de-
nversely related to
s are dull grey and
lac nuchal crest are
an the strikingly di-
ving from Gilliard's
smaller and less dec-
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roposed as an expla-
r exaggerated traits
rick 1982, 1986) and
r the female prefer-
e numbers of bower
vers as seen in Satin

Bowerbirds (Borgia *et al.* 1985; Borgia 1986; Diamond 1988). However, because runaway models do not make explicit predictions in general and specifically about male display behaviour they have proven difficult to test, and the data presented here cannot be used to evaluate them.

Several other models that purport to explain female preferences are amenable to such tests. Females may prefer aggressively dominant males as sires for their offspring because these males have been tested in direct competition with other males (Alexander 1975; Borgia 1979; Borgia *et al.* 1985). The strong effect of destructions (Borgia 1985a) and stealing (Borgia & Gore 1986) on the quality of bower displays and female choice of males with high quality displays in Satin Bowerbirds supports predictions of this model. Our finding here that stealing and destruction occur at very low rates makes it unlikely that these types of interactions affect patterns of assessment in Spotted Bowerbirds and, as such, it opens to question the generality of the suggestion that females use bower and decoration quality to assess male dominance status. It should be noted, however, that Spotted Bowerbirds may be highly divergent in many important aspects of their bower building and display around bowers, even when compared with the closely related Great Bowerbird *C. nuchalis* (Borgia unpubl. data). Thus, the low rate of stealing and destruction may be a result of recent evolutionary or ecological change (possibly related to bower spacing). The presence of stealing and/or destruction in other bowerbird species (e.g. *Amblyornis macgregoriae*, Pruett-Jones & Pruett-Jones 1982; *A. inornatus*, Diamond 1988; *Scenopoeetes dentirostris*, *C. nuchalis* and *Prionodura newtonia*, pers. obs.) leaves open the possibility of an important and general effect on female assessment by males. The ability to hold a bower, even without destructions and stealing, may provide females information about relative male quality and perhaps dominance. In Satin Bowerbirds there are many sexually mature adult plumaged males that do not hold bowers and it is from this class of males that replacement bower holders are recruited. Often these males attempt to establish bowers but the owners are excluded by nearby bower owners (Borgia unpubl. data). These observations show, at least for Satin Bowerbirds, that the ability to hold a bower depends on a male's ability to gain a minimal level of resource holding power (*sensu* Parker 1974). In Spotted Bowerbirds, we do not have detailed observations of attempts by young males to establish bowers, but there appear to be many similarities with Satin Bowerbirds including the presence of a sizable group of males who aggregate at the bowers of other males and participate in male-male displays. We do not know why these males fail to hold bowers but a likely explanation is that they have not acquired sufficient local dominance to do so. In Satin Bowerbirds this hypothesis is supported by the observation that it is invariably young males without well established bower sites that become involved in these aggregations. Thus, until this question is resolved, some care must be exercised before rejecting an important role for the assessment of dominance even in mate choice by Spotted Bowerbirds.

Similarities in the bowers of successful males in Spotted and Satin Bowerbirds suggest that criteria not directly related to male dominance may be important in mate selection. Females of both species tend to choose males with especially well-built bowers and, at least for Satin Bowerbirds, these are characteristic of older males. It has been hypothesised that females choose older males as sires because they have been tested by the environment (Halliday 1978; Howard 1979). In Satin Bowerbirds we found that bower quality is highly correlated with male age, even if the effects of male dominance are removed (Borgia 1985a), and that older males are able to build bowers faster than their younger counterparts (Borgia unpubl. data). This suggests that experience is a necessary component in bower building (see also Vellenga 1970). If this is also true in Spotted Bowerbirds, then the large differences we see in bower quality may function as indicators of male age to females. For Spotted Bowerbirds, the relative rareness of bower destructions suggests that effort directed at bower-building translates into cumulative improvements in bower quality.

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Patterns of l
Cacatua pas

G.T. Smith[1] and L.A

[1] CSIRO Division of V
[2] CSIRO Tropical Fore

Summary: Observation
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Introduction

The movements under
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