Complex male display and female choice in the spotted bowerbird: specialized functions for different bower decorations

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Abstract. Male bowerbirds build and decorate bowers to attract females as copulation partners. Spotted bowerbirds, *Chlamydera maculata*, are atypical in having widely spaced display sites, bowers that are greatly diverged from those of closely related species, and extremely intense, aggressive displays. Results from the continuous monitoring of bowers show that (1) a few males account for the majority of matings, (2) the two most common decoration types, bones and glass, explain a large proportion of the variation in male mating success and (3) large inter-bower distances relate to low levels of decoration stealing and bower destruction. Components of male mating success, male ability to attract female visitors to the bower, and male courtship success correlate respectively with counts of bones and glass. Bones are spread widely around the bower and glass is placed close to it supporting the hypothesis that bones act to attract females towards the bower and glass functions later to stimulate females in the bower. This temporal sequencing of courtship functions represents a novel explanation for the evolution of complex male display traits.

Mate selection in species with elaborate male display traits is a topic of much interest in evolutionary and behavioural biology (Fisher 1930; see Bradbury & Andersson 1987). In such species, males commonly make no material contribution to females or their offspring and females often show preference for a limited set of males (e.g. Andersson 1989; Höglund & Lundberg 1987; Pruett-Jones & Pruett-Jones 1990; and references in Bradbury & Gibson 1983; Wiley 1991).

There are now numerous hypotheses explaining how extreme displays evolve. 'Good genes' models propose that extreme sexual displays function as indicators of male quality to choosing females (e.g. Trivers 1972; Zahavi 1975; Borgia 1979; Andersson 1982, 1986; Hamilton & Zuk 1982). Alternatively, the runaway model (Fisher 1930; see also Lande 1981; Kirkpatrick 1982, 1986) posits that female preferences produce greatly elaborated male display traits without providing enhanced vigour to offspring. Other models include: passive choice (Andersson 1982; Parker 1983), intra-sexual signalling (Halliday 1978; LeCroy et al. 1980), proximate benefits (e.g. protection to females provided by well-constructed bowers; Borgia et al. 1985) and innate preferences (Burley 1985; Kirkpatrick 1987; Ryan et al. 1990).

Recent empirical studies have shown that elaborated traits in polygynous species are often complex sets of traits (Borgia 1985a; Borgia et al. 1987; Andersson 1989; McDonald 1989; Prum 1990; Zuk et al. 1990; Gibson et al. 1991; Møller & Pomiankowski 1993). The function of these traits and reasons for their complexity is just beginning to be explored.

Bowerbirds have among the most complex set of display traits of any organism. Bowerbird bowers are built of sticks on the ground in association with decorated display courts. Bowers and display courts provide a stage for male behavioural display that includes plumage, acoustical and dancing elements directed at females during courtship. Comparisons of different species led Gilliard (1956, 1963) to suggest that bowers and decorations serve as a replacement for elaborate plumage characters, but recent tests of this hypothesis have led to ambiguous results (Kusmierski et al. 1993).

Female satin bowerbirds, *Ptilonorhynchus violaceus*, prefer males with well-built and well-decorated bowers (Borgia 1985a; Borgia & Mueller 1992), indicating that bowers and decorations play an important role in mate attraction. For satin bowerbirds, bower destruction affects bower quality (Borgia 1985b) and decoration

stealing affects the number of decorations on bowers (Borgia & Gore 1986). The indicator hypothesis suggests that females may be able to assess male dominance and overall vigour by surveying the number of decorations and quality of the bower (Borgia et al. 1985). In satin bowerbirds, male mating success, bower quality and the number of bower decorations are correlated between years suggesting that their displays are not so costly as to be disabling in the subsequent field season. This contrasts with two sexual selection models (runaway and the epistatic version of handicap) that predict expensive male displays for satin bowerbirds (Borgia 1993). Recent comparisons with the toothbill bowerbird, *Scenopoeetes dentirostris*, a species that clears and decorates a display court but does not build a bower, suggest that bowers may have initially functioned in attracting females to the court to observe male display by lessening the threat of forced copulation (Borgia, in press a).

Comparisons between species can help determine the functional significance of display traits (Basolo 1990; Prum 1990; Ryan et al. 1990). Spotted bowerbirds, *Chlamydera maculata*, differ greatly from related species (Kusmierski et al. 1993) because of the unique architecture of their bowers and their highly energetic displays (see Borgia & Mueller 1992; Borgia, in press). Spotted bowerbird bowers have walls that are very thin, spread wide apart, made mostly of fine straw instead of sticks, and with a predominantly east–west orientation rather than north–south as is common in other species. Decorations are spread widely around the bower with small decorations (glass fragments and small stones) placed inside or near the bower, and larger decorations (sheep vertebrae) placed up to 2 m away (Chaffer 1984, pp. 69–71).

In other avenue-building species the female faces the male as he courts her at the bower entrance. In spotted bowerbirds, females face (usually north) into the bower wall and the male courts her through the see-through bower wall with especially loud calls, and rapid and wide-ranging body movements, including vigorous charges at the bower (see Borgia & Mueller 1992; Borgia, in press b; G. Borgia & D. Presgraves, unpublished data). Experimental destruction of a single bower wall results in males and females positioning themselves with the remaining wall between them during courtship (unpublished data). This supports the hypothesis that the unique design of the spotted bower functions to reduce threat to females during vigorous male display.

In a preliminary study, Borgia & Mueller (1992) found a low level of bower destruction and decoration stealing by males. This could be related to the wide separation of bowers characteristic of this species (McGill 1960). Bower quality (but not decorations) is significantly correlated with male mating success. The low level of interactions between bower owners suggests that bower quality and decorations may be less reliable indicators of male quality as sires in spotted bowerbirds than in satin bowerbirds. This led us (Borgia & Mueller 1992) to propose that the energetic displays of spotted bowerbirds have an enhanced role relative to decorations and bower quality in mate selection.

Here I describe the results of a much more detailed study made possible by the use of an automated camera system that continuously monitored behaviour of males and visitors at bowers. I test the hypothesis that females use bower components to assess male quality and the related prediction that numbers of decorations and bower quality correlate with male mating success. Multiple roles for decorations could come from different functions they play in attracting mates. I test the hypothesis that decorations spread widely around the bower (vertebrae) are used in long-distance signalling to attract females to bowers, whereas the close-in decorations (glass) function to enhance male courtship success. Studies of satin bowerbirds show a significant effect of decoration stealing and bower destruction on the number of decorations and bower quality. If similar mechanisms are operating in spotted bowerbirds then male mating success (and the proportion of successful courtships) should correlate positively with bower quality and the number of decorations, and negatively with the number of times a bower holder is a victim of decoration stealing and bower destruction. Finally, previous studies of the satin bowerbird have shown high between-year correlations for numbers of decorations on a bower, bower quality and male mating success. These results support the hypothesis of a low cost of display (Borgia 1993). I tested the same hypothesis in spotted bowerbirds.

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METHODS

Study Site

The study site was located in south central Queensland, Australia on a grazing property called 'Bullamon Plains' 3 km north 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 forest, with widely spaced trees (>10 m) and grassland (see Borgia & Mueller 1992, for a detailed description including a map with bower locations).

Field Techniques

Bowers were located between 1987 and 1989 by the owners and workers on the Bullamon Plains property, members of the Queensland Ornithological Society, my field assistants and me. This combined effort gave detailed coverage of the study site, and it is unlikely that many bower sites were missed. Thirteen bowers were available for monitoring in 1989. We found 12 bower sites in a preliminary study (Borgia & Mueller 1992) in 1987 and nine of these were occupied by the same owner in 1989. One site was destroyed by the clearing and planting of a large paddock (bower 9), and another (bower 4) was deserted, but a new bower (14) with a different owner was found in the same general area (150 m away). We located one new bower owner among the continuously occupied sites (bower 2) and two new bowers and their owners at two other sites (13 and 15) before we started monitoring bowers in 1989.

Bower owners were captured and banded with distinctive colour-band combinations, with the same two-band sequence repeated on each leg, and a metal band on the left leg above the plastic bands. In 1987 my field assistants and I observed bowers from blinds and found that all copulations occurred in the bower avenue. We monitored each permanent bower site with a camcorder (RCA CC 320) through the entire mating season from 8 October to 17 December 1989. The time and date of each event was recorded on videotape.

The camcorder was turned on automatically by an infra-red device when birds entered the bower. The camcorder started when the infra-red beam aimed through the bower was broken. The camcorder remained on until the beam was unbroken for 30 s. A specially designed interface circuit

responded to signals from the infra-red sensor to control camcorder functions. The equipment was powered by a 12-V automobile battery charged by one or more Solarex S10 solar panels. If lighting conditions prevented the full recharging of batteries, they were replaced before voltages dropped below a level that would impair camcorder function. Field assistants made direct behavioural observations from blinds situated 15–20 m from the bowers. These observations provided an independent assessment of the proper functioning of equipment. The birds did not seem to be affected by either the camera set-up or observers in blinds. In one instance a courtship and copulation occurred while an assistant and I were present to service a camcorder.

Behaviour patterns scored from videotapes included copulations, courtships, displays, bower destructions and courtship interruptions. Initially the courting male (almost always the bower owner) positions himself on the court adjacent to the bower and begins a very active dance with coordinated vocalizations. After perching nearby for a short period, females move directly into the bower, spending no more than a few seconds on the ground outside the bower. During courtship the male directs very rapid body and wing movements at the female in the bower. He commonly starts the courtships 3–4 m from the bower and charges at the bower with undulating body motions, head lowered and tail raised even with the body. The male often stops at the bower and energetically flips his wings and jumps, then hops a short distance, picks up decorations using his beak and throws them. Long runs at the bower and high activity levels of male courtship are both unique to spotted bowerbirds (Borgia & Mueller 1992). All copulations were preceded by courtship, but only a small proportion of courtships were successful. Thus, I refer to courtship sequences that culminated in copulations as copulations or 'successful courtships', and those that did not as 'unsuccessful courtships'. Display refers to typical courtship behaviour performed in the absence of a bird inside the bower. Displays appeared to be practice courtship dances rather than failed courtship attempts.

Most female spotted bowerbirds were not banded, so we could not determine whether females made multiple visits to mate at the same or different bowers. Observations of marked female satin bowerbirds, however, indicated that

while multiple copulations at different bowers by individual females are rare, it is not unusual for different females to visit a single male's bower on the same day to copulate (Borgia 1986). Based on these observations I developed rules for counting mating events, whereby a separate copulation was scored each time a female left the bower after copulation. If the male and female copulated twice in the same visit, this was scored as a single copulation.

Not all visitors courted at bowers are females. Borgia & Mueller (1992) observed marked males courting other marked males. The slight plumage dimorphism in spotted bowerbirds makes it difficult to use plumage to determine an individual's sex from videotapes. The infrequent expression of typical male behaviour patterns by visitors at bowers suggests that the proportion of male–male courtships during the breeding season was probably small.

Bower walls are composed of straw and sticks placed in a stick base. Sticks are generally restricted to the lower parts of the bower walls, but the relative proportion of the wall made of sticks and straw varies among bowers. Characteristics of bowers, including quality of bower construction, symmetry of bower structure, verticality of the walls and straw diameter, were scored subjectively by field assistants on a scale of 1–7. Those scoring the bowers had no previous knowledge of the reproductive history of individual birds. Individuals scoring bowers were instructed to give the quality rating of 1 to bowers with fine sculpturing and neat overall appearance and larger values for lower quality. Scores were also given for symmetry of bower walls, the verticality of walls, and the amount of thin straw used. Bowers that were most symmetrical, vertical and had the greatest proportion of thin straw were given rankings of 1 for these variables. (Because of this scoring method, negative values indicate a positive correlation.) The results show a significant correlation of bower quality scores between 1987 and 1989 in bowers built by the same bird. Different individuals scored bowers in each of these years suggesting that individual differences in scoring do not account for a large part of the variation in bower quality. These measures and scoring procedures were chosen to allow direct comparisons with information on bower shape from earlier studies (Borgia 1985a, 1986; Borgia & Mueller 1992).

Table I. Bower decorations used by spotted bowerbirds

Decoration	Description
Glass	Green, brown, light blue, dark blue, clear, purple, pink, red, white, orange, yellow, windscreen
Bones	Vertebrae (primarily sun-bleached sheep vertebrae)
Fruit	Quince, lemon, wilga, fig, other
Plant material	Silver seeds, red stems, green leaves, other
Plastic	Red, orange, black, other
Metal	Pull tops, wire/nails, aluminium foil, rifle cartridges
Stones	

Field assistants measured bowers and counted decorations on bowers on the same day. There were 32 categories of decorations including both natural objects such as bones (primarily sun-bleached sheep vertebrae), fruits or other plant material, and man-made objects such as glass, metal, or plastic objects (Table I). Items of the same type but of different colour (e.g. glass) were classed separately. To reduce the number of statistical comparisons, I classified decorations into seven general categories (bone, glass, metal, plastic, plant, stone and fruit) and used these categories in contrasts with other variables.

As noted above, Chaffer (1984) suggested that bones are placed at greater distances from bowers than glass. To test this hypothesis I used information on decoration placement from 1987. I mapped the positions of glass and bones using a grid placed around the bower (20-cm grid squares were defined using wooden rulers). These covered 4 m^2 with the bower at the grid centre. I recorded the position on the grid and type of decoration in each square. Glass decorations ($\bar{X} \pm \text{SD} = 0.632 \pm 0.079$ m) were closer to the bower centre than bone decorations ($\bar{X} \pm \text{SD} = 1.29 \pm 0.159$ m) at 11 of 12 bowers (paired $t = 5.03$, $df = 11$, $P < 0.001$).

Statistical Analysis

I used the SYSTAT statistical package (Wilkinson 1986) for data analysis. Means are expressed as $\bar{X} \pm \text{SD}$. I used Spearman rank correlations (r_s) for most bivariate comparisons. I estimate the variation explained by independent variables with linear, step-wise and multiple

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regressions, the latter two allowing comparisons of multiple independent variables. No transformations were necessary to meet the assumptions of normality and equality of variance for regression models. Tests of a priori hypotheses were one-tailed. An N of 13 is the basis for all comparisons of bower holders unless otewise noted. Because a priori hypotheses are tested in the contrasts below, there is no requirement to 'correct' alpha values for multiple tests of comparisons (Rice 1989).

RESULTS

Copulations

During the period in which we monitored bowers we observed 53 copulations. Nine of the 13 bower owners we observed copulated at least once. The copulations were not equally distributed among males (CV=1·016); three bower holders obtained 10 or more copulations (bower owners 5, 7 and 11) accounting for 59·6% of all copulations. Courtships leading to copulations lasted 6·62 ± 3·22 min. Copulations lasted 2·56 ± 0·27 s on average. A comparison of 1987 and 1989 mating success (number of copulations by a male) showed a positive but non-significant association between years (r_S=0·466, N=9, P>0·20).

Copulations were observed from 17 October to 9 December with a mean date of 41·91 ± 12·27 from the day observations began. A peak occurred in the last 10 days of November during which camcorders recorded 24 (45%) copulations. There was an earlier peak of 16 copulations in the first 10 days of November. Copulations were less frequent (six or less) in the subsequent 10-day intervals. There were no copulations in the last 10 days. Of the 23 copulations that occurred during the 6-day span from 20 November to 25 November, 14 occurred at two males' bowers (5, 7) and these accounted for two-thirds of all copulations at these bowers. The owner of bower 11, which was the only other male with 10 or more copulations, had copulations distributed more evenly throughout the mating season, with only three during the above-mentioned 6-day interval.

Male Mating Success and Bower Characters

There was a significant positive correlation between male mating success (number of copu-

lations) and the quality of bower construction (r_S= − 0·563, P<0·025; Fig. 1a). Comparisons between these years also showed a significant correlation in bower quality (r_S=0·686, N=9, P<0·04).

Male mating success showed a significant positive correlation with the total number of decorations at bowers (r_S=0·544, P=0·025; Fig. 1b). Decoration numbers in 1987 and 1989 were not significantly correlated (r_S=0·056, N=9, P>0·40). The general decoration categories were used in a step-wise regression model (alpha to enter=0·15) to determine their relative contribution to male mating success. Only the total numbers of bone and glass decorations entered the model and these were highly significant (total glass: t=3·22, P=0·009; total bones: t=3·93, P=0·003). A multiple regression model using these two independent variables explained a large proportion of the total variation (r^2=0·722) and was highly significant (F_{12}=13·0, P=0·002). These two classes of decorations were the most common at bowers (total glass, $\bar{X}$ ± SD=178·1 ± 272·5 and number of bones, 83·8 ± 72·8). The third most common class was total plant material (35·2 ± 37·6).

Quality of bower construction and total number of decorations were regressed on male mating success in a step-wise regression. Quality of construction entered the model first and did not allow total decorations to enter (r^2=0·413, P=0·018). The high correlation between total decorations and quality of construction (r_S=0·586, P=0·01) explains why only one of these variables entered the model. A multivariate regression model limited to the variables bower quality (F_{12}=4·86, P=0·052) and number of bones (F_{12}=5·84, P=0·048) showed that bower quality and decoration variables can significantly and independently explain variation in male mating success (r^2=0·61, F_{12}=7·85, P=0·009). In a step-wise regression procedure using the variables total bones, total glass and bower quality, only the first two entered the model, suggesting that male mating success can be best explained by two decoration variables.

Courtships

Only 4·13% (53 of 1284) of all courtships were successful (resulted in copulation). Unsuccessful courtships lasted 4·26 ± 10·86 min. There was a significant correlation between the number of
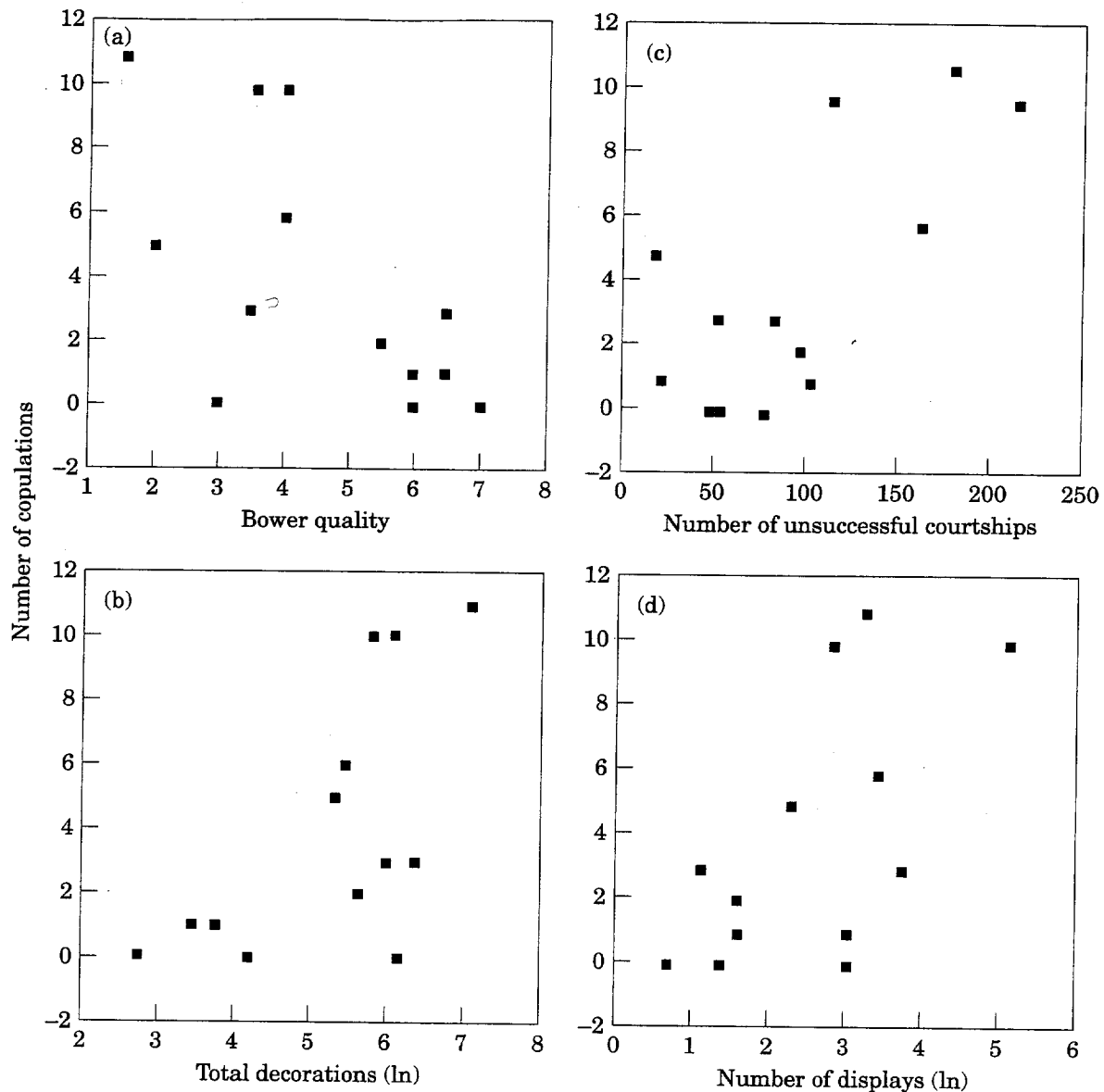
Figure 1. The number of copulations (successful courtships) that male spotted bower owners obtained versus (a) the quality of bower construction (lower values indicate bower of higher quality), (b) the total number of decorations (ln) on bowers, (c) the number of unsuccessful courtships and (d) the number of displays (ln).

copulations a male obtained and the number of unsuccessful courtships ($r_S=0.657$, $P=0.01$; Fig. 1c).

Displays

There were 359 displays by males at bowers with no visitor present (27.62 ± 44.87). These displays lasted 3.64 ± 3.18 min. If the number of displays indicate male investment in practice or an overall level of sexual interest, then a positive correlation between male mating success and the number of displays by males would be predicted ($r_S=0.570$, $P=0.02$; Fig. 1d). The number of displays was not correlated with the number of decorations ($r_S=0.028$, $P>0.40$) nor with bower quality ($r_S=-0.217$, $P<0.35$).

Partitioning Male Mating Success

Male mating success can be partitioned into two components: the male's ability to attract females to his bower and his success in copulating with visiting females. Both of these components

contribute significantly to explaining male mating success. The number of visitors to a male's bower was correlated with male mating success ($r_S=0.667$, $P<0.01$) and the proportion of successful courtships (copulations/(copulations + unsuccessful courtships)) by a male ($r_S=0.795$, $P<0.001$). In a multiple regression model these variables explained 59% of the variation in male mating success ($F_{12}=7.542$, $P=0.011$).

A male's ability to attract females to his bower may depend on characteristics of the bower and its associated decorations. Bones are scattered in large numbers up to several metres from bowers and are more exposed than the bower itself. This wide distribution makes them the most likely bower-related character to attract females. The number of bones was the only such character to correlate significantly with the number of visitors courted at males' bowers ($r_S=0.515$, $P=0.03$). Glass was the most common decoration type inside and in the immediate vicinity of bowers. The percentage of successful courtships was correlated with total glass ($r_S=0.599$, $P>0.02$) and quality of construction ($r_S=-0.572$, $P=0.02$).

Bower Destruction

There were 29 bower destructions (2.15 ± 1.86) occurring at a rate of 0.032 destructions/ bower/day. Destructions lasted an average of 2.89 ± 3.66 min. An average of $45 \pm 31\%$ of the bower was destroyed during each event. If the effects of bower destructions are assessed by females through their effects on bower quality, then there should be a positive correlation between bower quality and male mating success and a negative correlation between the number of bower destructions at a bower and the owner's mating success. There was no significant correlation of bower destruction with male mating success ($r_S=-0.261$, $P>0.30$) or bower quality ($r_S=0.225$, $P>0.20$). One male's bower suffered 20.7% (6 of 29) of the destructions, and he was the only male to desert his bower before the end of the mating season.

Timing of Behaviour

The timing of behaviour at the bower can be used to test hypotheses about their functions. The mean date of destructions was 31.24 ± 21.58 days from the day monitoring began, compared with 33.46 ± 18.84 days for courtships and 37.90 ± 19.67 days for displays. The average date of copulations occurred significantly later than that of bower destructions ($t=2.96$, $df=67$, $P<0.01$) and unsuccessful courtships ($t=3.15$, $df=68$, $P<0.01$). None of the other behaviour patterns showed significant differences in timing.

Decoration Stealing

Each bower gained an average of 1.96 ± 0.57 ($N=11$) marked decorations from other bowers from September 1989 to September 1990. The number of decorations moved was not significantly correlated with the total number of decorations ($r_S=-0.414$, $P=0.10$).

Courtship Interruption

There was a total of eight courtship interruptions in which an intruding male attempted to copulate with a female in the bower as she was being courted by the bower owner. If interruptions are affected by the status of the bower owner such that subordinate males are reluctant to interfere with successful and dominant males, then a negative relationship between interruption and male mating success is expected. Alternatively, if status of the bower owner is unimportant, then interruptions should be correlated with the frequency of female visitation. Interruptions occurred during 0.62% of total courtships, and three were successful for the intruding male. Interruptions were not distributed evenly; males with high mating success had higher rates of interruption ($r_S=0.5474$, $P=0.025$).

DISCUSSION

Several different aspects of male spotted bowerbird courtship behaviour contributed to their overall mating success. Successful males attracted more females to their bowers to observe courtships and mated with a larger proportion of these females. In addition, bower quality and the number of decorations were both significantly correlated with male mating success. This pattern is consistent with what we observed in 1987. As in 1987, bower destructions and decoration stealing were rare compared to other species.

Different decoration types appear to play specific roles in helping males obtain matings. A multiple regression shows that the number of bones and glass decorating a male's bower accounted for a very large proportion of the total variation in male mating success. Taken individually, bone and glass decorations showed higher correlations with the number of courted visitors and the proportion of successful courtships, respectively, than any other bower decoration. This result is consistent with the placement of these two decoration types. Bones function primarily to attract females to the bower, and glass enhances their willingness to mate once they arrive. Bones are arrayed further from the bower than glass, which is placed in the immediate vicinity of bowers, even in the bower avenue near where females stand while being courted. The wide distribution of bones is not paralleled by any other decoration type among closely related bowerbirds.

Because of their large numbers, bleached white colour and large size, bones may make bower sites visible from a distance and attract females unfamiliar with the location of the bower. The placement of the bower under trees (probably to shade courting birds from the intense sun) reduces its visibility to passing females and may necessitate an additional signal to help females locate bowers. Spotted bowerbirds are unique in having the combination of overhead cover and otherwise very open habitat around the bower that may permit this display tactic to be effective only for this species. Large inter-bower distances, which reduce the likelihood of decoration stealing, and the large size of bones, which are visible from afar and are difficult to steal, probably contribute to the effectiveness of this display tactic.

Long-distance displays may be valuable to females as cues for preliminary assessment of males prior to visiting a male's bower for courtship, which may create special risks for spotted bowerbird females because of males' attacks on visitors. There is, however, mixed evidence for preliminary assessment. Support comes from the high correlation between the number of courtships and male mating success in spotted bowerbirds, but preliminary assessment would predict a higher level of courtship success in this species than in other species, which has not been observed (Borgia, in press b).

The unusually wide area covered by displaying males (Borgia, in press b) could favour a corresponding spread of decorations used in display. This hypothesis was not supported because bones were often spread in a direction opposite that of the displaying males and males failed to use these decorations (e.g. pick and toss them) during displays even though they used other decorations that were closer to the bower. Thus, it is most likely that bones function as passive signals of bower location.

The sequential use of bones and glass in display suggests a new model for the evolution of complex display traits. This 'time sequence' hypothesis suggests that successful courtship may require a suite of traits with temporally distinct functions. This differs from Møller & Pomiankowski's (1993) multiple message hypothesis in that the multiple signals do not signal different kinds of male quality, but sequentially important tactical functions. In this case, bones may function as passive attractors (Andersson 1982; Parker 1983) and glass as a trait important in active female choice.

According to the indicator hypothesis (Borgia et al. 1985) the low rates of stealing and bower destruction in spotted bowerbirds make decorations and bowers less reliable indicators of male dominance in this species than they are for satin bowerbirds. Even without stealing, however, decorations could have value as indicators of male status. The decorations used by spotted bowerbirds (bones and glass) are long lived, re-used in successive years (many we marked in 1987 were still present in 1990) and accumulate over time. Ownership of bowers with accumulated decorations could indicate male vigour if males engage in contests for control of these sites. This predicts that new owners should quickly occupy deserted, well-decorated bower sites. In the two cases where males disappeared from undisturbed sites between 1987 and the end of 1989, only one of the two sites, the more decorated one, was rapidly reoccupied. In the second case, a new bower site was established in the same general area. More information on replacement of bower owners is needed to test this hypothesis.

The general female preference now found in several bowerbird species for well-decorated and well-built bowers (Borgia, in press b) could result from a variety of different mechanisms. Møller & Pomiankowski (1993) claimed that complex traits in polygynous species are 'Fisher traits' based on

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the absence of evidence for fluctuating symmetry in the plumages of males from polygynous clades. This conclusion is questionable because of the lack of statistical power of their test (it relies on accepting the null hypothesis with a sample size of 6), and because of their failure to consider other measures of male condition, exclusive consideration of plumage traits, and predictions from other good genes and other non-Fisherian models.

Lande's (1981) version of the runaway sexual selection model predicts a balance between the force of sexual selection and the cost of male display, and his prediction can be used to test this model. The force of sexual selection can be measured as a selection gradient associated with male display traits, which should be balanced against the costs reflected in the loss of male ability to reproduce due to the expression of these traits. Results of my study of satin bowerbirds (Borgia 1993) do not show the predicted balance. For spotted bowerbirds, several results showed patterns similar to those observed in satin bowerbirds: a steep selection gradient as indicated by the large proportion of variation in male mating success explained by display characters, and a low mortality rate (2 of 11 males disappeared over three field seasons). The high constancy in the quality of bower decoration among bower-owning males, and the positive but non-significant correlation between coefficients for the number of decorations and male mating success between years argue against a high cost of male display as predicted by the Lande model for spotted bowerbirds. A high cost of displaly is also predicted for the epistatic version of Zahavi's (1975) handicap model (see Maynard Smith 1991), and the above results also fail to support that prediction.

The display traits that are the most likely candidates for expressions of a pre-existing preference are glass and other novel types of man-made decorations. The importance of glass is problematical because of the short time interval during which it has been available (since European settlement). A pre-existing female preference for bright display objects might explain the use of glass. It is possible, for example, that a preference for shiny, natural objects could have created the preference for glass, but I have found no evidence that spotted bowerbirds regularly use natural, glass-like decorations on their bowers.

Most models for the evolution of new sexually selected traits are co-evolutionary and are thus limited by the need for the coincident appearance and simultaneous evolution of the male trait and the female preference, and, in the case of runaway models, conditions to create a genetic correlation between the male trait and the female preference. In bowerbirds, however, significant male display traits (decorations) are collected and are thus not part of male morphology. The same preferences that cause males to collect particular decorations may cause females to be attracted to the bower. This presents a much simpler model for trait evolution in which female preference for a given trait can favour copies of itself, as expressed by males.

Learning could also be important in the rapid acquisition of male display traits. There is good evidence both from observations of same-sex courtship displays at bowers (Borgia 1986) and from studies of satin bowerbird courtship vocalizations (Loffredo & Borgia 1986) that males learn display elements. West & King (1988) also found that male cowbirds, *Molotherus ater*, can improve their ability to court females by observing female reactions to their displays. Male bowerbirds probably learn through success in courtships and from other males what decorations are effective in stimulating females. If this is so, then male displays involving decorations could change rapidly to accommodate new female preferences and novel decorations that are attractive to females.

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