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Threat Reduction as a Cause of Differences in Bower Architecture, Bower Decoration and Male Display in Two Closely Related Bowerbirds *Chlamydera nuchalis* and *C. maculata*

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Summary: Major structural differences in the bowers of different bowerbird species have long been recognised, but the evolutionary significance of these differences has never been determined. I compared the bowers and displays of two congeneric species, the Spotted Bowerbird *Chlamydera maculata* and the Great Bowerbird *C. nuchalis*, and used the Satin Bowerbird *Ptilonorhynchus violaceus* as an outgroup to define ancestral characters. Spotted Bowerbird bowers and display courts differ from the more typical bower of avenue-building species in having a wide bower avenue, see-through walls, dispersed decorations, an E-W (rather than N-S) orientation, walls that are nearly vertical, and straw instead of sticks in the bower walls. These differences are coordinated with changes in male courtship patterns and female orientation in the bower. In addition, male displays are extremely vigorous, with aggressive elements not observed in other species. I evaluate three hypotheses that could account for the unique aspects of Spotted Bowerbird bower structure and display. Of these, the threat reduction hypothesis best explains changes in both patterns of male display and in the bower. It proposes that increased separation between bowers has caused selection for vigorous male display as part of mate assessment. An effect of this change is that female visitors to bowers are threatened by the increased vigour in male display. Male Spotted Bowerbirds utilise structural changes in their bowers to allow females to view male display with reduced threat. A threat reduction hypothesis is consistent with a general hypothesis that bowers function to enhance female willingness to attend male display courts and observe male courtship.

Darwin (1859, 1871) pointed out that many of the most bizarre morphological and behavioural traits in animals are associated with courtship and sexual display. The bowers built on display courts of male bowerbirds (Ptilonorhynchidae) are among the more remarkable of these curiosities, and their evolutionary origin has been the subject of speculation for over a century (see reviews by Marshall 1954; Gilliard 1963). After observers recognised that bowers were built by male birds and were not used for nesting, the view emerged that bowers functioned symbolically as nests to stimulate female reproduction (Sodderberg 1929; Davies in Cooper & Forshaw 1977; Diamond 1982a,b). There is little resemblance between a nest and bower apart from the use of sticks to build them. Moreover, females build nests in trees and males build bowers on the ground. The existence of bowerbird species in which males clear courts but do not build bowers shows that males in this family are capable of stimulating female reproduction without a bower (Borgia et al. 1985, but see Diamond 1986).

Gilliard (1956, 1963, 1969) proposed that bowers are an element of male courtship display. Among bowerbirds of the genus *Amblyornis*, he observed an inverse relationship between the brightness of male plumage and the degree of bower complexity. This led him to conclude that the display functions of plumage had been transferred to the bower. Within that genus and among those species with avenue-type bowers, Gilliard's hypothesis is supported; bowerbird species outside these groups show a conflicting pattern (Kusmierski et al. 1993; Borgia unpubl. data.).

Recent discussions about the origins of bowers and their current function have taken into account developments in sexual selection theory. Currently, there are several popular explanations for how mate choice affects the evolution of elaborate displays.

'Good genes' models propose that female choice can be adaptive in that it leads to improved quality (vigour) of female offspring (e.g. Trivers 1972; Alexander 1975; Zahavi 1977; Borgia 1979; Hamilton & Zuk 1982). Females may gain from mating with dominant males because this dominance signals a high level of vigour that may be inherited by offspring (Borgia et al. 1985). Evidence from Satin Bowerbirds shows that females choose mates on the basis of bower quality and number of decorations (Borgia 1985a). The quality of

bowers was inversely related to the frequency with which they were destroyed by other males (Borgia 1985b). Male ability to obtain blue feathers, the most important decoration affecting female choice, depends on male ability to steal and resist stealing by other males (Borgia & Gore 1986). Recent studies of Spotted Bowerbirds (Borgia & Mueller 1992; Borgia in press a) indicate low rates of male interaction, suggesting that they may have evolved alternative compensating mechanisms to demonstrate male quality.

Fisher (1930) suggested that female choice can be self-reinforcing and cause both the spread of the choice trait and the male character(s) favoured by the female preference. In this so-called runaway process, males with a character favoured by females have a mating advantage and female choice spreads as a correlated character. Recently modellers have emphasised that traits with negative effects on the viability of female offspring may evolve by this process (e.g. Lande 1981; Kirkpatrick 1986, 1987). For example, if some male bowerbirds had a propensity to manipulate sticks which then resulted in simple structures, it is possible that a female preference for this behaviour could have resulted in runaway selection leading to a widespread tendency to build large complicated stick structures (Borgia 1986; Diamond 1986, 1987). Advocates of the runaway hypothesis have often suggested that display characters that evolve by this process may be entirely arbitrary. That is, apart from their role in mate attraction, male display traits may have no other functional role.

The occurrence of pre-existing but latent female preferences has been advanced as an explanation for the development of elaborate male displays in some species (Burley 1985; Ryan et al. 1990; Basolo 1990). These preferences can cause the spread of novel male traits soon after they appear. Latent preferences would seem most useful for explaining entirely novel male traits, but not for changes in the same display trait, as is commonly seen among related bowerbird species (Kusmierski et al. 1993).

Finally, it has been suggested that females may prefer mating with males who provide particular bower types because these bowers may confer benefits such as protection of the female during courtship (Borgia et al. 1985). There are several kinds of threats to females that might be mitigated by the presence of the bower on display courts: protection from predators, protection from marauding males seeking forced copulations, and protection from forced copulations by the courting male (Borgia in press b).

Here, I present new information about the bowers and displays of three avenue-building species. I describe differences among these species in bower form and male courtship display, and test the hypothesis that these interspecific differences are functional. Marshall (1954) recognised three major categories of male display structures in bowerbirds: avenue bower builders, maypole bower builders and court clearers that build no bower. The avenue builders form the largest group. Eight species in three genera (*Sericulus*, *Chlamydera*, and *Ptilonorhynchus*) build bowers which consist of two parallel walls of sticks and an adjacent display court decorated with a wide variety of objects. In this group there are important species differences in the size of bowers, the type and colour of decorations (Marshall 1954; Gilliard 1969; Cooper & Forshaw 1977) and where decorations are placed (Gilliard 1969). Previous descriptions of display in nearly all species are anecdotal (e.g. Chaffer 1945, 1984) and there have been few attempts to make quantitative comparisons between species and to relate these to differences in bower characteristics.

The Spotted Bowerbird *Chlamydera maculata* and the Great Bowerbird *C. nuchalis* appear to have diverged recently (Sibley & Ahlquist 1985; Kusmierski et al. 1993). Comparisons with the only other species outside the genus for which there is detailed information, the Satin Bowerbird *Ptilonorhynchus violaceus*, show that the Spotted Bowerbird bower and how it is used in display have changed radically from the more typical and widespread patterns seen in other species. Among the most likely reasons for the divergence of Spotted Bowerbirds is that males need to build and display at a bower that provides protection to the female being courted. Three alternative protection hypotheses are evaluated: protection from predators, protection from aggression by the courting male, and protection from marauding conspecific males attempting to force copulate with the female.

Study sites

Field studies were made at three different study sites. Satin Bowerbirds were observed at Wallaby Creek (28°00′S, 151°30′E), New South Wales, Australia. The study site is located 140 km SW of Brisbane in the Beaury State Forest and has been described elsewhere (Borgia 1985b). Satin Bowerbirds were studied for seven years starting in 1980 from September to mid-December; data presented here is primarily from 1984.

During this period 28-33 bowers were monitored on a regular basis through the mating season and counts of bower decorations were made on a daily basis. Great Bowerbirds were studied along the McLeod River on Curraghmore Holding (16°30′S, 145°00′E), 15 km NE of Mt. Carbine, Queensland, in November and December 1987, 1988 and 1989. Great Bowerbirds were observed at 11 bowers in 1987 and 1988 and 19 in 1989. Spotted Bowerbirds were studied at Bullamon Plains (28°30′S, 148°52′E), a grazing property and wildlife sanctuary, 3 km N of the town of Thallon in south-east Queensland; in 1987 and 1989 we studied 13 bowers. A map of this site with locations of bowers and a detailed description of the habitat is available elsewhere (Borgia & Mueller 1992). For the latter two species, the results reported here are from 1987 for descriptions of bowers and courtship behaviours, and 1989 for general patterns of behaviour including bower destructions, predation rates, and courtship interruptions.

Methods

Bowers were observed from hides positioned 15 m away from each bower. Bower owners were captured at bower sites before observations began. Each bird received unique combinations of colour bands with matched sequences on each leg. Observations were made at different bowers from sunrise until 1300. Detailed notes were taken on individual behaviour around bowers.

Behaviour at bowers was videotaped or, in the case of Satin Bowerbirds, recorded on super-8 film, using cameras controlled by an infrared sensor that began recording when birds entered the bower at any time through the mating season (see Borgia 1985a; Borgia in press a & b). Bowers of each species were monitored with cameras and were also kept under direct observation from hides. Total hours of observation were approximately: Spotted Bowerbird (2200 h of observation, 12 000 h of monitoring with video equipment), Great Bowerbird (2400 h of observation, 13 000 h of monitoring with video equipment) and Satin Bowerbird (12 250 h of observation and 120 000 h of monitoring with film cameras — both over seven years).

The orientation of the bower avenue was measured using a compass laid along its main axis. Mean compass orientation was calculated using the deviation from N. The position of bower entrances and walls were defined relative to compass direction. Measures of particular interest were platform length, bower avenue length, total outside width entrance width, and maximum inside width. The last three variables were measured at the middle of the bower wall at 100 mm height. Separate measures taken for each bower wall included length, thickness and height. Decorations were marked with a dab of paint, the colour being unique to each bower (Borgia & Mueller 1992).

Bower walls were composed of sticks (Satin and Great Bowerbirds) or straw placed in a stick base (Spotted Bowerbirds). On Spotted Bowerbird bowers sticks were generally restricted to the lower parts of the bower walls, although the proportion of sticks and straw differed among bowers. The maximum straw height and the maximum stick height were defined as the height of the tenth highest stick or straw, respectively. For Spotted Bowerbirds the straw portion of the bower walls was sufficiently thin to see through and was denser near the base where it was anchored in sticks.

Video tapes were scored using a Panasonic AG-1730 VCR equipped with a slow motion jog/shuttle control. The entire length of courtships and the time for individual display components were timed with a stop watch. Rates of display were taken as the amount of time a male exhibited a particular behaviour divided by the length of the total courtship. If males moved off screen, the total time of courtship was reduced by the time the male was off screen.

Definitions of behaviours were as follows: the term 'display' referred to male courtship behaviours that occurred at a bower in the absence of another bird. A 'courtship' was courtship behaviour occurring with another bird present. 'Successful courtships' were those courtships that ended with a copulation. 'Male mating success' was scored as the number of copulations (successful courtships) a male achieved in one season.

During displays and courtships males perform a variety of behaviour. Some of these were similar between all species while others differed. A description of these behaviours follows. *Bower circling:* the male moved completely around the bower in one continuous run. *Wing flicks:* very rapid wing raising and closing that occurred when the male was either stationary or moving. *Hop-flicks:* the male simultaneously hops vertically and flicks his wings. *Step-flicks:* the male stepped to the side while flicking his wings. *Wing lifts:* slow raising and lowering of the wings. *Hop-backward:* males standing upright hopped backwards. *Tail and wing drags:* males ran near the bower with their tail or wings held in an exaggerated, lower-than-usual position. *Puffs:* males puffed out their body feathers. *Body*

slams: a male charged into the bower and forcefully hit it with his chest or side. *Bower tugs:* a male grasped the bower with his beak and gently tugged it, causing it to vibrate during courtship or display. The distance of courtships and displays from bowers was estimated from videotapes at four randomly chosen times in the male's courtship or display at the bower.

Statistical analysis was performed with the Systat statistical package (Wilkinson 1986). Interspecific comparisons of behaviour attempted to include observations from all males and to represent individual males equally in samples. Spearman rank correlations (r_s) and *t*-tests were used for statistical comparisons. Means are shown as $\bar{X} \pm s.d.$ One-tailed *P* values are used for tests in which an expected relationship could be defined *a priori*.

Table 1 Comparisons of bower characteristics in three avenue-building bowerbird species

Bower character	Species Satin *n* = 36	Spotted *n* = 12	Great *n* = 10
Avenue length	260.4 ± 66.5	585.1 ± 111.7	587.0 ± 105.5
Avenue width	140.4 ± 27.6	196.0 ± 18.4	153.9 ± 21.9
North (east)* entry width	—	225.3 ± 23.7	128.8 ± 7.9
South (west)* entry width	125.4 ± 24.9	216.3 ± 12.4	140.6 ± 18.1
Outside width	304.8 ± 51.4	476.7 ± 61.0	540.0 ± 79.8
Height	228.1 ± 36.9	338.1 ± 76.1	311.3 ± 35.3
East (north)* wall thickness	97.6 ± 24.8	141.2 ± 26.4	263.5 ± 150.7
West (south)* wall thickness	99.7 ± 58.3	140.4 ± 38.6	213.0 ± 42.7
Exposed platform length	450.7 ± 143.7	1174.9 ± 451.8	565.7 ± 137.3
Covered (rear) platform length	—	1150.1 ± 445.0	466.2 ± 115.0
Orientation (deg.)	2.7 ± 31.0	89.4 ± 41.2	358.9 ± 34.0
Number of decorations	51.0 ± 15.2	713.3 ± 733.2	987.4 ± 796.0
Primary materials used in walls	sticks	straw	sticks
% of bowers that could be seen through bower wall	0	100	0

The values given represent distance (mm) except where otherwise noted. *n* is the number of bowers. * Indicates direction for Spotted bowers.

Results

Comparisons of bower structure

The bowers of mature Satin and Great Bowerbirds (males that maintain a bower site during a whole season) were composed entirely of densely packed sticks. Sticks in the bower avenue had an outward bow at approximately 100 mm and then curved back toward the midline of the bower higher up. Young Satin Bowerbirds tended to have less sculpturing of their bowers and the bending in at the top of the bower was more pronounced in the bowers of older males (Borgia 1985a; Borgia unpubl. data). Even the best formed Great Bowerbird bowers were relatively rough outside, but inside the sticks were neatly arrayed. Typically these bowers had a neatly trimmed indentation at the north-east corner near where males commonly displayed. Spotted Bowerbird bowers were constructed of straw inserted into a base of sticks (see Marshall 1954). The straw of Spotted Bowerbird bowers was less densely packed than the sticks of other species, becoming thinner in higher portions of the wall. Walls of Spotted Bowerbirds were unbowed and could be seen-through at a relatively low height (about 100 mm) but this was not so for other species (Table 1). Great and Satin

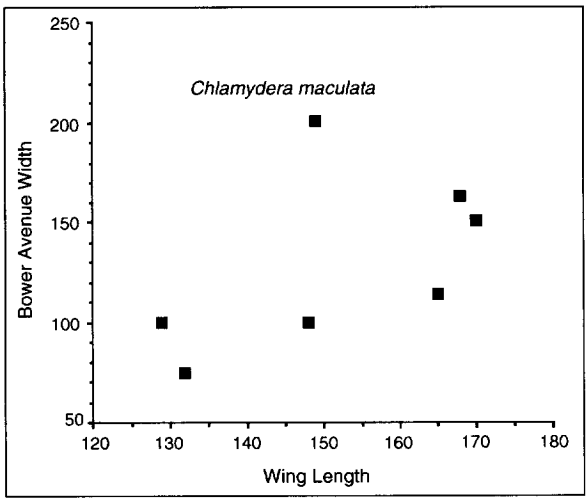

Figure 1 Plot of bower avenue width at 100 mm *vs* wing length of females for seven avenue building bowerbird species. The Spotted Bowerbird *Chlamydera maculata* has an especially wide bower relative to the size of the bird as estimated by wing length (mm). This permits females to stand perpendicular to the walls inside the bower to observe display.

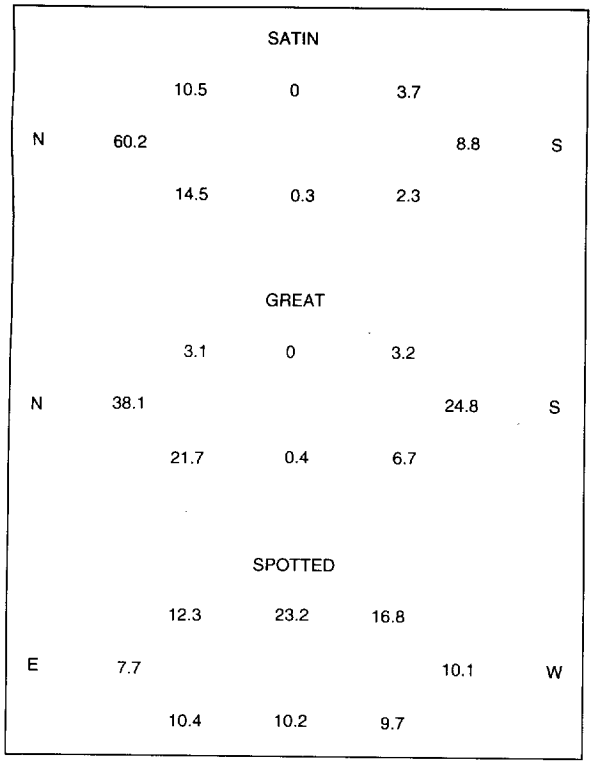

Figure 2 The position of male courtship around the bower and the percentage of time males spend displaying from those positions. In this figure bower walls run N-S for Satin and Great Bowerbirds and E-W for Spotted Bowerbirds.

Bowerbird bowers had a N-S orientation to bowers, while Spotted Bowerbird bowers had a predominantly E-W orientation (Table 1).

In avenue-building species the width of the bower avenue was typically slightly wider than the width of an individual of that species. Spotted Bowerbirds were exceptional in that they had a bower avenue nearly twice as wide as expected for their body size (Table 1, Fig. 1).

Bowers also differed among species in how they were situated with respect to cover. Great Bowerbird bowers were typically built (10 of 11 cases) with one court and the bower entrance on that side partially enclosed within a bush. Satin Bowerbird bowers generally were uncovered above the display court but were surrounded by vegetation and characteristically had a log situated behind the south bower entrance. Twenty-two of 31 bowers had logs behind at a median distance of 410 mm. In the remaining cases there was either dense vegetation or an earthen bank behind the bower. By contrast, Spotted Bowerbird bowers commonly did not have dense vegetation near either bower entrance although they were typically situated under a tree; only one of 15 bowers was near dense vegetation typical of Great Bowerbirds.

Dispersion of decorations

For all species the length of the bower platform was defined by the outer limit of where decorations were regularly placed. Decorations on Spotted Bowerbird bowers were more dispersed with a platform nearly twice as long as for the other two species (Table 1). The mean distance of decorations along the main axis of the bower from the bower entrance on the exposed court side was 721 mm for Spotted Bowerbirds, which was much greater than the 309 mm and 285 for Great and Satin Bowerbirds respectively (Table 1). For Spotted and Great Bowerbirds, decorations were present in nearly equal numbers at courts at both ends of the bower (Spotted Bowerbirds 58%; Great Bowerbirds 54%; on exposed side). Satin Bowerbird decorations were heavily concentrated at the north end of the bower (96%).

Displays

The Satin Bowerbird courtship/display was highly eurhythmic in that specific vocalisations were closely associated with particular dramatic body movements. A male began the courtship/display at a spot near the north bower entrance (Fig. 2), his body directed toward the visitor. He vocalised with the rising and falling pitch of the mechanical call that was coordinated with a rapid flick of his wings and he moved with an explosive rapidity and flicks of his wings as he step-flicked across the bower entrance emitting a short popping buzz (Table 3). After mechanical buzzes there was a trill and mimicry portion of the call followed by low twittering notes. During this period the male was stationary in a stretched position and engaged in very rapid and precise 'knee bends' during which he adjusted his height while holding an object in his beak directed toward the female in the bower. The extreme position of the courting male's body, his rapid movements, rapid changes in body form (from sleek to puffed), his strained voice and the darkening and bulging of his eyes all suggested that his displays were demanding. He attempted to copulate by rapidly moving around to the back of the bower, sometimes in response to the female lifting her tail.

Male Great Bowerbirds typically started their display from the north-east corner of the bower near the

bower entrance. Here the male performed a stationary display by leaning forward and turning his head to expose his lavender-pink nuchal crest to the female (Marshall 1954). He might bob his head, pick up and drop decorations, and occasionally grasp the bower with his beak and gently shake it. Bouts of stationary display were interrupted by periodic movements along the outside of the adjacent bower wall towards the far end of the bower. He then returned to where he began his stationary display. During movements along the wall the male held his head high and took a unique posture with legs close together, wings and tail held low and head erect. During circling moves the male commonly faced into the wall, gave characteristic churring calls and occasional wing flicks. Movements along the wall were repeated, becoming longer with successive repetitions until the male had moved the whole length of the wall. These last and longest movements commonly resulted in a copulation attempt.

For most bowers, the east wall has slightly shorter with sticks at the end trimmed to form a slight indentation where the male stood to start his courtship. Decorations were more numerous along the east than west wall and certain types of decorations (e.g. red plant stems) were typically found at the end of the wall and on the platform near where the male stood during the stationary part of his display.

Spotted Bowerbird courtship was unique in that males engaged in a series of runs at the bower wall from 3-4 m away and were generally farther from the bower than displaying males of other species (mean distance during display (cm) Satin = 6.0 ± 1.1, n = 37; Spotted = 43.9 ± 23.4, n = 80; Great = 10.0 ± 2.3, n = 33). In these runs the male was highly animated, moving very quickly with fast, jerky movements and undulations reminiscent of swimming. His head was slightly raised and then lowered as a wave of undulation passed down his body. His folded wings were tilted first down, then up; the tail was held low throughout. The male often suddenly stopped, and picked up and violently threw objects. He occasionally jumped up or backwards, sometimes flicking his wings, and then resumed the swimming movements either in place or as he moved towards the bower (Table 3). The male continued this behaviour toward the bower wall, displayed there briefly, then retreated to start a new run at the wall (Fig. 2).

Males used two specialised postures in moving away from the bower after a run. In the 'rooster' posture they held their heads and tails high, wings away from the body and in a horizontal position, and lifted their legs, in a prancing gait. In the 'penguin' posture the male's body was held erect, with his neck extended and his head held high; his tail was down and wings compressed against the body. He moved with small rapid steps as if his legs were bound together. Loud vocalisations occurred with movements toward the bower but were much less common in movements away.

The male Spotted Bowerbird nuchal crest differed from that of Great Bowerbirds in that it was held more erect during display and was fan shaped rather than circular. He presented his crest to the female as he leant forward during display; he did not show the slow, emphatic head turning to expose the crest as Great Bowerbirds did. (C. Frith, pers. comm., has observed occasional head turning in northern populations of Spotted Bowerbirds).

Comparisons between species (Table 2) showed large differences in the time males spent holding decorations in their beaks during courtship and display. Satin Bowerbirds held objects in their beak nearly 66% of the time, Great Bowerbirds nearly 19% and Spotted Bowerbirds only 2.2%. The difference between the latter two was largely due to the very short period male Spotted Bowerbirds held decorations before dropping or tossing them. An exception was when male Spotted Bowerbirds moved around the bower wall to copulate, when in 29 of 53 cases males held decorations throughout this period. Male Spotted Bowerbirds tossed decorations at a higher rate than the other species (Table 2) and tossed them farther.

In Satin and Great Bowerbirds the narrowness of

Table 2 Comparisons of decoration use and related behaviours in display of three species of avenue-building bowerbirds

	Species		
Decoration character	Satin n = 37	Spotted n = 80	Great n = 33
% time* object in beak	65.9 ± 29.0	2.18 ± 2.80	19.3 ± 17.4
Decorations picked up per min	2.63 ± 2.38	2.10 ± 0.84	2.46 ± 2.28
Decorations tossed per min	0.004 ± 0.03	0.56 ± 0.89	0.38 ± 0.83
% time head turned	0	0	6.9 ± 15.4

* Combined display plus courtship for all variables. Time refers to the duration of the courtship or display. n = number of courtships or displays.

Table 3 Unique display behaviours in three bowerbird species (frequency per s of display or courtship).

	Species		
Behaviour	Satin $n = 37$	Spotted $n = 80$	Great $n = 33$
Hop-flicks	0	0.34 ± 0.75	0
Step-flicks	2.71 ± 2.76	0	0
Hop backwards	0	0.17 ± 0.31	0
Tail-wing Drags	0	0	0.19 ± 0.28
Body slams	0	0.07 ± 0.13	0
Body puff	2.21 ± 1.33	0	0
Swimming	0	0.12 ± 0.13	0
Tug on wall	0	0	0.15 ± 0.23

n = number of courtships or displays.

the bower avenue constrained all female visitors to be aligned with the main axis of the bower. The wide avenue of Spotted Bowerbird bowers allowed females to position themselves perpendicular to the main bower axis, often facing the north wall. Males typically responded to visitors by courting them from the direction they were facing. Thus, the different style of bower construction and positioning of females was related to the distinctive orientation of male Spotted Bowerbird display. Visitors that did not crouch and that showed unsettled, uninterested behaviour during courtship might have been males (see Borgia 1986), and commonly these birds, even in Spotted Bowerbirds, face out of the bower entrance. Somewhat different behaviours were observed in a male- male courtships. For example, in Spotteds there appeared to be a greater tendency toward courtships at bower entrance rather than through the wall in apparent male-male courtships.

In summary, males of these three species differed in the position where bower displays occurred relative to the bower entrance. Satin and Great Bowerbirds mostly displayed at or near the bower entrance and were generally in the immediate vicinity of the bower (Table 3, Fig. 2). Satin Bowerbirds displayed almost exclusively at the north side of bowers, moving around the front of the bower during display. Great Bowerbirds also showed a bias toward the north entrance but were confined more to corners of the bower and movements close to the wall during display. Male Spotted Bowerbirds differed in their use of long runs and their tendency to direct them toward the northern wall of the bower. Spotted Bowerbird displays are more animated and occurred over larger areas compared with the other two species. Spotted Bowerbirds differed in that females commonly positioned themselves perpendicular to the main axis of the bower while being courted.

Vocalisations

Male Satin Bowerbird displays consisted of components that occurred in a predictable sequence (Loffredo & Borgia 1986). A preamble of guttural squeaks, buzzes and churring sounds was followed by two distinctive, almost stereotyped, elements: the mechanical call and mimicry of two and sometimes three other species, usually the Kookaburra *Dacelo gigas* and Lewin's Honeyeater *Meliphaga lewinii* and sometimes an Australian corvid *Corvus* sp. The mechanical call was an alternation of broad-band buzzing vocalisations that varied in pitch and amplitude, followed by a trill. The usual sequence was a long buzz of increasing pitch, a rapid decline in pitch, and several short low pitch buzzes. This sequence was repeated several times and then was followed by a high-pitched trill. The call sequence was most regular when the male was displaying to an empty bower in what appeared to be practice. When females were present components of the call might be left out, there was a greater range of amplitude and the display was more likely to be stopped midway through components. These changes in the call pattern appeared to be reactions to the behaviour of the female (Borgia & Loffredo unpubl. data).

Spotted and Great Bowerbirds had simpler courtship calls than Satin Bowerbirds. Neither species showed the sequence of buzzes and trills of the Satin Bowerbirds mechanical call. Although both species were good mimics (Chaffer 1945), neither included mimicry as a regular part of its courtship display. On one occasion a Great Bowerbird was heard to mimic a barking dog during his display but that was exceptional. Great Bowerbirds had a characteristic churring call with a consistent ringing sound given at one second intervals. They used this call as they circled the bower during courtship. The ringing note might have provided females information about the male's location since she could not see through the thick bower wall as he circled to the rear of the bower. In addition to their loud screech calls male Spotted Bowerbirds uttered a unique and very faint squeaking sound, like water bubbling over rocks, during their courtships.

Comparisons of courtship behaviour

Table 4 summarises comparisons of 40 display behav-

Table 4 Character states for display-related traits in three avenue building bowerbirds.

	Species		
	Satin	Great	Spotted
Bower width = bird width	P	P	A
Stick bower walls	P	P	A
Long bower avenue	A	P	P
N-S bower orientation	P	P	A
End of bower protected	P	P	A
Rise in bower avenue	A	P	A
See-through bower wall	A	A	P
2 display courts	A	P	P
Decoration number large (>500)	A	P	P
Decorations in avenue	A	P	P
Decoration on wall	A	P	P
Decoration spread	A	A	P
Decorations heavy	A	P	P
Decorations on platform	P	P	P
Dimorphic plumage	P	A	A
Neck crest	A	P	P
Crest shape round	—	P	A
Simple courtship call	A	P	P
Mimicry in courtship	P	A	A
Stereotyped vocal sequence (including mechanical call)	P	A	A
Circling of bower	A	P	P
Location notes while moving around bower	A	P	A
Bubbling vocalisation	A	A	P
Runs to bower	A	A	P
Display at entrance wall	P	P	A
Decoration throwing	A	P	P
Decoration holding	P	P	A
Head turning	A	P	A
Swimming	A	A	P
Hop-flip	A	A	P
Standing wing flips	A	P	A
Step-flip	P	A	A
Female sideways in bower	A	A	P
Attacks on bower visitors	A	A	P
Tug on bower wall	A	P	A
Body slam at bower	A	A	P
Body puff	P	A	P
Tail/wing drag	A	A	P
Courtship interruption	P	A	P

P = character present, A = character absent.

iours among the three species. The closely related Spotted and Great Bowerbirds show more differences (24) than Great and Satin Bowerbirds (20), and the largest number of differences occur between Spotted and Satin Bowerbirds (30). This pattern supports the hypothesis that Spotted Bowerbirds have, since their divergence from Great Bowerbirds, undergone substantial changes in their display behaviour in ways that make them the most distinctive of the avenue-building species.

Male Spotted Bowerbirds were generally very energetic and aggressive in courtship even to the point of attacking birds in their bowers. When a visiting male moved outside the bower during a display, the courting male would attack him, either by moving toward him with a beak thrust or with a 'body slam' into the bower wall very near to where the male stood (Table 3). This behaviour had the effect of moving the visitor back into the bower. No attacks or slams were seen in either Satin or Great Bowerbirds.

Spotted Bowerbirds appeared more aggressive than the other species in several other regards. As noted above they tossed decorations more often and further. In addition, they showed rapid movements directed at the bower during display. Satin Bowerbirds also moved quickly but these movements were often of shorter duration and were not directed at the bower and female as they were in Spotted Bowerbirds. Also, male Spotted Bowerbird courtship calls were more harsh and broad-banded and were similar to aggressive calls shared by the three species.

Decoration stealing

Decoration stealing was common in Satin Bowerbirds, less common in Greats and extremely rare in Spotteds. The mean percent of decorations on Spotted Bowerbird courts that had marks from other males' courts was 0.014 ± 0.006, compared with 6.3 ± 0.56 for Great Bowerbirds (t = 37.3, $d.f.$ = 30, $P < 0.001$). This contrasted with a range of 15-80% for different decoration types on the courts of Satin Bowerbirds (Borgia unpubl. data).

Bower destruction

In 1989 there were 29 destructions of Spotted Bowerbird bowers ($\bar{X}$ = 2.15 ± 1.86) occurring at a rate of 0.032 destructions/bower/day. Great Bowerbirds had a higher rate of destruction, with 67 bower destructions ($\bar{X}$ = 4.47 ± 1.76) occurring at a rate of 0.094 destructions/bower/day (χ^2 = 10.1, $d.f.$ = 1, P = 0.005). Satin

Bowerbirds had an even higher destruction rate (0.2 destructions/bower/day).

Courtship interruption

Courtship interruptions involved one or more marauding males flying into the bower during courtship and attempting to land on top of the female and to forcibly copulate with her. Spotted Bowerbird courtship interruptions occurred 8 times (0.62% of all courtships). When the courting male noticed the marauding male he quickly moved around the bower and attempted to copulate with the female. In most cases there was a successful copulation, as shown by the typical (3 s) length of cloacal contact and characteristic shaking of the female afterward, but because the males approached the female nearly simultaneously, it was difficult to determine in what proportion of cases the marauding male was successful. No courtship interruption/forced copulation attempts were seen in Great Bowerbirds. On several occasions I have seen males attempt forced copulations in Satin Bowerbirds. In one instance the bower owner from an adjacent bower flew in and landed on top of a female as she was being courted by the owner of the bower. A fight ensued and the female left, but it was clear by the manner in which the intruding male mounted her that he was attempting to forcibly copulate. In numerous other instances sexually mature males still in green plumage (see Marshall 1954) alone or in groups would arrive at bowers during courtship and attempt to mount courted females.

Predation at bower sites

Observations from hides, videotape and film records of behaviour at bowers (161 850 h) showed no evidence of predation at bowers of the three species.

Discussion

The results show that many characteristics of male Spotted Bowerbird display differ radically from the congeneric Great Bowerbird, which shows an unexpectedly high similarity to the more distantly related Satin Bowerbird. Other characters are consistent with the closer relationship of Spotted and Great Bowerbirds. Three differences in bowers can be related to unique aspects of Spotted Bowerbird courtship. The see-through bower walls made of straw, the wide bower avenue, and the bower orientation all appear to be necessary to allow females to view male courtship through the bower wall. In particular, the wide bower avenue allows females to face the displaying male as he courts her through the bower wall.

The highly integrated nature of changes in bower structure in relation to male courtship argues against the possibility that sexually selected male traits are entirely arbitrary, independently determined and unrelated. If changes in display are associated with changes in habitat, there is reason to expect that such changes are functional in the sense that they are dictated by the peculiar conditions where the species occurs.

There are three plausible reasons for changes in the elements of male display and structure of Spotted Bowerbird bowers. First, the predator protection hypothesis suggests that the openness of Spotted Bowerbird habitat and the sparse cover immediately around their bowers may make them particularly susceptible to predation. Bowers might have been modified to reduce some of this threat while females are on the ground.

Several results suggest evidence contrary to the predictions of this hypothesis. First, there is no evidence that predators present a problem for females in the bower. Second, peculiar attributes of Spotted Bowerbird bowers do not suggest modification for predator protection. Its lighter construction with thin straw, wide avenue, and vertical walls that do not cover the female suggest a bower less secure from predators than those of either Satin or Great Bowerbirds.

The protection from marauding male hypothesis suggests that changes in bower structure and display may function to reduce the possibility of forced copulation by marauding males interrupting courtships. There is a large difference in the amount of cover available to Spotted and to Great Bowerbirds, and this difference may make visiting female Spotted Bowerbirds more susceptible to forced copulations by marauding males. In the relative absence of logs and protective bushes males may have evolved to change the bower so that the bower wall is behind the female, providing her protection from this kind of interference.

The hypothesis that bowers offer protection from intruding males is attractive because both the bower builder and the visiting female benefit directly. Bower owners lose in successful forced copulations by marauders. Even if the marauder is unsuccessful, females often leave the court after a failed attempt; it is also possible that she will not return and will choose to mate elsewhere. Females that are forced to copulate lose the advantage of being able to choose their mate. If adjustment of bowers discourages forced copulation attempts

by marauding males, then the bower owner might gain from both a lower rate of disrupted copulations and a preference by females to mate at bowers that offer protection.

In Satin Bowerbirds, interference in courtships by intruding males has been frequently observed, although bower owners build their bowers with the back near a log or dense vegetation, which may be an adaptation to reduce interference from marauding males (Borgia 1986). In another species, *Amblyornis macgregoriae*, Pruett-Jones & Pruett-Jones (1982) found that 39% (7/18) of courtships were disrupted by other males. Low rates of forced copulation attempts were noted at Spotted Bowerbird bowers but none were observed at Great Bowerbird bowers. This between-species difference could be interpreted as evidence either for or against the protection from marauding male hypothesis. It may signify that courtship interruptions are a problem for Spotted but not Great Bowerbirds, or it may show that Great Bowerbirds have built and situated bowers in ways that are more effective in discouraging courtship interruption.

The threat reduction hypothesis suggests that males have rotated the bower orientation to reduce threat to visiting females from themselves. In other bowerbird species there is evidence that females assess males on the basis of bower quality and number of decorations. In an environment where decorations are commonly stolen and bowers are destroyed, bower owners resisting these intrusions can maintain a well decorated and well built bower, and thereby demonstrate a high level of vigour. Spotted Bowerbirds' bowers are widely spaced and there is little decoration stealing or bower destruction so alternative indicators of male vigour may be necessary. Enhancement of the intensity of male courtship may serve this function, but may also have the side effect of intimidating the visiting female. The positioning of a see-through bower wall between the courting pair allows the male to perform his vigorous display while reducing the threat to the female.

I tested these hypotheses in an experiment in which one of the two bower walls was randomly destroyed to evaluate how females positioned themselves relative to the wall left standing during courtship (Borgia unpubl. data). I predicted that to gain protection from forced copulation by marauding males females should orient with the standing wall behind them. To gain protection from displaying males females should stand facing the wall with the male on the other side. The second hypothesis (threat reduction) was supported by two results. First, in 25 of 26 courtships females spent most time facing the wall with the male on the other side. Second, displaying males showed a higher rate of aggressive behaviours when displaying outside the standing than outside the destroyed wall. This result supported the hypothesis that males adjusted the intensity of their display in relation to the protection available to the female.

Additional evidence for a specialised threat reduction function for a Spotted Bowerbird's bower wall was shown in comparisons of display behaviours with other species. Male Spotted Bowerbirds were more inclined than other species to carry out aggressive acts against visitors, e.g. body slams at the bower and attacks on visitors that were never or rarely seen in other species. Even so, male Spotted Bowerbirds failed to or infrequently utilised other common threat reduction behaviours used by congeners that include holding decorations in their beak and head turning during courtship. Decorations held in the beak or head turning probably signalled a disinclination to attack a visitor at the bower. I saw no head-turning by displaying male Spotted Bowerbirds and they held decorations for only a very short time during courtship. Because males were separated from females by the bower wall they probably had less need for decoration holding and head turning than other species. The observation that male Spotteds commonly held decorations when not separated from females by the wall, as when they moved around it to copulate, supports this view.

The vigour in Spotted Bowerbird courtships may be the result of an arbitrary female preference rather than selection for assessing male quality. Bowers were then modified for threat reduction. There are, however, two reasons to favour the hypothesis that the increased vigour of male display is functional rather than a result of an arbitrary preference. First, there is an unique association in Spotteds between the lack of decoration stealing and bower destruction and the enhanced vigour of male display. An arbitrary preference model does not explain this association. Second, the increase in intensity of the male display may bring added costs to females. Recent models of arbitrary preferences suggest that such costs can significantly limit the spread of such preferences (Pomiankowski et al. 1991). If there were a compensating benefit, e.g. the selection of more fit males, then these costs might be less limiting. Male Spotted Bowerbird mating success is highly correlated with the numbers of two types of bower decorations suggesting that decorations still play an important role

in mate choice despite there being low levels of stealing in this species (Borgia in press b).

Emphasis on proximate benefit explanations, i.e. protection for females, is consistent with the likely causes for the origin of bower building. Elsewhere, I have suggested that bowers originally functioned to enhance the females' willingness to visit male bowers by providing protection from forced copulations (Borgia in press a). Observations in Spotted, Satin, Fawn Breasted and especially Toothbill Bowerbirds indicate that the female bowerbirds are susceptible to forced copulations at the bower either by the bower owner or marauding males (Borgia 1986; Borgia in press a,b, unpubl. data). Male Toothbills have no bower and the typical copulation involves aggressive capture of the female by the male, often with him biting her behind the neck as he mounts her. Combined with observations of display across bowerbird species indicating that even highly divergent bower types force the male to run around a wall or maypole, thereby allowing the female to leave if she is not ready to mate, these observations support the hypothesis that the bower offers protection to females from unwanted copulations by the bower owner. This hypothesis is most attractive as an explanation for the origin of bower-building because it is consistent with the simplest bower type such as an undecorated sapling, all existing bower types and the behaviour of species that only clear courts (Borgia in press b). Other forms of selection have affected bower evolution. For example, females may use bowers as part of their assessment of males (Borgia 1985a; Borgia & Mueller 1992; Borgia in press a; Borgia unpubl. data) but this appears to be a secondary adaptation that occurred after bower-building evolved (Borgia in press b).

These interspecific comparisons of bowerbird display illustrate how large differences can emerge between closely related species. In most cases the reported changes do not involve the development of entirely new structures or behaviour, but rather a modification of traits common across bowerbird species, often, as in the case of behavioural traits, with some amplification of intensity. These changes are not universal, but affect specific aspects of courtship. Bower traits that have changed are connected functionally and these operate primarily in improving conditions for female visitation and observation of courtship at bowers. These changes are consistent with models for the origin of bower-building that claim bowers evolved to encourage female visitation at male courts by reducing the threat of forced copulation by the bower owner (Borgia in press b).

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