



Coevolution of elaborated male display traits in the spotted bowerbird: an experimental test of the threat reduction hypothesis

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ABSTRACT

Elaborated male sexual displays commonly involve multiple elements that may differ greatly among closely related species, but there have been few studies of the causes of this divergence. Male spotted bowerbirds, *Chlamydera maculata*, have unusually intense, aggressive courtship displays and highly divergent bowers. Male and female courtship positions differ from related species in that males court females separated by a modified see-through bower wall. Here we experimentally tested hypotheses that could explain the unique features of spotted bowerbird display relative to other *Chlamydera* species. Our results support the threat reduction hypothesis, which suggests that accessory traits evolve because they mitigate the threat associated with intense, aggressive male displays that are most effective in causing females to become sexually receptive. In spotted bowerbird males, the highly modified and unique see-through bower walls allow females to view intense displays while reducing threat that would otherwise be associated with these same displays. We found that (1) females preferred males with the most intense displays, (2) males and females at experimentally manipulated bowers consistently moved to courtship positions so that the standing bower wall separated them and (3) males reduced display intensity when not separated from the female by an intact bower wall. Comparisons with other *Chlamydera* species suggest that bower architecture coevolves with other display elements to allow maximally effective male displays. Such coordinated adaptive changes of display elements suggest an alternative to the runaway divergence of arbitrary traits as the cause of rapid divergence in multifaceted male display traits among closely related species.

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Recent empirical studies have shown that elaborated displays in polygynous species are commonly a complex sets of traits (Borgia 1985; McDonald 1989; Zuk et al. 1990, 1992; Gibson et al. 1991; Hasson 1991; Møller & Pomiankowski 1993; Omland 1996a, b; Brooks & Caithness 1995) that are often highly divergent between closely related species (Basolo 1990; Prum 1990; Kusmiński et al. 1997). There are several hypotheses that attempt to explain how elaborate, multifaceted male display traits evolve (see Andersson 1994), and among these, only the runaway model (Fisher 1930; see also Lande 1981; Iwasa & Pomiankowski 1995) is commonly used for describing rapid, large-scale divergences in sexually selected traits (Lande 1981; West-Eberhard 1983; Prum 1990; Andersson 1994). The lack of evidence

supporting runaway (Borgia 1987, 1993; Kirkpatrick & Ryan 1991), restrictive assumptions about levels of genetic variation and genetic correlations (Turelli 1984; Borgia 1987; Nichols & Butlin 1989, 1992; Breden et al. 1994; but see Bakker & Pomiankowski 1995), and the support for alternative hypotheses (Loffredo & Borgia 1986; Basolo 1990; Zuk et al. 1990, 1992; Ryan et al. 1991; Petrie 1994) have led some to view runaway as unimportant in the evolution of extreme traits (e.g. Kirkpatrick & Ryan 1991; Kirkpatrick 1996). However, there are no alternative models to explain how multiple elements of complex traits might rapidly diverge. Møller & Pomiankowski (1993) argue that elaborated display traits in polygynous species are commonly made up of multiple elements. Here we propose that these multiple elements are often coevolved and functionally dependent. Changes in one or more elements drives compensatory adjustments in an entire suite of display traits creating

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the rapid large-scale shifts in elaborated displays that seem to characterize many polygynous taxa (e.g. Prum 1990).

Phylogenetic relationships among bowerbirds are now well established (Kusmierski et al. 1993, 1997) and these show extreme lability in display traits between sister species (Borgia 1995c; Kusmierski et al. 1997). In the genus *Chlamydera* there is a high level of divergence of bower and courtship behaviours with the most extreme differences occurring between the spotted bowerbird (*C. maculata*) and its close relatives (Borgia 1995a). Here, we experimentally test hypotheses that may explain the dramatic divergence of multifaceted, male display characters in spotted bowerbirds.

Bowerbird bowers are stick structures built by males adjacent to display courts which they clear on the ground (Marshall 1954; Gilliard 1969). In avenue-building species like the spotted bowerbird, the bower is made up of two walls creating a central avenue, which the female enters for courtship. Bowlers are attractive to females, and males with well-built bowers mate proportionately more often than males with bowers of lower quality (Borgia 1985, 1995b; Borgia & Mueller 1992). Like all other court-clearing bowerbirds, neither female spotted bowerbirds nor their offspring receive direct material contributions or parental assistance from males apart from sperm.

Courtship by male spotted bowerbirds is conspicuously more energetic and aggressive than in closely related species (Borgia & Mueller 1992; Borgia 1995a). Male spotted bowerbirds are unique because they charge towards the bower wall from several metres away with extremely rapid hops and exaggerated undulating movements, sometimes crashing into the wall. They also pick up decorations in their beaks and toss them, up to a metre away, in contrast to tosses of less than 10 cm typical in their close relatives. Courtship calls are loud and more similar to threat calls than are those of other species (Borgia 1995a). Spotted bowerbirds are also unique among avenue-building bowerbirds in that males sometimes aggressively attack females (Borgia & Mueller 1992). Although the causes for these attacks are unknown, they may be by-products of mechanisms needed to produce high-intensity displays.

Spotted bowerbird bowers differ from all other avenue-building species because of their disproportionately wide (relative to the size of the bird) avenue, see-through walls of fine straw instead of dense sticks, the concentration of bright decorations in the bower avenue, and an east-west rather than north-south orientation (Borgia & Mueller 1992; Borgia 1995a). Courted females commonly stand in the bower avenue perpendicular rather than parallel to the bower walls and look through the north wall at the courting male. The uniqueness of these characters relative to closely related species indicates that this suite of characters has evolved recently in the lineage leading to spotted bowerbirds.

The association between the development of intense male display and the modified bower with the wall separating the male and female during courtship suggests the possibility of conflicting effects of high-intensity

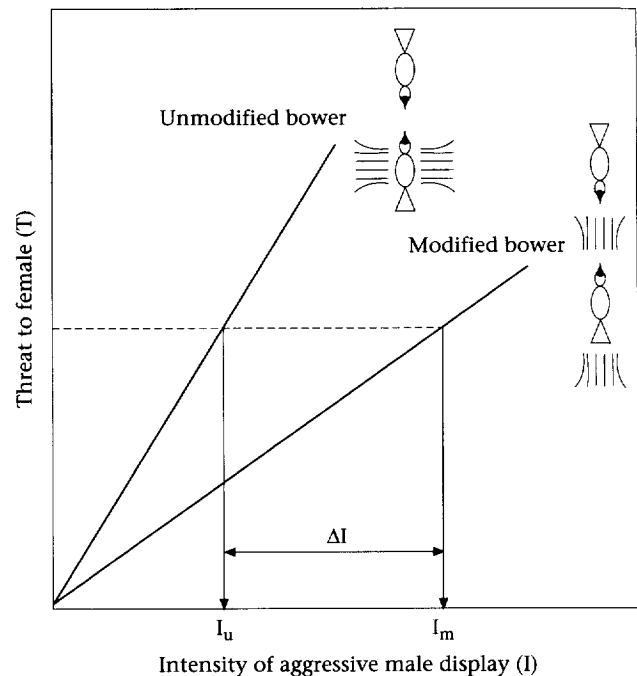


Figure 1. The threat reduction hypothesis suggests that intense male displays that are useful to females in assessing males may also be threatening to females. Threat to females increases as a function of the intensity of male display. At unmodified bowers, the rate of increase is greater than at modified bowers, like those of spotted bowerbirds that protect females with the bower wall. ΔI is the difference in intensity of male display at a fixed level of threat at modified and unmodified bowers. The threat reduction model predicts that when females are protected from threatening display elements males will produce more intense displays.

male display. The threat reduction hypothesis (Borgia 1995a) proposes that males develop specialized display elements, in this case the modified bower wall, to allow them to more effectively court females with high-intensity displays. Under this hypothesis, intense, aggressive male display is attractive to females because it provides information about overall male vigour and, ultimately, genetic quality of males. However, intense displays may also be threatening, causing females to leave before courtship is complete because of the risk of attack. An ideal display would be one in which females are stimulated by high-intensity aggressive displays, but the negative consequences of these behaviours perceived as threatening by females are filtered out. The modified bower of spotted bowerbirds, with the wall positioned between the male and the female, may function as such a filter, allowing the female to view aggressive, high-energy male displays from a protected position (Fig. 1).

Several other hypotheses could also explain the unique male and female orientation in spotted bowerbirds. Recently, pre-existing preference models of display trait evolution (Burley 1985; Ryan et al. 1991) have received much attention, in part because of their relative simplicity of evolution in not requiring the coevolution of female preferences and male traits (Kirkpatrick & Ryan

1991). In spotted bowerbirds, for example, there could be an arbitrary novel female preference for facing into the bower wall. It is also possible that females may retain the ancestral preference for males that court from the north, which is present in other species that build avenue bowers (Vellenga 1980; Borgia 1986).

Here we report the results of an experiment designed to evaluate predictions from the threat reduction hypothesis as part of an analysis of large-scale changes in bower design. In this experiment, we destroyed one of two bower walls and observed the effect of this destruction on male and female display behaviour. If threat reduction is the cause of unique attributes of spotted bowerbird bower structure, then we would expect compensating behaviours by males and females during courtship that adjust for changes brought about by the removal of the bower wall. Three testable predictions from this hypothesis are: (1) males should display from behind the standing wall; (2) females should move to face the standing wall; and (3) males should reduce the intensity of their displays when the bower wall is not present to screen the female during courtship. Alternative hypotheses, however, may involve different predictions. For example, a female preference for facing north would predict no effect of wall destruction on male orientation during display or on intensity of display.

METHODS

This experiment was conducted in Queensland, Australia, 3 km north of the town of Thallon (28°30'S, 148°52'E) beginning 4 September 1990. Most of the bower sites were found in 1987 (see Borgia & Mueller 1992 a detailed description of the study area) and remained occupied in 1989 and 1990. Of the 12 bowers used in this experiment, half had the north wall destroyed, and half had the south wall destroyed. We removed sticks from the destroyed wall every 2 days as bower owners attempted to rebuild that wall. To control for the effects of destroying the north and south wall, midway through the experiment (4 days after the initial destruction), we slid a piece of flat iron under the bower and rotated it 180° so that the positions of the walls of each bower were reversed. We continued to destroy the same wall that had initially been destroyed, the only difference being that the positions of all walls were now reversed. Each bower was monitored throughout the experiment using a camcorder (model RCA CC320) controlled by an infra-red detector that projected an invisible beam through the bower (see Borgia 1995b for a description of the apparatus and methods). Video and sound recording were initiated automatically when a bird in the bower interrupted this beam.

We scored the videotapes to determine male and female position in and around the bower during courtship relative to standing and destroyed walls. We used variables showing significant correlations from the 1989 comparisons (see below) in our 1990 analysis of male aggressive behaviour at experimentally manipulated bowers. We compared levels of activity and intensity of aggression on the standing and destroyed wall side of

each bower. Methods for monitoring bowers generally paralleled those of a previous study (Borgia 1995b), except that in the earlier study, bowers were monitored with no experimental manipulation. We captured individual males at bowers and marked them with unique colour leg-band combinations beginning in 1987; by 1990 all male bower owners were marked. Typically mature males prevent other males from using their bowers for courtship, and colour bands allowed us to confirm that the displaying male was the bower owner. We captured a few females away from bowers and banded only a small proportion (<10% receiving courtships).

We conducted a prospective analysis so that we could identify intense elements of male display that were attractive to females at intact bowers. In 1989, we continuously monitored the behaviour of 13 males with camcorders through the mating season (Borgia 1995b). We used courtships recorded on videotape during that season to determine whether there was a general female preference for aggressive male traits, and to identify which of the display traits that appeared aggressive were attractive to females. We measured attractiveness using Spearman correlations between intensity (e.g. the rate with which these elements were used in displays) and that year's mating success (number of copulations) of individual displaying males. For each male display variable, we calculated intensity from the mean value of three unsuccessful and three successful courtships. Not all males copulated so the number of successful courtships scored ranged between 0 and 3.

We selected seven variables as possible indicators of intensity of male display.

(1) Long calls. Male courtship vocalizations are predominantly raspy, broad-banded calls given repetitively and lasting no more than a few seconds. These calls vary in length, and the longer form is identical to a threat call. We classified calls as long (>1.0 s) or short (<1.0 s), and measured the proportion of long calls (long calls/(long calls+short calls)) uttered by each male.

(2) Body shudder. Often as the male approaches the female in the bower, he leans forward with head down, and rapidly jerks his wings back against his body while undulating rapidly from head to tail. We calculated the rate of body shuddering.

(3-4) Wing flip. A rapid mechanical extension and retraction of the wings and a common element of courtship display in several bowerbird species. We calculated the rate and duration of wing flipping.

(5-7) Decorations. During courtship, males often pick up bower decorations in their beaks and either drop them or toss them. We measured the rate at which decorations were picked up, the rate at which decorations were tossed, and the proportion of decorations tossed (i.e. not merely dropped).

We also examined four variables of courtships recorded in 1990 that were shown to correlate significantly with male mating success in 1989. We measured the rate at which males displayed each of these four selected elements on the side of the bower that was destroyed and left standing.

Table 1. Number of courtships at each bower classed as to the predominant orientation of the courting male and the courted female relative to the standing wall

Bower	Female facing standing wall, male facing standing wall	Female facing standing wall, male facing destroyed wall	Female facing destroyed wall, male facing standing wall	Female facing destroyed wall, male facing destroyed wall
1	2	1	0	0
2	1	0	0	0
3	2	0	1	0
5	1	0	0	0
7	3	1	0	0
8	5	0	0	0
9	3	0	0	0
11	2	1	0	0
14	2	0	0	0
16	1	0	0	0
17	0	0	0	0
18	1	0	0	0
Totals	23	3	1	0

We used Spearman correlations (r_s) for bivariate comparisons to identify variables showing positive relationships with male mating success. This test is robust under conditions associated with small sample size; its use does not suggest an inability to identify independent and dependent variables. Because we were selecting only for variables that showed positive associations, we used one-tailed tests in these comparisons. We used a chi-square (χ^2) test to determine female direction preferences. The Statistica program (Statsoft 1995) we used to evaluate male and female positioning relative to standing walls reports Z scores for both the Wilcoxon signed-ranks (Z_w) test and the sign test (Z_s). For tests of preference for the standing versus the destroyed wall, male position, and the intensity of display, none of the hypotheses predicted a preference for facing or displaying on the side of the destroyed wall. Thus, the appropriate tests are one-tailed. Experimental results found to be statistically significant ($P < 0.05$) were also significant as two-tailed tests.

RESULTS

The hypothesis that females may retain an ancestral preference for facing north was not supported. There was no association between direction (north or south) and the orientation of females in bowers during courtship ($\chi^2 = 0.731$, $P = \text{NS}$). Females faced the standing wall 87.9% of the time at the beginning of courtships when males were not yet present on the court (sign test: $Z_s = 2.27$, $N = 7$, two-tailed $P = 0.023$).

Females spent more time facing the standing than the destroyed wall at all bowers ($Z_{w,10} = 2.93$, $P = 0.0066$) and in 26 of 27 total courtships (Table 1). Similarly, males courted more from outside the standing wall than the destroyed wall for all bowers ($Z_{w,10} = 2.87$, $P = 0.0088$) and in 24 of 27 courtships. Overall, males and females positioned themselves such that the standing wall was between them the majority of time in 23 of 27 courtships. In one case, the pair had the destroyed wall between

them, and in the three remaining cases, the female faced into the standing wall, but the male displayed more from the side of the destroyed wall.

In one case, a courtship began with the male standing inside the bower and the female facing him, looking through the wall from the outside. The male then moved away briefly and the male and female reversed positions. These results indicated that separation by the wall may be more important than the usual positions taken by each sex at the bower, and that females will only move towards their usual position if the male is not in a position to threaten her.

Using information from the previous field season, we tested the prediction that intense displays are attractive to females by contrasting male mating success with seven variables that might indicate the level of vigour in male courtships. Four of these variables showed significant positive correlations with male mating success, suggesting their importance in female mating decisions (Table 2).

To determine whether the presence of the wall affected the intensity of male display, we compared the rates of the four behaviours shown to be important in mate

Table 2. Spearman rank correlations of male mating success with seven variables selected as possible indicators of the intensity of male display

Variables ($N = 13$)	Spearman rank correlation
Proportion of long calls	0.594*
Body shudder rate	0.832**
Wing flip rate	-0.083
Wing flip duration	0.391
Decoration toss rate	0.575*
Proportion of decorations tossed	0.208
Decoration pick-up rate	0.564*

* $P < 0.05$, ** $P < 0.001$.

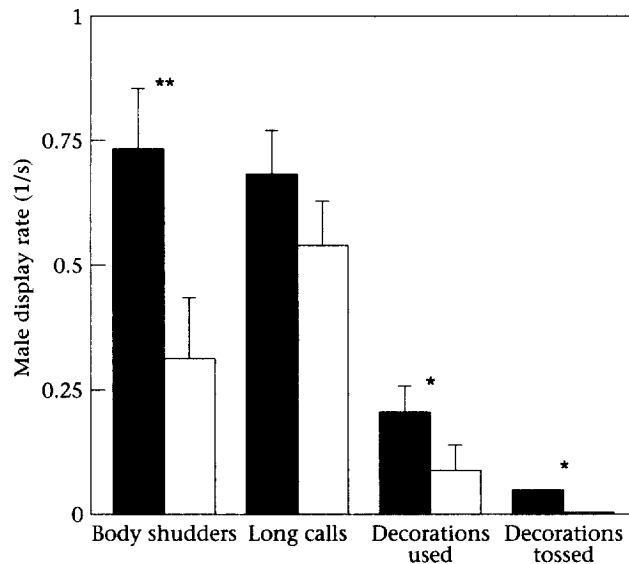


Figure 2. Comparisons of rates of male display on standing and destroyed sides of bowers. Variables that showed significant correlations with male mating success in the previous year (1989), indicating their likely importance to females in mate selection, were selected for this comparison. The figure shows overall mean \pm SE rate. ■=Unmanipulated wall; □=destroyed wall. * $P < 0.05$ (Wilcoxon signed-ranks test).

choice on the standing and the destroyed wall sides of bowers. Consistent with predictions from the threat reduction hypothesis, three of the four variables showed significantly higher rates of display on standing side than on destroyed side of the bower (body shudder rate: $Z_w = 2.09$, $P = 0.015$; percentage of long calls: $Z_w = 1.48$, $P = 0.065$; decoration pick-up rate: $Z_w = 2.6$, $P = 0.0047$; decoration toss rate: $Z_w = 2.07$, $P = 0.022$ (one-tailed tests; Fig. 2). A combined probability test (Fisher 1954; Sokal & Rolf 1995) revealed a highly significant overall difference in display rate for these variables ($\chi^2_2 = 25.82$, $P = 0.005$).

DISCUSSION

Our results are consistent with predictions developed from the threat reduction hypothesis suggesting that changes in spotted bowerbird bowers represent a coevolved suite of changes that allow males to give higher intensity displays to females than might be given at a bower of more typical design. Results from the analysis of unmanipulated bowers suggest that females prefer males with more intense displays. Experimental modifications of bowers showed that both males and females spent more time facing into the standing wall than into the destroyed wall of the bower during courtship. Females faced into the standing wall before males arrived on the court, suggesting a bias to face into the wall even when males were not present. The consistent tendency for males to use the bower wall to orient their displays at manipulated bowers despite the northerly bias found at unmanipulated bowers suggests that separation by the

wall was of greater importance at manipulated bowers than the directional bias commonly expressed at unmanipulated bowers. The higher intensity of male display on the standing versus the destroyed side of the bower supports the prediction from the threat reduction hypothesis that the wall allows males to give more intense displays.

Pre-existing female preferences for facing the displaying male or the standing wall represent alternative hypotheses that could explain male and female responses to bower wall manipulations. A pre-existing female preference for facing the male does not explain differences in male behaviour at unmanipulated bowers, where males most often displayed from behind the north bower wall (Borgia 1995a), and at experimental bowers, where males consistently positioned themselves behind the standing wall.

Courtship through the bower wall could result from an arbitrary female preference for facing standing walls, and the male choosing to face the female for display. But this hypothesis does not explain the lowering of display intensity on the destroyed side of the bower. Hypothetically, display intensity might be higher behind the standing wall because males are less visible, and displays of a minimum perceived intensity may be needed to stimulate females. However, this is unlikely because (1) the bower wall is sufficiently open to allow a reasonably clear view of the male's movements, (2) acoustical characters were among those enhanced during courtship displays, and thus the perception of these characters is unlikely to be unaffected by the presence of a thin bower wall, and (3) males reduced the intensity of their display on the destroyed side of the bower. Conceivably, males could save energy by reducing display intensity, because in the absence of the wall, they would be more visible, but such savings would be small and would not be expected in the relatively novel situation presented by wall destruction in our experiments. On the other hand, if threat was critical in affecting female receptivity and males monitor female reactions to their own courting behaviour, then males should show effective and appropriate changes in display intensity even under the relatively novel condition when the bower wall is removed.

The male threat in display has probably affected the evolution of display in other bowerbird species. In avenue-building bowerbirds, excepting spotted bowerbirds, males hold bower decorations in their beak during courtship as they directly face the female. Attacks involving lunges with an open beak are sometimes directed at visiting birds at the bower. The presence of a decoration in the beak could soften this blow and may signal reduced threat to females, because the male's beak is closed on the decoration. Male spotted bowerbirds frequently pick up and throw decorations, but are unique because males do not hold decorations in their beak over prolonged periods of display (Borgia 1995a). The separation of the male and female by the bower wall during courtship in spotted bowerbirds may obviate the need for threat reduction gained by males holding decorations in their beaks. Among species in the genus *Chlamydera*, the male's ability to move away from the bower allows the male

to modulate negative effects of intense courtships (G. Borgia, unpublished data). Two species have independently evolved small courts and bowers raised on tall stick platforms (fawn breasted, *C. cerviniventris*, and yellow breasted, *C. lauterbachii*), and both have low-intensity courtships. Males in species with bowers on the ground (spotted, great, *C. nuchalis*, and western, *C. guttata*, bowerbirds) have displays that are much higher in intensity and often court at much greater distances from the female.

Most models of elaborate male display have focused on the exaggeration of individual display traits (e.g. Lande 1981). Møller & Pomiankowski's (1993) comparisons show, however, that for most polygynous species, elaborate displays consist of multiple display traits. They propose that multiple traits can evolve because some signal different types of information valuable to females, and some provide redundancy to increase the accuracy of assessment, while others have lost their function. They conclude that traits in most polygynous species are functionless either as the result of runaway selection or as indicators that have lost their ability to reliably signal male quality (but see Borgia 1995b). Alternatively, Hasson (1990, 1991) has suggested that secondary display elements evolve because they enhance the female's perception of major indicator traits (see also Brooks & Caithness 1995). Schluter & Price (1993) suggest that secondary traits increase signal detectability. We suggest a different reason why secondary traits (e.g. modified bower architecture or decorations held in the male's beak) evolve: because they reduce costs of assessment to females.

In recent models that consider the evolution of multiple display traits, the cost to females, such as increased time in mate searching, may limit the number of traits that can evolve (Pomiankowski & Iwasa 1993; Iwasa & Pomiankowski 1994). However, if novel traits lower the overall costs to females, then constraints on the addition of new traits should be removed, and allow large numbers of new traits to be added. In spotted bowerbird lineage, the many traits associated with a dramatic change in courtship display may have evolved because these traits have reduced the negative elements associated with aggressive courtships and allowed further intensification of male display. In general, traits that reduce the costs of choice to females should (1) increase the number of display elements that females can afford to prefer and (2) allow further elaboration of already existing display traits.

The recurrent evolution of displays with aggressive elements in species with nonresource-based mating systems (Loffredo & Borgia 1986; Höglund & Alatalo 1995) suggests that these displays are not arbitrary. Instead, threatening displays may result from the co-option of already available signals that evolved in the context of male-male threat display (Borgia 1979; Berglund et al. 1996). Male threats used in aggressive interactions are probably most effective when they indicate a high level of vigour by the displaying male such that the signal recipient can anticipate losing in an escalated contest; this same signal may also be useful in indicating male quality

to females. Display systems involving these types of signals should evolve readily relative to those requiring coevolved male traits and female preferences (Turelli 1984; Borgia 1987; Nichols & Butlin 1989, 1992; Breden et al. 1994) because it would only require the evolution of a female preference for the already existing male trait that reliably confers information about male genetic quality to females. However, while such displays may be valued by females, their design may need modification to function effectively in the new context of male-female display. Thus, trait elaboration in bowerbirds, and probably in other species, often involves the co-evolution of behaviours, postures and structures that enhance the utility of threat displays for use in courtship by modulating their negative effects on females. Co-option of other male traits useful in mate selection by females (e.g. choosing bright feathers evolved for other functions as a signal of disease resistance) could involve similar adjustments.

The common use of aggressive elements in male courtship display in species with nonresource-based mating systems (Borgia 1979; Loffredo & Borgia 1986; Berglund et al. 1996) suggests the possibility that threat reduction could affect display elaboration in species other than bowerbirds. For example, the male bluebird of paradise, *Paradisaea rudolphi*, and oropendolas, *Psarocolias montezuma*, may reduce threatening aspects of their very loud displays by hanging upside down from display perches, a position from which it would be difficult to attack females. These examples suggest that hypotheses considering threat reduction, and more generally, reducing costs to females, may be useful for understanding functional roles for the curious patterns of elaborate and extreme displays assumed to be artefacts of arbitrary sexual selection.

The coevolution of large numbers of display elements as part of a functional display system provides an alternative to runaway selection of arbitrary traits as an explanation for rapid and large-scale changes in display traits between even closely related species. This hypothesis is supported by our observation that changes in display between spotted bowerbirds and close relatives are highly integrated functionally, indicating a high level of adaptation.

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References

- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Arnold, S. 1983. Sexual selection: the interface of theory and empiricism. In: *Mate Choice* (Ed. by P. Bateson), pp. 67–107. Cambridge: Cambridge University Press.
- Bakker, T. C. M. & Pomiankowski, A. 1995. The genetic basis of female mate preferences. *Journal of Evolutionary Biology*, **8**, 129–171.
- Basolo, A. 1990. Female preference predates the evolution of the sword in swordtail fish. *Science*, **228**, 340–344.
- Berglund, A., Bisazza, A. & Pilastro, A. 1996. Armaments and ornaments: an evolutionary explanation for traits of dual utility. *Biological Journal of the Linnean Society*, **58**, 385–389.
- Borgia, G. 1979. Sexual selection and the evolution of mating systems. In: *Sexual selection and Reproductive Competition in Insects* (Ed. by M. S. Blum & N. A. Blum), pp. 27–49. New York: Academic Press.
- Borgia, G. 1985. Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour*, **33**, 266–271.
- Borgia, G. 1986. Sexual selection in bowerbirds. *Scientific American*, **254**, 92–101.
- Borgia, G. 1987. A critical review of sexual selection models. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 55–66. Chichester: J. Wiley.
- Borgia, G. 1993. The costs of display in the non-resource-based mating system of the satin bowerbird. *American Naturalist*, **141**, 729–743.
- Borgia, G. 1995a. 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*. *Emu*, **95**, 1–12.
- Borgia, G. 1995b. Complex male display and female choice in the spotted bowerbird: specialized functions for different bower decorations. *Animal Behaviour*, **49**, 291–301.
- Borgia, G. 1995c. Why do bowerbirds build bowers? *American Scientist*, **83**, 542–550.
- Borgia, G. & Mueller, U. 1992. Bower destruction, decoration stealing and female choice in the spotted bowerbird. (*Chlamydera maculata*). *Emu*, **92**, 11–18.
- Breden, F., Gherardt, C. & Butlin, R. K. 1994. Female choice and genetic correlations. *Trends in Ecology and Evolutionary Biology*, **9**, 343
- Brooks, R. & Caithness, N. 1995. Manipulating a seemingly non-preferred male ornament reveals a role in female choice. *Proceedings of the Royal Society of London, Series B*, **216**, 7–10.
- Burley, N. 1985. The organization of behavior and the evolution of sexually selected traits. *Ornithological Monographs*, **37**, 22–24.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Fisher, R. A. 1954. *Statistical Methods for Research Workers*. 12th edn. Edinburgh: Oliver & Boyd.
- Gibson, R. M., Bradbury, J. W. & Vehrencamp, S. L. 1991. Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. *Behavioral Ecology*, **2**, 165–180.
- Gilliard, E. T. 1969. *Birds of Paradise and Bowerbirds*. London: Weidenfield & Nicholson.
- Hasson, O. 1989. Amplifiers and the handicap principle in sexual selection: a different emphasis. *Proceedings of the Royal Society of London, Series B*, **235**, 383–406.
- Hasson, O. 1990. The role of amplifiers in sexual selection. An integration of the amplifying and the Fisherian mechanisms. *Evolutionary Ecology*, **4**, 277–289.
- Hasson, O. 1991. Sexual displays as amplifiers: practical examples with an emphasis on feather decorations. *Behavioral Ecology*, **2**, 189–197.
- Höglund, J. & Alatalo, R. V. 1995. *Leks*. Princeton, New Jersey: Princeton University Press.
- Iwasa, Y. & Pomiankowski, A. 1994. The evolution of sexual preferences for multiple handicaps. *Evolution*, **48**, 853–867.
- Iwasa, Y. & Pomiankowski, A. 1995. Continual change in mate preferences. *Nature*, **377**, 420–422.
- Kirkpatrick, M. 1996. Good genes and direct selection in the evolution of mating preferences. *Evolution*, **50**, 2125–2140.
- Kirkpatrick, M. & Ryan, M. 1991. The evolution of mating preferences and the paradox of the lek. *Nature*, **350**, 33–38.
- Kusmiński, R., Borgia, G., Crozier, R. & Chan, B. 1993. Molecular information on bowerbird phylogeny and the evolution of exaggerated male characters. *Journal of Evolutionary Biology*, **6**, 737–752.
- Kusmiński, R., Borgia, G., Uy, A. & Crozier, R. 1997. Molecular information on bowerbird phylogeny and the evolution of exaggerated male characters. *Proceedings of the Royal Society of London, Series B*, **264**, 307–313.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the U.S.A.*, **78**, 3721–3762.
- Loffredo, C. & Borgia, G. 1986. Sexual selection, mating systems, and the evolution of avian acoustical display. *American Naturalist*, **128**, 773–794.
- McDonald, D. 1989. Correlates of male mating success in a lekking bird with male-male competition. *Animal Behaviour*, **37**, 1007–1022.
- Marshall, A. J. 1954. *Bower-birds, Their Displays and Breeding Cycles*. Oxford: Oxford University Press.
- Møller, A.P. & Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology*, **32**, 167–176.
- Nichols, R. A. & Butlin, R. K. 1989. Does runaway sexual selection work in finite populations? *Journal of Evolutionary Biology*, **2**, 299–313.
- Nichols, R. A. & Butlin, R.K. 1992. Sexual preference and genetic correlations. *Trends in Ecology and Evolutionary Biology*, **7**, 29–30.
- Omland, K. 1996a. Female mallard mating preferences for multiple male ornaments. I. Natural variation. *Behavioral Ecology and Sociobiology*, **39**, 353–360.
- Omland, K. 1996b. Female mallard mating preferences for multiple male ornaments. II. Experimental variation. *Behavioral Ecology and Sociobiology*, **39**, 361–366.
- Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, **171**, 598–599.
- Pomiankowski, A. & Iwasa, Y. 1993. Evolution of multiple sexual preferences by Fisher's runaway process of sexual selection. *Proceedings of the Royal Society of London, Series B*, **253**, 173–181.
- Prum, R. O. 1990. Phylogenetic analysis of the evolution of display behavior in the neotropical manakins (Aves: Pipridae). *Ethology*, **84**, 202–231.
- Ryan, M., Fox, J. H., Wilczynski, W. & Rand, S. 1991. Sexual selection by sensory exploitation in the frog *Physalaemus pustulosus*. *Nature*, **343**, 66–67.
- Schluter, D. & Price, T. 1993. Honesty, perception and population divergence in sexually selected traits. *Proceedings of the Royal Society of London, Series B*, **253**, 117–122.
- Statsoft 1995. *Statistica*. Tulsa, Oklahoma: Statsoft.

- Sokal, R. & Rohlf, J. 1995. *Biometry*. 3rd edn. San Francisco: W. H. Freeman.
- Turelli, M. 1984. Heritable genetic variation via mutation-selection balance: Lerch's zeta meets abdominal bristle. *Theoretical Population Biology*, **25**, 138–193.
- Vellenga, R. E. 1980. Distribution of bowers of the satin bowerbird at Leura, NSW, with notes on parental care, development and independence of the young. *Emu*, **80**, 97–102.
- West-Eberhard, M. J. 1983. Sexual selection, social competition and speciation. *Quarterly Review of Biology*, **58**, 155–183.
- Zuk, M., Johnson, K. & Thornhill, R. 1990. Mechanisms of female choice in the red jungle fowl. *Evolution*, **44**, 477–485.
- Zuk, M., Ligon, D. & Thornhill, R. 1992. Effects of experimental manipulation of secondary sex characters in the red junglefowl. *Animal Behaviour*, **44**, 999–1006.

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