Satin bowerbird displays are not extremely costly

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Sheldon (1996) presents an inaccurate critique for my arguments concerning the costs of display. In Borgia (1993), I reported results from my studies of satin bowerbirds, *Ptilonorhynchus violaceous*, that conflicted with predictions from two particular sexual selection models. I pointed out that Zahavi's (1975) and Lande's (1981) models predict extremely high costs of display for satin bowerbirds and that the size of male display should show effects of high cost such as male mortality and/or a decreased ability to produce large displays in successive years. I provided strong evidence from life history and experimental data against these predictions. I then discussed how honest advertising could occur without expensive male displays.

Sheldon constructs a straw man by suggesting that I argue that there is no cost of display and by applying my results as tests of models I did not claim to test. His title implies that I claim that male satin bowerbird displays are 'cheap' and says that I '. . . interpret positive correlations between variables (in this case between-year values of bower characteristics) as particularly strong evidence against a cost of display' (Sheldon 1996, page 646). Nowhere in my paper do I argue that satin bowerbird displays are cheap, nor do I suggest that there is no cost of display. I test and am able to support the very different hypothesis that there are no 'formidable' (page 730) or 'high absolute costs' (page 731) of display (Borgia 1993). I indicate that some displays are 'unambiguously expensive' (page 740) and conclude that 'The results here suggest that, at least for some cases, male display traits are not as expensive as has been commonly assumed' (Borgia 1993, page 471).

Sheldon (1996) claims that I 'do not take into account the fact that theory predicts and empirical

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studies frequently find that, positive covariances exist between the phenotypic value of pairs of life history traits (page 645). However, neither the Zahavi (1975) nor the Lande (1981) model that I explicitly identify as the focus for my tests makes this prediction of positive covariances. Maynard Smith (1991) pointed out that the Zahavi model is not a condition-dependent model in the usual sense, where positive covariances between male vigour and size of the display trait are predicted. Lande's model explicitly rules out covariances between trait attractiveness and male vigour (Arnold 1983).

The Zahavi and Lande models lead to predictions for a very high cost to males from display. The Zahavi (1975) model is unique among good genes/indicator models, in that males first produce a display character, and then their subsequent survival is the test of male quality. Because of this requirement, very high levels of male mortality are necessary for females to mate with the highest echelon of male sires. For example, the trait must be expensive enough to cause 75% of males bearing it to die for females to mate with males in the top 25% of male sires. Similarly, the Lande model predicts that with steep selection gradients that occur in satin bowerbirds, there must be high costs to males bearing display traits.

The suggestion by Zahavi (1975) that predation costs associated with display are a major source of male mortality led to the first prediction in Borgia (1993), that males should die at a higher rate during the mating season when they are producing display characters than outside it. Predictions 2 through 6 were designed to test for other likely outcomes of having extremely high cost display traits. These include (prediction 2) the expectation of a high overall level of male mortality associated with the full expression of male display traits, and (prediction 3) an inverse correlation between the size of the display trait and male survivorship.

In Borgia (1993) I was n of the predictions of high c addition, I pointed out that unexpectedly positive and reference to the hypotheses ing both that male displa expensive and that for m quality displays, 'male gene related to the marginal cos quality' (page 738).

Sheldon (1996) summaril predictions 2 through 6, b only experimental data can variances, failing to recog I tested do not predict Sheldon restates an argum my results are consistent w indicator models (pages 73 takenly argues that this vie conclusions.

Sheldon's claim that 'The tality is not higher during th outside it (point 1) has no be of whether display is cos ignores that this test was m ment made by Zahavi (Bo that displays test males b predators. If these displays and only occur during the contrary to Sheldon's claim, to expect higher mortality season. Sheldon criticizes me effects of costly display m mating system, but fails to c the same observation (page 7 that this mortality differenc by my other tests.

Sheldon argues that my concerning male mortality af are inadequate because of power associated with accept esis. He assumes an inaccu statistical power for my test u 11 rather than the 14 indivi used in the experiment. He fa with the very extreme increa bower building caused by the high costs demanded by the even a test with low statistical evidence for extreme costs importantly, however, is the mortality from displays that,

In Borgia (1993) I was not able to support any of the predictions of high costs of male display. In addition, I pointed out that some correlations are unexpectedly positive and significant, at least in reference to the hypotheses being tested, suggesting both that male displays are not extremely expensive and that for males with the highest quality displays, 'male genetic quality is inversely related to the marginal cost of enhancing display quality' (page 738).

Sheldon (1996) summarily dismisses my tests of predictions 2 through 6, because he claims that only experimental data can test for positive covariances, failing to recognize that the models I tested do not predict positive covariances. Sheldon restates an argument that I made that my results are consistent with other more recent indicator models (pages 738–739) and then mistakenly argues that this view is at odds with my conclusions.

Sheldon's claim that 'The observation that mortality is not higher during the mating season than outside it (point 1) has no bearing on the question of whether display is costly: ...' (page 646) ignores that this test was motivated by an argument made by Zahavi (Borgia 1993, page 733) that displays test males by exposing them to predators. If these displays are extremely risky and only occur during the mating season, then contrary to Sheldon's claim, it is quite reasonable to expect higher mortality during the mating season. Sheldon criticizes me by arguing that some effects of costly display may be felt after the mating system, but fails to credit me for making the same observation (page 733) and for my claim that this mortality difference could be measured by my other tests.

Sheldon argues that my experimental results concerning male mortality after bower destruction are inadequate because of the low statistical power associated with accepting the null hypothesis. He assumes an inaccurate estimate of the statistical power for my test using a smaller size of 11 rather than the 14 individuals per treatment used in the experiment. He fails to recognize that with the very extreme increase in time spent in bower building caused by the experiment and the high costs demanded by the models being tested, even a test with low statistical power should show evidence for extreme costs of display. More importantly, however, is the overall low rate of mortality from displays that, at their base level,

are supposed to be extremely costly, and especially for the experimental group for which the level of effort devoted to display is greatly increased. No males died during the mating season, and only three of 28 died (two experimental and one control) between the end of the experiment and the following season. In addition, rates of male mortality from 1980 to 1988 indicate that display costs associated with deaths are nowhere near the magnitude necessary for the tested hypotheses to be supported.

Sheldon makes the interesting suggestion that, in the blue chip addition experiment, the tendency of males with augmented decorations to use fewer chips may result, because the use of additional choice would increase the risk of bower destruction. This interpretation is unlikely for the following reasons, however. In another experiment (G. Borgia, unpublished data) I offered males 20 blue chips that were not fixed to the bower platform as they were in the above mentioned experiment. In that experiment, no males removed decorations from their bowers, as might have been expected if those decorations brought on high costs. In general, decorations probably have a neutral and perhaps even moderating effect on bower destruction in that, at well decorated bowers, marauding males focus more on stealing decorations than on bower destruction (Borgia & Gore 1986). Neighbouring subordinate bower holders may be tolerated by dominant bower holders if the benefits of having them nearby (e.g. as a source for prized decorations) is greater than reproductive losses due to their presence.

In conclusion, the particular hypotheses being tested predict very high levels of male mortality and do not predict positive covariances between male survival and the size of the male trait, and are thus suited to both the experimental and non-experimental tests I described. The absence of evidence for high male mortality, extremely costly display and an inverse relationship between display size and male mortality argues against these hypotheses. As I point out in Borgia (1993), tests of the role of cost of display with respect to other indicator hypotheses that require costly advertising to promote honest advertising are less clear. It is commonly assumed that costly displays are required to allow honest advertising, but there has been little consideration of alternative possibilities (e.g. Horn et al. 1995). Positive covariances

may be part of explanation for the absence of conspicuous costs in bowerbirds, but perhaps more important are alternative explanations (e.g. traits that are acquired with experience) that could also produce honest advertising without high cost (Borgia 1993). Lastly, Sheldon's commentary errs severely and unfairly by invoking arguments that are not pertinent to the models under discussion and in failing to credit me for arguments I made that anticipate and fully explain his criticism.

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