Bower decorations attract females but provoke other male spotted bowerbirds: bower owners resolve this trade-off

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Elaborate secondary sexual traits offset the costs that they impose on their bearer by facilitating reproductive benefits, through increased success in intrasexual contests or increased attractiveness to choosy mates. Some traits enhance both strategies. Conversely, I show that spotted bowerbirds *Chlamydera maculata* may face a trade-off. The trait that best predicts their mating success, numbers of *Solanum* berries exhibited on a bower, also provokes increased intrasexual aggression in the form of bower destructions by neighbouring bower owners, which reduce the quality of the male's bower. At natural berry numbers, levels of mating success in the population are skewed, but levels of destruction do not vary with berry number. When berry numbers are artificially exaggerated, increased levels of destructions occur, but mating success does not increase. When offered excess berries, either to add to the bower or artificially placed on the bower, bower owners preferred to use numbers of berries related to the number that they displayed naturally. This decision is made without direct experience of the attendant changes in destruction or mating success. This indicates that bower owners may assess their own social standing in relation to their neighbours and modulate their display accordingly.

Keywords: bowerbird; male competition; female choice; condition dependence

1. INTRODUCTION

The evolution of elaborate secondary sexual traits puzzled Darwin (1871) who suggested that the costs of males exhibiting such traits could be offset by reproductive benefits. Elaborate traits may enhance a male's chance of success in intrasexual competition. Alternatively, they may enhance his attractiveness to choosy females. In some cases, traits function in both intrasexual contest and intersexual choice. Berglund *et al.* (1996) review 48 cases of traits that function as both ornaments (used in intersexual choice) and armaments (used in intrasexual contests), including visual, acoustic, chemical and electrical signals. These two selective forces, inter- and intrasexual selection, usually operate in the same direction. For example, Bisazza & Marconato (1988) showed that female bullheads *Cottus gobio* preferred large males and that large males did better in intrasexual competitions. Male golden-headed cisticolas *Cisticola exilis* with artificially shortened tails were able to defend higher quality territories against other males and also achieve increased reproductive success independent of territory quality, possibly due to enhanced aerial displays (Balmford *et al.* 2000). In cases such as these, a successful male gains fitness benefits via both inter- and intrasexual selection through exaggeration of the same trait.

In some cases however, traits favoured by female choice do not enhance the male's status. Work on house finches *Carpodacus mexicanus* (McGraw & Hill 2000) showed that males bearing bright plumage (a trait favoured by females)

were dominated by duller males during the non-breeding season when competing for access to food.

Numerous studies have demonstrated that males exhibiting the most elaborate secondary sexual traits within a population enjoy the highest levels of mating success (for reviews see Andersson 1994; Johnstone 1995; Kotiaho 2001). However, relatively few studies then go on to manipulate these correlates in order to test how such traits drive variation in mating success. Only one-third of the 232 studies of sexually selected traits reviewed by Andersson (1994) combine field observations with confirmatory experiments. One reason for the paucity of such experiments is that altering a morphological trait correlated with an organism's mating success is likely to have other effects outside the context of sexual selection. For example, male golden-headed cisticolas *C. exilis* with artificially shortened tails—a trait that increases their mating success—showed reduced aerodynamic performance during slow-speed foraging flights (Balmford *et al.* 2000).

Male bowerbirds build and decorate bowers, which act as the target of both intersexual choice by females (Borgia 1985b; Borgia & Mueller 1992; Lenz 1994; Uy & Borgia 2000; Madden 2001a), and intrasexual contest, with neighbouring males destroying the bower structure and stealing decorations (Borgia & Gore 1986; Borgia & Mueller 1992; Lenz 1994). This reduces the possibility that manipulating such traits will confound mating success by altering other aspects of male behaviour. Despite this apparently ideal situation, to my knowledge, only a single previous study (Borgia 1985b) has attempted to determine whether widely reported correlations between numbers of decorations and male mating success reflect causal relationships. This experiment, which involved removing all decorations except for three yellow leaves from satin

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Ptilonorhynchus violaceus bowers, was only able to conclude that decorations *per se* enhance mating success, rather than specifying which were of particular significance.

At Taunton National Park (Central Queensland, Australia), spotted bowerbirds *Chlamydera maculata* displaying large numbers of *Solanum* berries were observed to obtain increased mating success in 2 consecutive years (Madden 2001a). I tested whether these berries were responsible for variation in levels of mating success by experimentally manipulating berry numbers at bowers. During the experiment, I observed that the manipulations that I was making provoked a surprising side-effect: altering levels of bower destruction.

This presents a situation where males may face a trade-off between whether to increase numbers of berries and enjoy increased mating success, or reduce berry numbers and hence avoid intrasexual destructions. I tested this trade-off experimentally with a series of cache experiments, investigating whether males offered large numbers of berries forego the opportunity to use them, despite the potential for increased mating success.

2. METHODS

(a) *Do numbers of Solanum berries cause variation in mating success?*

This experiment ran from 26 October to 14 November 2000, coinciding with the height of the 2000 breeding season. Nine bowers were selected for their ease of access under wet conditions and unimpeded monitoring by automated video equipment (described in Madden (2001a)). They were randomly assigned to one of two groups of four and five bowers, respectively. All existing *Solanum* berries were cleared off the bowers. Thirty new berries were added to each bower in group one. This was approximately equal to the mean number of *Solanum* berries found in 10 avenues on 28 August 2000 (29.7 ± 10.6 ($\bar{x} \pm 1$ s.e.)). Bowers from group two were kept free of *Solanum* berries. Under natural conditions, at least 20% of bowers carried an average of less than one berry over the breeding season: in 1998 4 out of 19 bowers; in 1999, 6 out of 18 bowers. In both 1998 and 1999, no copulations were observed at any of the bowers lacking berries, compared with average copulation rates of 0.0067 and 0.0055 copulations per hour (respectively) for bowers holding more than a single berry (1998: $t = -5.04$, d.f. = 14, $p < 0.001$; 1999: $t = -2.60$, d.f. = 11, $p = 0.025$). Bowers were revisited every 2 days and any excess berries removed, or lost berries replaced. These visits were also used to replace videotapes and batteries. Monitoring continued for 10 days, until 4 November, when the treatments for each group were reversed, ensuring that each bower acted as a control for itself. Videotapes were examined and rates of copulation, display, destruction and bower maintenance were calculated, correcting for length of time monitored.

(b) *Do males with higher levels of Solanum berries experience higher levels of destruction under natural conditions?*

Destruction rates were estimated from the videos of bowers monitored in 1998 and 1999 following the methods outlined in Madden (2001a). Destructions were clearly visible, typified by a non-owner bird tugging vigorously at the base of the avenue, pulling out large clumps of grass and sticks. Numbers of *Solanum* berries present on the bowers were also recorded over

these 2 years. Data used in this analysis, relating to natural levels of destruction, were confined to those collected during the breeding seasons of 1998 and 1999. This allowed me to compare average destruction rates from these 2 years with the rates recorded during the experimental period, which covered the breeding season in 2000. Attendance rates in 1998 and 1999 were also collected from the videos in order to investigate whether destruction rate was related to attendance at the bower.

(c) *Do males exhibit the maximum numbers of Solanum berries available?*

Two experiments were conducted to address this question. First, a 'harvesting' (Diamond 1987) experiment was conducted at 19 bowers. All berries were removed from the avenue and placed in a cache 1.5 m from the avenue entrance. An equal number of new berries, or 30 berries in total (equating to the mean number of berries; see above) if there were few (less than 15) berries naturally on the bower, were added to the cache and thoroughly shuffled, thereby providing easy access to at least twice as many *Solanum* berries as were initially present on the bower. Old berries were marked with a small cross using a permanent pen, while new berries were marked with a circle. The cache was left for 2 days, and when I returned I recorded the number of berries placed in the avenue. A second 'weeding' (Diamond 1987) experiment was conducted at 17 bowers. These had all been used in the harvesting experiment. In this case, the original number of berries was recorded and a further 30 berries were added to all avenues. Old and new berries were marked as before and left for 2 days. I returned and recorded the number of berries remaining in the avenue. At the end of each experiment, all new berries were removed.

3. RESULTS

(a) *Do numbers of Solanum berries cause variation in mating success?*

Contrary to expectations, bower owners provided with 30 berries did not enjoy greater mating success than when they had all their berries removed (table 1). Equally, the presence of *Solanum* berries did not alter the total time that owners spent at their bowers, the proportion of time that they spent maintaining the bower, the proportion of time spent displaying to visiting birds or the rate at which such displays took place (table 1). However, when bowers exhibited elevated numbers of berries, they were subject to significantly more and longer bower destructions by marauding males (table 1). Interestingly, mating success at bowers over the experimental period was significantly correlated with the number of *Solanum* berries that were present on the bower on 28 August, my first recording session of 2000, and 24 November, 10 days after the experiment had finished and the occasion of my last visit to all bowers (28 August: $r_s = 0.715$, $n = 9$, $p = 0.03$; 24 November: $r_s = 0.817$, $n = 9$, $p = 0.007$).

I compared four out of the nine bowers used in the experiment that naturally held fewer than 20 berries (30 – 1 natural s.e. (10.6)) with the five bowers that naturally held around 30 berries or more. Bowers with naturally high numbers of berries received significantly higher numbers of copulations during the experimental period than those that had naturally low numbers. This effect was seen when comparing the periods of berry addition (one-sample *t*-test: $t = 3.58$, $n = 5$, $p = 0.023$). None of the

Table 1. The effects of berry manipulation on behaviours occurring at the bower.

(Destructions carried out by visiting males. All other activities performed by the known bower owner. Comparisons between behaviour percentages and rates in the absence or presence of berries all use paired-sample *t*-tests. All *p*-values are two-tailed.)

	percentage of time spent on activity								rate of activity (events min ⁻¹ × 1000)							
	total time at bower		bower maintenance		display		destruction		display		destruction		copulation			
berries absent (–)	–	+	–	+	–	+	–	+	–	+	–	+	–	+	–	+
or present (+)																
mean	8.75	10.43	6.76	9.09	0.80	0.69	0.04	0.10	0.98	1.22	0.09	0.29	0.28	0.14		
<i>T</i>	–1.21		–1.97		0.55		–3.13		–0.89		–3.53		1.05			
<i>P</i>	0.26		0.08		0.60		0.01		0.44		0.01		0.32			

bowers with naturally low numbers of berries obtained any copulations when berries were added. When berries were removed, bowers with naturally high numbers of berries obtained somewhat higher levels of mating success than those with low berry numbers (Mann–Whitney *U* test: $W = 12.5$, $p = 0.086$).

(b) Do males with higher levels of *Solanum* berries experience higher levels of destructions under natural conditions?

I found that number of berries varied hugely from 0 to 158 under natural conditions. However, bowers exhibiting naturally large numbers of berries were not subject to significantly higher levels of destruction (natural number of *Solanum* berries versus rate of destructions in 1998: $r = 0.005$, $n = 19$, $p = \text{n.s.}$; 1999: $r = -0.229$, $n = 18$, $p = \text{n.s.}$). It is unlikely that variation in destruction rate is confounded by differences in bower attendance as such rates are not correlated in either 1998, 1999 or during the experiment in 2000 (attendance at the bower versus destruction rate in 1998: $r = -0.087$, $n = 19$, $p = \text{n.s.}$; 1999: $r = 0.056$, $n = 18$, $p = \text{n.s.}$; 2000: $r = -0.149$, $n = 9$, $p = \text{n.s.}$). However, artificially increasing the number of berries at a bower led to correspondingly higher levels of destruction. Furthermore, the rate of destruction when berries were added was significantly higher than that of the observed destruction rate over the breeding seasons of 1998 and 1999 (figure 1). The destruction rate at bowers with berries removed did not differ significantly from destruction rates in 1998 and 1999 (figure 1).

(c) Do males exhibit the maximum numbers of *Solanum* berries available?

Males did not exhibit the maximum number of *Solanum* berries available to them, even when there was a cost to removing them. In the first ‘harvesting’ experiment, the number of berries that a male took was significantly related to his natural number of berries ($F_{1,17} = 47.1$, $p < 0.001$; figure 2*a*). Avenues naturally contained a mean of 24.4 berries at the start of the experiment, compared with 27.7 at the end. However this was not due to males choosing the original old berries over the new berries. The proportion of new berries taken from the cache did not differ significantly from the proportion of new berries available at the cache (paired *t*-test: $t = 1.839$, d.f. = 18, $p = 0.082$). The second ‘weeding’ experiment revealed that males actively removed *Solanum* berries from their bowers from a mean of 34.6 berries immediately after

Figure 1. The rate of destruction at bowers does not vary between years, but significantly increases when numbers of berries are artificially enhanced (ANOVA: $F_{3,51} = 3.09$, $p = 0.035$; Tukey tests 2000 + berries versus 1998, 1999 and 2000 – berries, all $p < 0.05$). However, rates of destruction do not vary between 1998, 1999 or 2000 at bowers with artificially reduced numbers of berries (Tukey tests, all $p = \text{n.s.}$). Bars indicate $\bar{x} \pm 1$ s.e.

supplementation, to only 17.4 after 2 days (paired *t*-test: number of berries in avenue at start of experiment after 30 had been added versus number of berries in avenue at end of experiment, $t = 13.85$, d.f. = 16, $p < 0.001$). The number of berries that males removed was related to the number naturally present on the bower ($F_{1,16} = 73.1$, $p < 0.001$; figure 2*b*). However, they did not revert to the natural number of berries. At the start of this experiment there was an average of 4.6 berries, significantly lower than the 17.4 left after 2 days (paired *t*-test: natural number of berries in the avenue versus number of berries in avenue at end of experiment, $t = -10.26$, d.f. = 16, $p < 0.001$).

4. DISCUSSION

Although number of *Solanum* berries was the best predictor of mating success over 2 years, it did not appear to affect the mating success of the bower owner when manipulated experimentally. The fact that number of *Solanum* berries both before and after the experimental period was significantly correlated with mating success during the experimental period indicates that these decorations retained their predictive powers in 2000, as well as in 1998 and 1999. However, the manipulation did affect other

Figure 2. (a) The number of berries that bower owners add to their bowers from caches is related to the number of berries they naturally displayed on the bower ($F_{1,17} = 47.05$, $p < 0.01$, $r^2 = 0.73$, $y = 0.63x + 12.5$). (b) Males remove excess berries to return to a level that is related to the number of berries they naturally displayed on the bower ($F_{1,16} = 73.1$, $p < 0.001$, $r^2 = 0.81$, $y = 1.05x + 24.5$).

events occurring at the bower, specifically increasing the number and duration of destruction events at bowers with supplemented berries. Such destruction events, common in several bowerbird species including spotted bowerbirds, act to reduce the overall quality of the bower and are generally carried out by other bower owners (Borgia 1985a; Borgia & Mueller 1992; Pruett-Jones & Pruett-Jones 1994). Studies of several other species of bowerbirds have shown that an anthropomorphic measure of bower quality is related to mating success (Borgia 1985a; Borgia & Mueller 1992; Lenz 1994; Uy & Borgia 2000). Therefore, the high levels of destruction experienced at bowers when supplemented with berries may negate any advantage that the berries themselves bring in terms of female choice. Bowlers that naturally held numbers of *Solanum* berries similar to or greater than the 30 used in the experiment experienced higher levels of mating success under both supplementation and depletion treatments. These results are intriguing and provide, to my knowledge, the first evidence that levels of destruction depend on aspects of the bower, suggesting that not only females, but also other males pay close attention to bower design.

These results indicate that there may be a trade-off for a male between maintaining a high number of berries, and appearing attractive to females, and the increased risk of destruction of the bower associated with displaying high numbers of berries. Under natural conditions I found that number of berries varied from 0 to 158. Although bowers with high numbers of berries hosted high levels of mating success, bowers exhibiting naturally large numbers of ber-

ries were not subject to significantly higher levels of destruction. These results imply that some males can exhibit large numbers of berries and hence gain enhanced mating success, and yet not suffer from high levels of destruction. Such males may be more socially dominant or physically vigorous and so can deter marauders.

A similar condition-dependent outcome of trait manipulation was shown by Qvarnstrom (1997) in her work on collared flycatchers *Ficedula albicollis*. When their forehead patches were experimentally enlarged, old males were more likely to establish a breeding territory, while young males receiving the same treatment suffered a reduced likelihood of territory establishment. In humans, men with dominant facial appearance attained higher social standing (in the form of military rank) and subsequently enjoyed greater reproductive success, but only if they were professionally competent (Mueller & Mazur 1997). For men performing below the average, dominant facial appearance was a handicap for military promotion. It appears that certain traits may be highly beneficial to a male in terms of his mating success, but only if he is able to meet the cost of bearing them. If he cannot meet the cost, such a trait becomes instead, a hindrance.

The results from the 'harvesting' and 'weeding' experiments indicate that the male spotted bowerbird is, to some extent, aware of the potential trade-off and so alters his display accordingly. Males were seen to replace lost berries, but only to a level related to that they had previously exhibited, despite the low cost of acquisition needed to potentially double the natural level. Furthermore, when acquisition costs were removed entirely, by placing the berries on the bower, males actively removed excess berries. The 'harvesting' and 'weeding' experiments were carried out over a period that was too short (2 days each) to actually suffer destructions or enjoy mating success, indicating that the awareness of excess berries is not directly linked to the experience of increased destructions or sexual success. Previous studies (Madden 2001a) show that *Solanum* berries (when offered in small numbers) are the most popular decorations in a series of male choice tests. Obviously, males are required to make a choice: take it or leave it? The incentives to enhance the signal (take it), and hence increase mating success, are intuitive. Yet, theoretical work by Grafen & Johnstone (1993) suggests that it may become advantageous for an individual below a certain quality level not to signal at all (leave it).

In conclusion, males capable of holding a large number of berries, without incurring elevated harassment by neighbouring males may offer a signal to visiting females of their social dominance or physical prowess. As such, berries may act as an 'honest' indicator to females of male quality, constantly patrolled by other males to ensure against cheats. The unusually large brains of the spotted bowerbird (Madden 2001b) may facilitate accurate comparisons of bower components between bowers in relation to others within the population. Therefore, the number of *Solanum* berries displayed can be viewed as a condition-dependent trait, in which trait expression is constrained by a male's relative quality within a population, and is closely monitored by peers. This view implies that bower owners possess an innate or learnt assessment of their social standing in relation to their neighbours, and modu-

late their display accordingly to resolve the crucial trade-off between sexual success and vigorous persecution.

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