CSIRO PUBLISHING
www.publish.csiro.au/journals/emu *Emu*, 2009, **109**, 237–243

Do male Great Bowerbirds (*Ptilonorhynchus nuchalis*) minimise the costs of acquiring bower decorations by reusing decorations acquired in previous breeding seasons?

Natalie R. Doerr[A,B]

[A]School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia.
[B]Present address: Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA. Email: doerr@lifesci.ucsb.edu

Abstract. In many species, males must acquire resources from the environment in order to produce the sexual signals attractive to females, and indicator models of sexual selection suggest that the costs of resource acquisition may contribute to honest sexual signalling. I used data collected during a 5-year field study of the Great Bowerbird (*Ptilonorhynchus nuchalis*) to test the hypothesis that acquiring decorations is costly to males in time and energy, and that males minimise costs by reusing decorations acquired in previous breeding seasons. Males reused 240 ± 30 decorations, which represents 30% of the decorations at their bowers. Males that reused a higher proportion of their decorations were more likely to equal or exceed the numbers of decorations they displayed at their bowers during the previous breeding season than males that reused a lower proportion. Males that inherited bower-sites, where they were able to reuse decorations acquired by the previous owner, had more decorations than males that built at new sites, where decorations were not available to reuse. Males only reused a high proportion of rocks, a common decoration type, when the distance over which they had to carry the rocks was small, but they reused less common decoration types regardless of distance. These data suggest there are costs associated with acquiring decorations, and males reuse decorations to minimise costs.

Introduction

Indicator models of sexual selection propose that elaborate male traits evolve to reveal honest information about male quality to females (Zahavi 1977). Male traits are honest because they are costly to produce or maintain, and only high-quality males are able to bear the costs associated with the most extreme development of traits (Grafen 1990*a*, 1990*b*). In many species, males must acquire resources from the environment in order to produce the sexual signals attractive to females, and males with the largest or most conspicuous signals may be the most capable foragers, adept at minimising the time and energy costs of resource acquisition (Endler 1980; Hill 1991). Correlational evidence in Eurasian Siskins (*Carduelis spinus*) (Senar and Escobar 2002) and experimental evidence in guppies (*Poecilia reticulata*) (Karino *et al*. 2007) supports this possibility.

Bowerbirds (Ptilonorhynchidae) provide a unique system for studies examining the cost of elaborate male traits, and the strategies that males adopt to produce these traits. Males of most species are polygynous, and they build and decorate stick structures, called bowers, to attract the females with whom they mate. In many species, mating success of males is correlated with the numbers of specific types of decorations at bowers (Borgia 1985*a*; Borgia and Mueller 1992; Uy and Borgia 2000; Madden 2003; Coleman *et al*. 2004; N. R. Doerr, unpubl. data), suggesting males should maximise the numbers of decorations they collect. However, many studies have found that individual males vary greatly in the numbers of decorations at their bowers (reviewed in Frith and Frith 2004), so there may be costs associated with acquiring and retaining decorations.

Most empirical and theoretical work examining the cost of display in bowerbirds has considered only two methods by which males acquire decorations: collecting decorations from the environment and stealing decorations from rival males (Borgia 1993; Pruett-Jones and Pruett-Jones 1994; Madden and Balmford 2004; Morrell and Kokko 2004; Wojcieszek *et al*. 2007). However, there may also be a historical component to the numbers of decorations at bowers. Bower-owning males of all species studied to date exhibit high annual survivorship (90–93%), and they return to the same location each breeding season, typically building a new bower within 50 m of the previous year's structure (Frith and Frith 2004). Many species also use a large number of non-perishable decorations, including stones, bones and snail shells, which are likely to remain near the bower-site over time. These factors make it possible for males returning to established bower-sites to reuse decorations they acquired in previous breeding seasons.

Understanding the significance and extent of reuse of decorations is fundamental to our understanding of the costs associated with acquiring decorations. First, males returning to established bower-sites have immediate access to a large and varied cache of decorations, all located at a relatively short distance from the current season's bower. This should reduce the search and transport costs that a male would face if he had to collect all of these decorations anew, and it may allow established

 10.1071/MU09022 0158-4197/09/030237

males to begin the breeding season facing lower display costs than males building in a new location for the first time. Second, the number of decorations that a male reuses represents his long-term success at collecting and stealing decorations over the course of several breeding seasons, so older males may have more decorations on average than younger males. However, bower-sites and accompanying decorations are sometimes inherited by males upon the death of the original owner. If females prefer older males, bower-site inheritance could lead them to make inaccurate mate-choice decisions.

Anecdotal accounts of the reuse of decorations have been reported in several species of bowerbird (Marshall 1954; Gilliard 1969; Frith and Frith 2004), and the historical accumulation of objects at bower-sites may have relevance to climatologists (Gilliard 1969) and archaeologists (Dwyer *et al*. 1985) alike. Here I quantify the numbers of decorations reused each breeding season in the Great Bowerbird (*Ptilonorhynchus nuchalis*), and I use data collected during a 5-year field study to test the hypothesis that acquiring decorations is costly in time and energy, and that males minimise costs by reusing decorations.

Methods

Species and study site

Male Great Bowerbirds build bowers from June to September, and most copulations occur between September and December (Frith *et al*. 1996; N. R. Doerr, unpubl. data). Bowers are decorated with hundreds of objects, including rocks, bones, snail shells, leaves and fruit. Many bowers also contain man-made objects, such as green glass, red wires and aluminium foil (N. R. Doerr, unpubl. data). Once a male has established ownership at a particular site, he returns to it during subsequent breeding seasons, typically building a new structure within 33 ± 43 m (s.d.) of the previous one (Doerr 2008). Males that do not own a bower-site can acquire one in two ways: they can inherit a site and its accompanying decorations upon the death of the original owner, or they can build a bower in a new location. It is not known whether males that inherit sites differ in quality from males that build in new locations. Like other species of bowerbird (Borgia and Gore 1986; Frith and Frith 2004), males steal each other's decorations, and red wires were the most commonly stolen type of decoration in Townsville in 2003 (N. R. Doerr, unpubl. data).

The study site was located in the city of Townsville, north-eastern Queensland, Australia (19°19′S, 146°46′E). The habitat in Townsville consists of man-made gardens and eucalypt woodland. Bowers were located at James Cook University, the Lavarack Barracks military base, and the suburb of Annandale.

Quantifying the numbers of decorations reused

At the end of the breeding season in December 2003, I placed a small mark on all decorations at 19 Townsville bowers with a black, waterproof pen. At the beginning of the following breeding season (July 2004), I searched the study site to determine the location at which males had rebuilt their bowers. After I located bowers, I counted all decorations and determined how many had been retained from the previous breeding season. Some of the marks I placed on decorations faded with the sun and rain, so my results are likely to underestimate the actual number of decorations reused. Studies conducted during other breeding seasons suggest that 5–10% of marked decorations lose their marks within three months (N. R. Doerr, unpubl. data).

Predictions regarding the cost of acquiring decorations

In 2000, researchers in Townsville began banding Great Bowerbirds and conducting behavioural observations at their bowers, and I continued this program from 2003 to 2007. These data allowed me to calculate the minimum number of years that each male had owned a bower for most individuals in the study population. I also counted all decorations at bowers at least two times each breeding season, though I only counted decorations at a subset of bowers in 2007. In 2004, I conducted transect surveys to determine the availability of three categories of non-perishable types of decoration in the environment: rocks, man-made objects and snail shells. Following the procedure of Madden and Balmford (2004), I counted all potential decorations encountered within 1 m of a transect line that extended for 50 m in eight cardinal directions (N, NE, E, SE, etc.) from the bower. In 2006, some bowers were involved in a decoration removal experiment, so it was not appropriate to include these bowers in the predictions described below. Together with data quantifying the numbers reused in 2004, I was able to address the following predictions, two of which are not unique. If acquiring decorations is costly in time and energy, and if decoration reuse minimises costs, then:

(1) Males should reuse fewer decorations as the distance over which they have to transport the decorations increases. This prediction should only apply to abundant types of decoration that have low search costs.
(2) Males that reuse a higher proportion of decorations should be more likely to equal or exceed the numbers of decorations they displayed at their bowers during the previous breeding season than males that reuse a lower proportion.
(3) Males that inherit bower-sites should have a higher mean number of decorations at their bowers than males that build in new locations because males that inherit bower-sites are able to reuse decorations acquired by the previous owners. However, this relationship could also occur if males that inherit sites are of higher quality than males that do not.
(4) There should be a correlation between years of bower ownership and the numbers of decorations at bowers. This relationship could also occur if inexperienced males are less skilled at acquiring and retaining decorations than experienced males.

Statistical analysis

I used non-parametric tests (Mann–Whitney *U* tests, Spearman rank correlations) for all analyses, using SPSS for Windows version 11.5 (SPSS Inc. 2002), and I used the false discovery rate (FDR) to correct for multiple tests. All tests are two-tailed, and means are expressed ±s.d.

Results

Baseline description of decoration reuse

At the end of the breeding season in December 2003, 19 Townsville bowers contained a mean of 1333 ± 641 decorations.

At the beginning of the 2004 breeding season (July), newly rebuilt bowers contained a mean of 820 ± 345 decorations, of which 240 ± 126 decorations (30%) had been present at bowers during the previous breeding season. The mean numbers of decorations in 2004 was probably lower than the mean in 2003 because males had only recently begun building bowers when I took the samples that year, and they continued to acquire decorations throughout the season (Doerr 2008).

The total number of decorations at bowers in 2003 was correlated with the total number at bowers in 2004, though this value was not quite significant ($r_s = 0.447$, $P = 0.055$, $n = 19$). When the abundant rocks were excluded (see Prediction 1 below), this value was significant ($r_s = 0.667$, $P < 0.002$, $n = 19$). Strong between-year correlations were present for most common, non-perishable decoration types, and these correlations were significant even when comparing numbers of decorations between 2003 and 2005 (Table 1). In contrast, the numbers of organic items were not correlated between years (Table 1).

Prediction 1. Males should reuse fewer decorations as the distance over which they have to transport the decorations increases. This prediction should only apply to abundant types of decoration that have low search costs

In 2004, Townsville males built new bowers within 34 ± 36 m (range 4–127 m, $n = 19$) of the structures they had built the previous breeding season. Transect surveys revealed that rocks were more than 100× as common in the environment as man-made objects and snail shells (mean number encountered on eight transects per bower: rocks = 18 038 ± 21 091; man-made objects = 123 ± 67; snail shells = 0.1 ± 0.2).

There was an inverse correlation between the proportion of rocks that Townsville males reused and the distance between their current and former season's bower-sites ($r_s = -0.586$, $P < 0.008$, $n = 19$; Fig. 1). There was no correlation between the proportion of snail shells or man-made objects that males reused and the distance between their current and former season's bower-sites (both $P > 0.60$). Males reused a higher proportion of snail shells and man-made objects than rocks (snail shells, 0.44 ± 0.37; man-made objects, 0.30 ± 0.18; rocks, 0.14 ± 0.15; Friedman test, $\chi^2 = 7.63$, $P < 0.022$, $n = 16$).

Prediction 2. Males that reuse a higher proportion of decorations should be more likely to equal or exceed the numbers of decorations they displayed at their bowers during the previous breeding season than males that reuse a lower proportion

There was a positive correlation between the proportion of decorations that males reused and the between-season difference in numbers of decorations at their bowers (season 2 – season 1; $r_s = 0.544$, $P < 0.016$, $n = 19$; Fig. 2*a*). This correlation was also significant when the abundant rocks were excluded ($r_s = 0.623$, $P < 0.004$, $n = 19$; Fig. 2*b*).

Table 1. Between-year correlations for five common types of decoration
Cell values are Spearman's rho. *, $P < 0.05$; **, $P < 0.01$; †, $P < 0.05$ after FDR correction for multiple tests

	2003–04 ($n = 19$)	2004–05 ($n = 16$)	2003–05 ($n = 16$)
Green glass	0.735**†	0.811**†	0.794**†
Green plastic	0.917**†	0.760*†	0.693*†
Red wire	0.781**†	0.495	0.609*†
Snail shell	0.889**†	0.596*†	0.746*†
Organic items	0.271	–0.002	–0.226

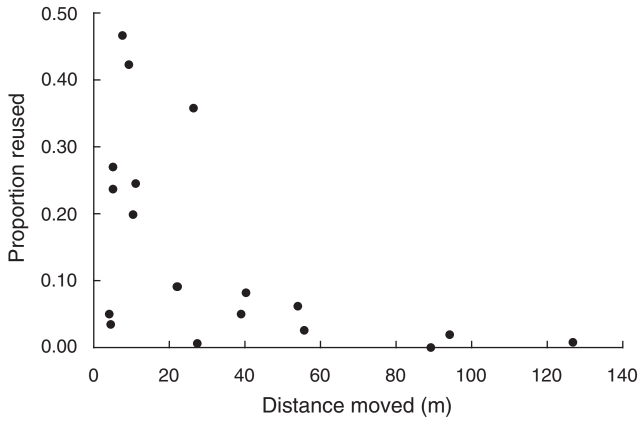

Fig. 1. The proportion of rocks that males reused and the distance between bowers of the current and former seasons (m).

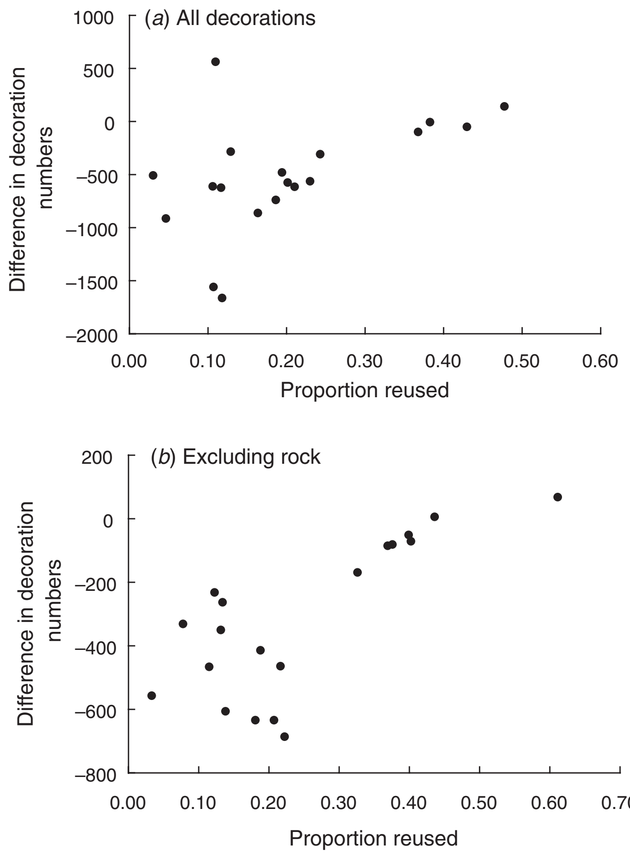

Fig. 2. The proportion of decorations that males reused and the between-season difference in numbers of decorations at their bowers (season 2 – season 1) for: (*a*) all decorations at bowers, and (*b*) all decorations except rocks.

Prediction 3. Males that inherit bower-sites should have a higher mean number of decorations than males that build in new locations

Over the five years of my study, I acquired data for six Townsville males that successfully established bowers in new locations, and eight males that inherited existing sites. To my knowledge, none of these males had previously owned a bower. However, three of the six males that built in new locations did so late in the breeding season, while seven of eight males that inherited sites were present at the start of the breeding season. Thus, differences in numbers of decorations between groups might reflect the fact that males differed in the amount of time they had to collect decorations.

To account for this problem, I used a conservative test: I determined the numbers of decorations at newly established bowers in September of the season following their inception. All newly established bowers had more decorations at this time than they had in the previous season. I compared these numbers with the numbers at established bower-sites in two time periods: in September of the first season they inherited the site, and in September of the following breeding season. The numbers of decorations at new bower-sites was significantly lower than the numbers at established bower-sites in both periods (new = 337.2 ± 248.3, inherited = 1365 ± 760.5 (season 1), Mann–Whitney $U = 45$, $P < 0.005$, $n_1 = 6$, $n_2 = 8$; inherited = 1426.7 ± 644.7 (season 2), $U = 36$, $P < 0.002$, $n_1 = 6$, $n_2 = 6$; Fig. 3*a*), even when rocks were excluded from the sample (new = 214.8 ± 159.2, inherited = 751.8 ± 412.2 (season 1), $U = 45$, $P < 0.005$, $n_1 = 6$, $n_2 = 8$; inherited = 830.2 ± 267.5 (season 2), $U = 35$, $P < 0.004$, $n_1 = 6$, $n_2 = 6$; Fig. 3*b*). The sample size was smaller in season 2 because two males that inherited sites did not return the following year.

Males that inherited sites also had more red wires than males that built in new locations (new = 10.7 ± 7.7, inherited = 32.25 ± 14.4 (season 1), $U = 45$, $P < 0.005$, $n_1 = 6$; $n_2 = 8$; inherited = 37.0 ± 18.2 (season 2), $U = 34$, $P < 0.009$, $n_1 = 6$, $n_2 = 6$). This type of decoration is reused by males, but it is also frequently stolen (Doerr 2008).

Prediction 4. There should be a correlation between years of bower ownership and the numbers of decorations at bowers

The relationship between years of bower ownership and the total numbers of decorations at bowers was not significant in either 2004 ($r_s = 0.379$, $P = 0.062$, $n = 25$) or 2005 ($r_s = 0.360$, $P = 0.109$, $n = 21$), though there was a trend in the predicted direction. Because my sample size was small, I divided males into two groups in order to maximise differences between them. Group 1 contained males that were in their first year of ownership; these were the same individuals used in Prediction 3 ($n = 14$). Group 2 contained males that had owned bowers for at least six years ($n = 10$). These two groups did not differ in the total numbers of decorations at their bowers (Mann–Whitney $U = 52$, $P < 0.312$). If males that inherited bower-sites were excluded from the sample, all first-year males had fewer decorations than males in their sixth year of ownership ($U = 60$, $P < 0.0001$, $n_1 = 6$, $n_2 = 10$).

Years of bower ownership was significantly associated with the numbers of red wires at bowers (2004: $r_s = 0.587$, $P < 0.004$, $n = 22$; 2005: $r_s = 0.452$, $P < 0.046$, $n = 20$), even when males that inherited sites were included in the sample (2004: $r_s = 0.531$, $P < 0.006$, $n = 25$; 2005: $r_s = 0.485$, $P < 0.026$, $n = 21$). Similarly, males in their first year of ownership had fewer red wires than males in their sixth year ($U = 34.5$, $P < 0.038$, $n = 24$).

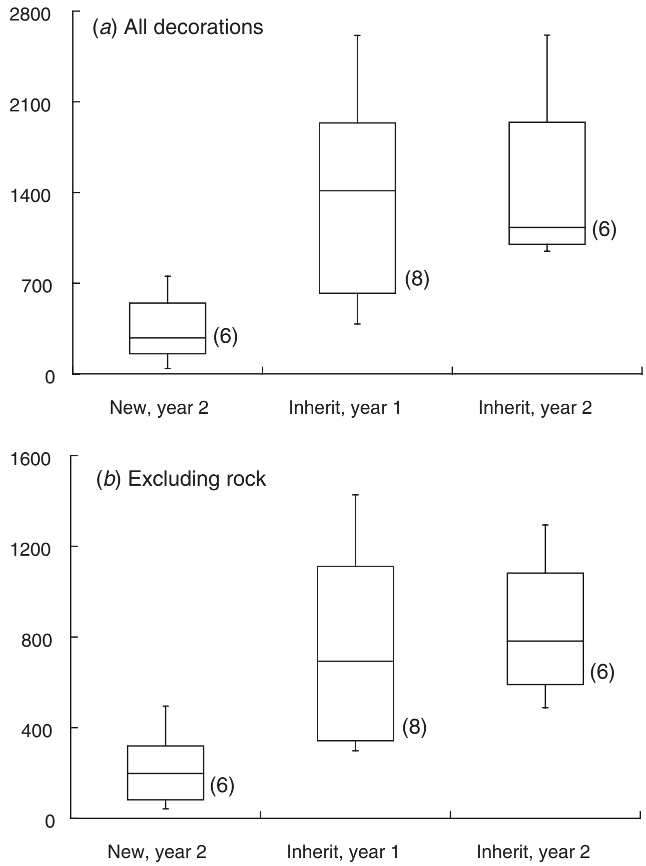

Fig. 3. The number of decorations at bowers of males that inherited bower-sites and at bowers of males that built in new locations for: (*a*) all decorations, and (*b*) all decorations except rocks. The sample size is given in parentheses to the right of each box.

Discussion

Bower decorations acquired by Great Bowerbirds in one breeding season appear to make an important contribution to the quality of the bower display in future seasons. Males reused 240 ± 30 decorations, which represents 30% of the decorations at their bowers, and they reused both natural and man-made objects. Previous studies of decoration reuse have been anecdotal and limited to observations of specific man-made items: a tin can was observed at the bower of a Vogelkop Bowerbird (*Amblyornis inornatus*) for seven years, and man-made objects that disappeared from a farm building were found at Regent Bowerbird bowers (*Sericulus chrysocephalus*) twelve years later (Frith and Frith 2004).

My results suggest that males reuse decorations to reduce the costs associated with producing attractive visual displays. Males that inherited bower-sites were able to reuse decorations acquired by the previous bower owner, and these males had almost four times as many decorations as males that built in new locations, where no decorations were available to reuse. Males that reused a higher proportion of their decorations were more likely to equal or exceed the numbers of decorations they had at their bowers during the previous year. In a related study, males that had their decorations removed at the end of the breeding season were unable to re-acquire a similar number the following year, and they always had fewer decorations than males at control bowers where decorations were not removed (Doerr 2008). The association between reuse of decorations and high-quality displays suggests that the time required to create a highly attractive bower display may exceed the time available in one breeding season alone. Reuse of decorations allows males to reduce these time costs and outcompete their rivals.

Males may also face a trade-off between search and transport costs when constructing their mating signals. Males reused a higher proportion of rocks as the distance over which they had to carry the rocks decreased, and transect surveys revealed that rocks were more than 100 times as common in the environment as any other non-perishable types of decoration used by males. Because rocks are not a limiting resource, males may reuse them only when transportation costs are small. Males reused a higher proportion of man-made objects and shells than rocks, and there was no relationship between the proportion reused and the distance over which these items were carried. These decorations are less common in the environment, so the cost of searching for new ones may exceed the cost of transporting old ones, causing males to reuse these types of decoration regardless of the distance of transport. Displaying males also present man-made objects and shells to females more often than rocks (N. R. Doerr, unpubl. data), so the types of decorations that males reused could also have been influenced by their value in terms of mating success.

Though a few studies have suggested that acquiring decorations is costly to males, most have addressed social costs, such as theft of decorations (Borgia and Gore 1986; Wojcieszek *et al*. 2007) or destruction of bowers (Borgia 1985*b*; Madden 2002). Others have provided anecdotal evidence suggesting that preferred decoration types are rare in the environment and may require considerable time, experience or both to locate (Borgia and Gore 1986; Frith and Frith 1990; Bravery and Goldizen 2007). Only two studies have attempted to quantify the cost of acquiring decorations from the environment, and both have suggested that the process is not extremely costly. Male Satin Bowerbirds (*Ptilonorhynchus violaceus*) experienced no increase in mortality from bower-building activities, and males exhibited strong between-year correlations in the numbers of decorations at their bowers (Borgia 1993). If decorating bowers was costly, males should not be able to produce high-quality displays year after year. Male Spotted Bowerbirds (*Ptilonorhynchus maculatus*) appeared to face minimal acquisition costs because many preferred decoration types were common in the environment, and neither males nor females had a preference for decoration types that were rare over decoration types that were common (Madden and Balmford 2004).

My results suggest that we should re-examine the cost of acquiring decorations, particularly in species that reuse decorations. Like Borgia (1993), I found strong between-year correlations in the numbers of decorations at bowers, even across two years. Males reusing decorations could explain why bowers looked similar from year to year. Decoration reuse has also been recorded in Satin Bowerbirds (Marshall 1954), so some of the decoration types for which Borgia (1993) found strong between-year correlations may have been those that were reused, and this could affect his interpretation that acquiring decorations is not costly. Indeed, the strongest correlations occurred for man-made objects ($r = 0.71$) and snail shells ($r = 0.63$), both of which were commonly reused by Great Bowerbirds in my study. However, strong between-year correlations also occurred for several perishable decoration types (Borgia 1993), so decoration reuse is not the sole explanation for the repeatability of display in Satin Bowerbirds.

Previous studies examining bowerbird display costs have also tended to focus on the rarity or abundance of preferred decoration types in the environment, but this may not provide useful information about the time and energy costs males face when acquiring decorations. Male Black Wheatears (*Oenanthe leucura*) carry hundreds of stones to their nest-sites, a display that may reveal their parental ability to females (Moreno *et al*. 1994). Though stones are common around the Wheatear's nest-site, the process of transporting stones requires near-maximal levels of muscle exertion (Møller *et al*. 1995) and can negatively affect the male's immune system (Soler *et al*. 1999). Thus, decorations could be both common in the environment and costly to acquire. Males that leave the bower to collect hundreds or thousands of decorations could also be forced to compromise on other aspects of their displays. Females appear to select mates based on a variety of characteristics, including vocalisations (Loffredo and Borgia 1986), intensity of display (Coleman *et al*. 2004), the quality of the bower-structure (Borgia 1985*a*), the rate at which males paint the bower (Robson *et al*. 2005), and the numbers and types of decorations (Borgia 1985*a*; Uy and Borgia 2000; Madden 2003; Coleman *et al*. 2004). If males must be proficient in multiple forms of display, this may decrease the time available for searching for decorations. Modelling work has shown that males should spend most of their time near the bower (Pruett-Jones and Pruett-Jones 1994), and some species spend more than 70% of daylight hours guarding the bower (Frith and Frith 2004).

Reuse of decorations and honest sexual signalling

Because decorations appear costly to acquire, they may function as indicator traits providing females with honest information about male quality. Males with many decorations could be in better condition; or they could be more skilled, experienced, or efficient at locating resources in the environment. Because decorations accumulate at bower-sites over time, decoration numbers could also reflect the age of males. The numbers of decorations at bowers increases with age of males in Satin Bowerbirds (Borgia 1986).

However, bowerbirds differ from most species because the resources they acquire for sexual display remain external to their bodies. Males that inherit bower-sites have not undergone the process of searching for decorations in the environment, so the numbers at their bowers may not accurately reflect their quality as mates. In my study, several males that inherited sites had small nuchal crests (N. R. Doerr, unpubl. data), the size of which increases with age (Frith and Frith 2004; Eguchi *et al*. 2007), so they may have been younger than males that had owned bowers for many years. I only found a significant relationship between years of bower ownership and the numbers of decorations at bowers when males that inherited sites were excluded from the sample. If females prefer older males, inheritance of bower-sites could lead them to make inaccurate mate-choice decisions. Interestingly, female Black Wheatears involved in the mate-choice process ignore rocks that males collected during previous breeding seasons, presumably because these do not provide accurate information about the male's current condition (Soler *et al*. 1996).

However, signalling theory only specifies that signals be honest on average (Johnstone and Grafen 1993). Because bower-owning males exhibit high annual survivorship (90–93%; Frith and Frith 2004), only a few males inherit bower-sites each year, keeping the frequency of 'cheaters' to a minimum. I only obtained limited information about the characteristics of males, so males that inherited sites could have been older, more aggressive, or in better condition – and thus not 'cheaters' at all. Furthermore, bower decorations are often washed away by storms, thrown away by humans, and discoloured by the sun and rain (Marshall 1954; Frith and Frith 2004; N. R. Doerr, unpubl. data). These environmental factors ensure that males are never able to reuse all of their decorations.

Honest sexual signalling may also be maintained by both social and environmental costs. Males frequently steal from each other (Doerr 2008), so males with many decorations could be more successful at stealing and defending their own decorations against theft. This could provide females with information about a male's social status in relation to his neighbours (Borgia *et al*. 1985; Wojcieszek *et al*. 2007). In my study, half of the males that inherited bowers were among the most frequently stolen from: one individual lost 100 decorations in two months (N. R. Doerr, unpubl. data). I also found a significant correlation between years of bower ownership and the numbers of red wires at bowers; red wires are one of the most frequently stolen types of decoration (Doerr 2008). This suggests that numbers of decorations are not an arbitrary by-product of history: males experience search and transport costs when acquiring decorations from the environment, and social costs when attempting to retain these decorations. Both social and environmental costs contribute to honest sexual signalling in Three-spined Sticklebacks (*Gasterosteus aculeatus*) (Candolin 2000) and Red Junglefowl (*Gallus gallus*) (Parker and Ligon 2007).

In summary, Great Bowerbirds reuse decorations acquired in previous breeding seasons, and this may reduce the costs of display. Because some bowerbird species prefer perishable decoration types, which cannot be reused, they may not be able to acquire as many decorations in a single breeding season as species that do reuse. Future studies should compare the extent of decoration reuse in each species with the numbers and types of decorations at their bowers; this may shed light on how male decoration preferences influence signal size and complexity in bowerbirds.

Acknowledgements

This study was supported with a National Science Foundation International Travel Grant and a National Science Foundation Graduate Research Fellowship. Thanks to Allan McManus and the Australian Army for permission to work at Lavarack Barracks, and to John Endler, Kate Buchanan, and two anonymous referees for comments on the manuscript. This study was conducted with permission from Queensland Parks and Wildlife, the University of California Animal Care and Use Committee (IACUC), and the James Cook University Ethics Committee.

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Manuscript received 12 March 2009, accepted 29 June 2009