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Male great bowerbirds accumulate decorations to reduce the annual costs of signal production

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Indicator models of sexual selection suggest that honest mating signals are costly to produce or maintain. Animals that use extended phenotypes as courtship signals may be able to reduce these costs in a given year by reusing nonbodily ornaments acquired during previous years, perhaps affecting signal honesty. I examined whether male great bowerbirds, *Ptilonorhynchus nuchalis*, are able to reduce the annual costs of signal production by reusing bower decorations acquired during previous years. I paired males that had similar numbers of bower decorations and removed decorations from one member of the pair. Males that had decorations removed from their bowers collected more decorations from the environment the following year than did control males, and they tended to steal more decorations. However, they had fewer decorations at their bowers than did control males, most likely because control males reused almost 50% of the decorations that they had acquired during previous years. These results suggest that individuals that accumulate nonbodily ornaments can reduce the costs of signal production in subsequent years; and that resource accumulation can lead to differences in both behaviour and display quality between individuals that do and do not accumulate resources. I also found a positive correlation between the number of decorations at bowers before removal and the number of decorations acquired by males after removal, suggesting that decoration numbers indicate a male's past condition and present performance.

In many species, male mating signals provide honest information about their quality as mates (Johnstone 1995). Indicator models of sexual selection suggest that honest signalling occurs because mating signals are costly to produce or maintain (Grafen 1990a, b). High costs ensure that only high-quality males have the resources necessary to produce the largest or most conspicuous traits. Although costly mating signals occur in numerous taxa and signalling modalities (Johnstone 1995), few studies have examined whether honest signalling is affected by the amount of time that signals persist in the environment. Some mating signals last for only a moment; others last for a single breeding season; and still others are present for most of the individual's lifetime. Differences in the persistence time of signals could affect the costs of signal production and maintenance, as well as the degree of honesty of the signals (Karubian et al. 2011).

Animals that use extended phenotypes as courtship signals represent a unique opportunity to investigate how signalling costs are affected by the amount of time that signals last. Extended phenotypes consist of external objects that an animal incorporates into its phenotype, but which remain external to the animal itself (Schaedelin & Taborsky 2009). Black wheatears, *Oenanthe leucura*, collect stones to display at their nest sites (Moreno et al. 1994); the cichlid *Cyathopharynx furcifer* builds sand mounds on which to display (Schaedelin & Taborsky 2010); and Lawe's parotia, *Parotia lawesii*, decorates a display court with snake skin, chalk, feathers and bone fragments (Pruett-Jones & Pruett-Jones 1988). Even humans may acquire cars, designer clothing and beautiful objects to attract a mate (Haselton et al. 2007; Dunn & Searle 2010; Apostolou 2011). Because these objects are external to the signaller, the costs of signal production may differ relative to bodily ornaments. Indeed, many extended phenotypes are composed of objects that can persist in the environment for decades, so the costs of producing the initial display (i.e. acquiring the objects) may be much higher than the costs of maintaining the display over time (Schaedelin & Taborsky 2009). In long-lived species, extended phenotypes created during one breeding season could potentially be reused the following breeding season, thus functioning as 'accumulated wealth' that reduces the cost of display in future years, although this has not been directly investigated.

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Males of most species of bowerbird (Ptilonorynchidae) build and decorate stick structures, called bowers, to attract females. Individual bowers may contain fewer than 10 decorations to more than 10 000 (Frith & Frith 2004), and males with well-decorated bowers have higher mating success (Borgia 1985; Madden 2003a; Coleman et al. 2004), although other male and bower characteristics may also influence mate choice (Coleman et al. 2004; Robson et al. 2005). In many species, males can live for more than 20 years; they build a new bower structure at approximately the same site each year; and they use nonperishable objects as decorations, including stones, bones, shells and man-made objects (Frith & Frith 2004). These factors make it possible for males to reuse decorations acquired during previous years (Doerr 2009a). Since males can travel up to 5 km to collect decorations from the environment or to steal them from other males (Borgia et al. 1987; Borgia & Mueller 1992), males that reuse decorations are likely to experience lower time and energy costs associated with constructing their mating signals than males that do not reuse decorations.

I conducted a decoration removal experiment to determine whether male great bowerbirds, *Ptilonorhynchus nuchalis*, reduce the annual costs of signal production by reusing decorations acquired during previous years. At the end of the breeding season, I paired males that had similar numbers of bower decorations and removed decorations from one member of the pair (the ‘experimental’ male). I returned the following breeding season to count decorations at all bowers. If acquiring decorations is costly in time and energy, and males reuse decorations to reduce costs, then (1) experimental males should have fewer decorations during the breeding season that followed removal than control males whose decorations were not removed; (2) experimental males should have fewer decorations during the breeding season that followed removal compared to the breeding season that preceded removal, while control males should have an equal or greater number; (3) experimental males should collect and steal more decorations than control males; and (4) there should be a positive correlation between the numbers of decorations at experimental bowers before and after removal. Prediction 4 was based on the differential costs assumption of indicator models (Grafen 1990a, b), in which high-quality males should be better able to bear the costs of signal production than low-quality males.

METHODS

Species and Study Sites

Great bowerbirds build bowers between June and September, and breeding primarily occurs between September and December (Endler & Day 2006). Once a male has acquired a bower site, he usually returns to it each breeding season, typically building a new structure within a mean ± SD distance of 33 ± 43 m of the previous one (Doerr 2009a).

Field work occurred at two sites in north Queensland, Australia: Townsville (19°19′S, 146°46′E) and Dreghorn (20°15′S, 146°42′E; see Doerr 2009b for details). The habitat in Townsville is composed of man-made gardens and eucalypt woodland. Bowers were located at two adjacent areas in Townsville: James Cook University and the suburb of Annandale. Dreghorn is a cattle property with a habitat of open eucalypt woodland. Bowers were located along the Burdekin River and Six Mile Creek. I included the majority of bowers at each site in the experiment described below. However, I did not include one bower in Townsville at which the property owner did not wish to have decorations removed; and one bower each at Townsville and Dreghorn that were abandoned prior to the experiment but rebuilt during the second year of the study. In addition, there were five bowers in Townsville and five at Dreghorn that were located on the periphery of the study site. For all the bowers that I did not include in the experiment, I still labelled the decorations and monitored them for decoration theft (details below). This study was conducted with permission from Queensland Parks and Wildlife (WISP01994004), the University of California Institutional Animal Care and Use Committee (620), and the James Cook University Ethics Committee (A919).

Decoration Removal and Bower Monitoring Schedule

I counted all decorations at bowers at the end of the breeding season (Townsville: 6–12 December 2005; Dreghorn: 4–18 December 2006), and I paired males that had similar numbers of nonperishable decorations at their bowers (Townsville = 10 pairs; Dreghorn = 12 pairs). I paired males to help ensure that males of similar quality were compared to one another, and also to ensure that the two groups contained a similar sample of bower qualities. Nonperishable decorations included natural objects, such as shells and bones, and man-made objects, such as glass, metal and plastic. Although stones were the most numerous nonperishable decoration at bowers, I did not consider stones when pairing males. Stones appear to function as a background against which more conspicuous objects are displayed (Endler & Day 2006); and leaving stones at bowers allowed me to control for differences in disturbance between treatments (see below). Bowers also contained perishable decorations, such as fruit, leaves and seed pods. Because perishable decorations cannot be reused between years, I did not consider their numbers when pairing males. I randomly designated one male as the ‘control’ and one as the ‘experimental’ male. Neither the mean nor the variance in decoration numbers differed between groups (mean ± SD: Townsville: control = 559 ± 274; experimental = 588 ± 317; paired *t* test: $t_9 = 0.168$, $P < 0.870$; Dreghorn: control = 264 ± 187; experimental = 257 ± 155; $t_{11} = 0.061$, $P < 0.953$; variance ratio test: Townsville: $F_{9,9} = 1.71$, $P < 0.44$; Dreghorn: $F_{11,11} = 1.36$, $P < 0.62$). In addition, control and experimental males were generally distributed evenly throughout the study sites: males were no more likely to have a nearest neighbour that had undergone decoration removal than a nearest neighbour that had not (binomial test: control: $P = 0.832$, $N = 22$; experimental: $P = 0.524$, $N = 22$).

After pairing males, I removed all decorations from control and experimental bowers. I used a diamond-tipped engraver pen to permanently mark decorations from control bowers. Some decorations could not be marked with the engraver, so I used a permanent black marker. I marked decorations with a unique symbol signifying the bower from which they came, counted them, and returned them to control bowers. At experimental bowers, I counted all decorations but only marked and returned stones; this ensured that both control and experimental males experienced the process of decoration marking. As a post hoc check to ensure that decoration marking did not affect the numbers of decorations that control males reused, I compared the difference in decoration numbers at control bowers (season 2 − season 1) in Townsville (mean ± SD = 80 ± 143, $N = 10$) with the difference in decoration numbers at 13 Townsville bowers at which decorations were not marked (101 ± 248; J. A. Endler, L. B. Day & N. R. Doerr, unpublished data). The between-season difference in decoration numbers did not differ between groups (*t* test: $t_{21} = -0.200$, $P = 0.843$), suggesting that marking did not affect patterns of reuse. To minimize disturbance to the birds, I primarily removed decorations during night-time hours (after 1800) and returned them the following morning (before 0630).

During the breeding season that followed decoration removal and marking, I counted all perishable and nonperishable decorations at control and experimental bowers at regularly spaced intervals (Townsville: 1–5 July, 15–20 September, 7–11 December 2006; Dreghorn: 30 September–3 October, 2–6 December 2007). The symbols that I placed on nonperishable decorations at the end