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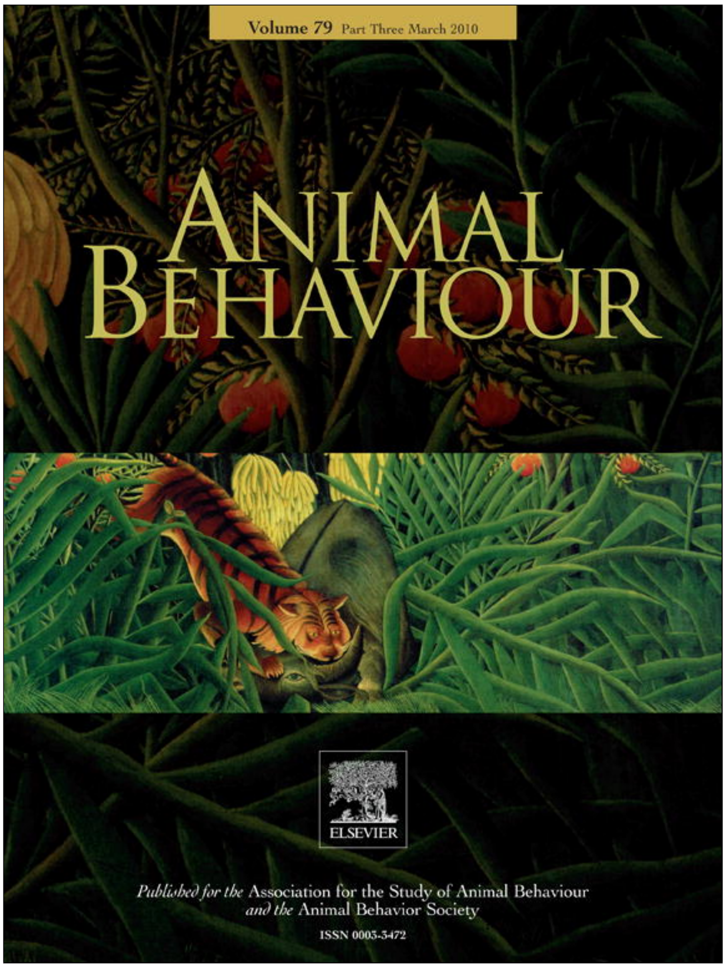

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Does decoration theft lead to an honest relationship between male quality and signal size in great bowerbirds?

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Male–male competition can contribute to honest sexual signalling. Because male bowerbirds steal each other's decorations, decoration theft could lead to an honest relationship between male quality and signal size. To test this hypothesis, I conducted an experiment in which I standardized decoration numbers at bowers of the great bowerbird, *Ptilonorhynchus nuchalis*, such that all males had equal numbers. I then monitored males for 11 weeks as they stole decorations from other males, defended their decorations against theft, and collected decorations from the environment. For two commonly stolen decoration types (red wire and green plastic), there was a correlation between the numbers at bowers before and after standardization. Males that had more red wires and green plastic pieces before standardization were less likely to have these decorations stolen from their bowers after standardization, although they were not more successful at stealing decorations. These males also collected more red wires and green plastic pieces from the environment, and collecting rate was unrelated to the numbers available near the bower. Males that were more successful at guarding their decorations had longer nuchal crests and had been bower owners for longer periods, although nearest-neighbour distance explained more of the variation in guarding ability than either male characteristic. These results suggest decoration numbers are an honest signal of the male's ability to guard his bower against theft and to locate decorations in the environment, although some variation in stealing behaviours may be related to the spatial arrangement of males rather than to male quality.
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Indicator models of sexual selection suggest that elaborate male traits evolve as costly and honest signals of male quality (Zahavi 1975; Grafen 1990a, b). Only males in good condition are able to incur the costs associated with the most extreme trait development, and females that choose these males as mates may receive direct benefits, such as improved parental care (Préault et al. 2005), or indirect benefits, such as good genes for their offspring (Møller & Alatalo 1999). The traits used in male–male competition may also be assessed by females during courtship, and the use of such traits may enhance signal honesty (reviewed in Berglund et al. 1996). Because males frequently test one another during aggressive encounters, frequent testing should expose cheaters, producing reliable signals of male quality.

Bowerbirds offer a unique system for studies examining the relationship between male–male competition and honest sexual signalling. Males of most species build and decorate stick structures, called bowers, to attract the females with whom they mate. Females prefer to mate with males that have well-decorated bowers (Borgia 1985b; Uy & Borgia 2000; Madden 2003; N. R. Doerr, unpublished data), although other male and bower characteristics may also influence mate choice (Borgia 1985b; Coleman et al. 2004; Robson et al. 2005). Because males engage in marauding behaviours (i.e. steal each other's decorations and destroy each other's bowers), male–male competition can influence the quality of a male's display. Males that are successful at stealing decorations and defending their display sites from rivals may consequently have more decorations than unsuccessful males, and this could provide females with honest information about male quality or social status (Borgia et al. 1985; Wojcieszek et al. 2007).

In support of the honest signalling hypothesis, male satin bowerbirds, *Ptilonorhynchus violaceus*, that frequently stole blue feathers had more blue feathers at their bowers (Borgia & Gore 1986; Wojcieszek et al. 2007), and this decoration type was the best correlate of mating success (Borgia 1985a). Male spotted bowerbirds, *P. maculatus*, that received supplemental decorations experienced increased bower destruction from rivals, and low-quality males rejected supplemental decorations added to their bowers,

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most likely to reduce aggression from rivals (Madden 2002). Male satin bowerbirds that dominated conspecifics at artificial feeding stations were more likely to destroy other males' bowers (Borgia 1985a), while those given testosterone implants stole more decorations than control males (Collis & Borgia 1993). These results suggest that bower destruction and decoration theft may be correlated with male quality or social dominance.

However, stealing behaviours could also be influenced by factors unrelated to male quality. Bower-owning males primarily interact with their near neighbours (Borgia & Gore 1986; Wojcieszek et al. 2007; Doerr 2009), so differences in stealing rates between males may simply be a consequence of intraspecific variation in the spatial arrangement of bowers. In addition, decoration theft and bower destruction often occur in the owner's absence (Borgia 1985a; Borgia & Gore 1986), so marauders may preferentially target males that spend less time at their bowers (Wojcieszek et al. 2007). Modelling work suggests that decoration theft and bower destruction are evolutionarily stable strategies, even when differences in male quality are not considered (Pruett-Jones & Pruett-Jones 1994; Morrell & Kokko 2004). Studies that examine how multiple factors contribute to the occurrence of marauding behaviours are needed to clarify the relationships between male–male competition, male quality and signal size. Male bowerbirds also collect decorations from the environment in addition to stealing them from other males, so studies that examine whether collecting behaviours contribute to signal honesty are essential for testing the honest signalling hypothesis.

I conducted an experiment to test the hypothesis that stealing behaviours contribute to an honest relationship between male quality and the numbers of decorations at bowers of the great bowerbird, *Ptilonorhynchus nuchalis*. At the beginning of the breeding season, I removed all decorations from bowers and subsequently gave all males an equal number of new decorations. I then monitored males for 11 weeks as they stole decorations from rivals, guarded their own decorations against theft, and collected decorations from the environment. If stealing behaviours lead to a relationship between decoration numbers and male quality, I predicted a positive correlation between the numbers of decorations at bowers before and after the experimental period, and I predicted that this relationship would be explained by the male's ability to steal decorations, his ability to prevent theft from his own bower, or both. In addition, I examined how these relationships were associated with the male's ability to collect decorations from the environment. Finally, I asked how much variation in male stealing behaviours could be explained by the spatial arrangement of bowers and by two male characteristics that may indicate status or quality: the length of the nuchal crest and the years of bower ownership. Nuchal crest length is correlated with blood testosterone levels (L. Day, unpublished data) and male age (K. Eguchi, Y. Yamaguchi, I. Nishiumi, H. Koike & R. Noske, unpublished data) in great bowerbirds, and the crest is displayed to females during courtship (Frith & Frith 2004) and to males during agonistic interactions at the bower (N. R. Doerr, unpublished data). Anecdotal evidence suggests that years of bower ownership influences the outcome of competitive interactions in several bowerbird species (Borgia & Gore 1986; Frith & Frith 2004).

METHODS

Study Site and Species

Great bowerbirds live throughout northern Australia and decorate their bowers with a variety of objects, including stones, bones, manmade objects, fruit and leaves. They typically begin building bowers in June or July, and peak breeding occurs between September and December (Frith et al. 1996; N. R. Doerr, unpublished data).

The 34 bowers included in this study were located in three adjacent areas along the southern edge of Townsville, Queensland, Australia (19°19′S, 146°146′E): James Cook University (JC, $N = 11$), the Lavarack Barracks military base (LB, $N = 12$), and the suburb of Annandale (AN, $N = 11$). The habitat in Townsville consists of manmade gardens and eucalyptus woodland (see Doerr 2009 for a map of the study site). The study occurred between July and December 2004.

Bower Search and Bird Banding

Great bowerbirds have been continuously monitored in Townsville since 2000, providing information on the location of all bowers at JC and LB. Beginning in 2003, bowers were also monitored at AN, and the majority of the time I spent searching for bowers during 2004 occurred at this location ($\approx$60 of 90 search hours). I primarily located bowers by listening for male advertisement calls, and I am confident that I located all active bowers within the study areas. However, I could not monitor one bower at AN because it was located on private property that I was not permitted to access. I also located four bowers that were peripheral to the bowers at AN and JC. Although I monitored theft of decorations to and from these bowers, I did not include these males in the decoration removal experiment described below. I used a handheld GPS unit (Garmin eTrex Vista, Garmin International, Olathe, KS, U.S.A.) to record the location of all bowers, and I determined the distance between each bower and its nearest neighbour, as well as the number of bowers within a 1 km radius of each bower. These aspects of the spatial arrangement of males may influence stealing rates in Townsville (Doerr 2009).

During July–November 2004, I caught and colour-banded 30 bower-owning males in spring-loaded live traps baited with fresh fruit and bower decorations. I measured each bird's weight and the length of the wing, tarsus, head/bill and nuchal crest. Head/bill was the length from the back of the head to the tip of the bill. I measured the maximum length of the left and right sides of the nuchal crest while extending the bird's head downwards; the mean of the two measurements was used as the nuchal crest length variable in all analyses. Morphological measurements were repeatable when birds were remeasured by the same person within $\approx$20 min (ANOVAs: wing length: $F_{9,10} = 114.7$, r (repeatability) $= 0.98$; tarsus: $F_{9,10} = 11.6$, $r = 0.83$; head/bill: $F_{9,10} = 11.8$, $r = 0.84$; weight: $F_{9,10} = 409.9$, $r = 0.99$; crest: $F_{9,10} = 891.1$, $r = 0.99$). For most males, I was able to use banding and behavioural data collected at the study site since 2000 to estimate the minimum number of years that each male had been a bower owner. If a male was in his first year of ownership, he received a score of one. Because males had only been monitored in Townsville for five breeding seasons, the maximum score was five. Males can own a bower site for more than 10 years (reviewed in Frith & Frith 2004), so this value is likely to be an underestimate. I did not band one bower-owning male because this male was located on private property, and banding was not acceptable to the property owners. I was unable to capture three other males, but two were banded in a previous season and still had colour bands, which meant they could still be accurately identified.

Experimental Approach

In great bowerbirds, the distribution of decorations across bowers remains relatively constant during the breeding season. In 2003, there was a correlation between the numbers of decorations at bowers at the beginning of the breeding season (mid-September) and the numbers at bowers at the end (early December) (Pearson

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correlation: $r_{20} = 0.893$, $P < 0.0001$; N. R. Doerr, unpublished data). Stealing behaviours were also consistent across the season in 2003: the rate at which males stole decorations during August–October was correlated with the rate at which they stole decorations during October–December ($r_{20} = 0.617$, $P < 0.002$; N. R. Doerr, unpublished data). These results form the basis of my experimental approach: if decorations are removed from bowers, and all males are given an equal number of new decorations, then stealing behaviours should redistribute decorations among bowers in a pattern that resembles their original distribution, provided that individual differences in male stealing behaviours explain why some males have more decorations than other males. Thus, a correlation should exist between the numbers of decorations at bowers before and after removal, and this correlation should be related to male stealing behaviours.

Decoration Removal

During 12–15 September 2004, I removed all decorations from bowers ($N = 34$). Immediately after removing decorations, I placed a new set of decorations upon each bower. Each set was identical and contained 655 decorations: 500 grey stones, 75 white stones, 36 pieces of green glass, 12 pieces of green plastic, 8 red wires, 2 purple wires, 2 red caps, 8 metal wires, 2 metal caps, 2 white wires and 8 snail shells. I placed two-thirds of the decorations on the court that had previously contained the majority of decorations, and one-third on the secondary court; males frequently decorate one court more extensively than the other under natural conditions (Frith et al. 1996). The numbers and types of decorations in the new decoration sets were designed using data on the decorations present at bowers during the 2003 breeding season. The number of stones in the set approximated the average number at bowers during 2003 (493 ± 424; N. R. Doerr, unpublished data). Stones appear to function as a background against which more colourful objects are displayed (Endler & Day 2006), and they are almost never stolen (5 stolen out of approximately 16 000 labelled in 2003; N. R. Doerr, unpublished data). I gave each bird far fewer than the average number of green and red decorations present at bowers in 2003 (337 ± 185; N. R. Doerr, unpublished data); green and red decorations were stolen significantly more often than grey and white decorations during 2003, particularly red wire and green plastic (N. R. Doerr, unpublished data). I followed this approach because I hoped that reducing the numbers of preferred decoration types at bowers would motivate males to steal. Hunter & Dwyer (1997) suggested that males are more likely to steal when decorations are relatively rare at bowers. I chose the other non-stone objects because they could be clearly marked with a pen, were nonperishable, and were common on most or all bowers. I marked decorations with a unique symbol signifying the bower upon which they were placed.

Once a week for 11 weeks, I visited bowers to record the numbers of stolen decorations and the numbers of new decorations collected from the environment. When I found a stolen decoration, I added the thief's symbol to the decoration. I assumed that decorations without marks had been newly collected from the environment. Because I visited bowers on a weekly basis, it is possible that I missed some incidents of theft, and that some of the decorations that I classified as 'collected from the environment' were actually stolen from other males. However, data from 2003 and 2004 suggested that monitoring males on a weekly basis provides accurate information on patterns of decoration acquisition. In both years, I labelled decorations and monitored theft by visiting bowers weekly (2004) or every 10–14 days (2003; Doerr 2009), and I used motion-activated video cameras to record all activity at a subset of bowers during each breeding season (described below). In both years, there was a positive correlation between the number of stolen decorations I recorded during bower visits and the number I recorded from watching the videotapes, which give continuous time data (Spearman rank correlation: number of decorations stolen by a male: 2003: $r_S = 0.789$, $N = 12$, $P < 0.002$; 2004: $r_S = 0.726$, $N = 11$, $P < 0.011$; number stolen from a male: 2003: $r_S = 0.684$, $N = 14$, $P < 0.007$; 2004: $r_S = 0.687$, $N = 14$, $P < 0.007$), suggesting that I accurately recorded patterns of decoration theft. Because the number of decorations that a male stole was uncorrelated with the number he collected from the environment (2003: $r_S = 0.073$, $N = 31$, $P < 0.695$; 2004: $r_S = -0.050$, $N = 34$, $P < 0.778$), it is unlikely that the patterns of decoration collection I observed were compromised by misclassification of stolen items.

Immediately upon conclusion of the experimental period (5–7 December 2004), I removed all decorations from bowers, returned the decorations that I had taken from males in mid-September, and arranged them in their initial locations (avenue, court, etc.) to the best extent possible.

Decoration Counts

On 15–16 October, 15–16 November and 5–7 December 2004, I counted all decorations at bowers, and I averaged the results to produce a single value for the numbers of decorations at bowers after decoration removal. Prior to decoration removal, I counted all decorations at bowers on 21–23 July and 12–15 September 2004, and I averaged these two counts to produce a single value for the numbers of decorations at bowers before decoration removal. Bowers were not regularly monitored for theft prior to decoration removal.

Ethical Note

This study was conducted with permission from Queensland Parks and Wildlife (WISP01994004), the University of California Institutional Animal Care and Use Committee (IACUC) (1101620), the Australian Bird and Bat Banding Scheme (2646), and the James Cook University Ethics Committee (A919). To minimize disturbance to the birds, I removed decorations from bowers during night-time hours (before 0500 hours and after 1830 hours), when males were not present. All males accepted the experimental decorations, and males were regularly observed maintaining their bowers, displaying to females and presenting experimental decorations to visitors during courtship. Eighty-eight per cent of banded males (28/32) returned to their bower sites the following breeding season, a return rate similar to that of other bowerbird species (90–93% return rate; Frith & Frith 2004) and not significantly different from the return rate of Townsville males during other breeding seasons (range 74–93% return rate; N. R. Doerr, unpublished data), suggesting the experimental manipulation did not interfere with the site fidelity or survivorship of males.

Collection and Availability of Decorations in the Environment

From 30 October to 3 November 2004, I conducted availability surveys at JC and LB to determine whether the numbers of decorations that males collected was influenced by their availability in the environment. I did not conduct surveys at AN because many transects were on private land that was unfortunately inaccessible. To conduct surveys, I followed the procedure of Madden & 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, etc.) from the bower. My procedure differed from Madden & Balmford's in two ways: I performed transects closer to the bower (beginning 5 m from the bower instead of 100 m), and I did not

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attempt to survey for organic items, such as leaves and fruit. Like satin bowerbirds (Wojcieszek et al. 2006), great bowerbirds seldom steal organic items (N. R. Doerr, unpublished data), and many organic items were located at the tops of tall trees, where I could not accurately count them. I compared the numbers of potential decorations found on transects with the numbers collected by males during the experiment; the hypothesis being that a positive correlation would suggest a relationship between the numbers of decorations collected and the numbers available.

Video Monitoring and Behavioural Observations

Because a male's involvement in decoration theft may be a function of other aspects of behaviour, such as time spent at the bower, I used motion-activated video cameras to monitor all activity at 14 of the experimental bowers from 14 September to 6 December 2004. Bowers that were monitored with cameras were located in areas where human interference with the equipment was unlikely to occur. An assistant visited bowers every other day to change tapes and batteries. When watching tapes, I recorded the number of displays and destructive events that occurred at each bower. I randomly chose 2 days during the breeding season to view additional behaviours at bowers: total time spent at the bower, total time spent displaying to another bird, total time spent displaying alone, and total time spent 'painting' the bower. The total time spent displaying was highly correlated with the number of displays (Spearman rank correlation: $r_s = 0.736$, $N = 14$, $P < 0.003$). Thus, I only considered the number of displays in the analysis because I recorded the number of displays for all days during the breeding season, while I recorded the time spent displaying for only 2 days.

Displays occurred when an individual arrived at the bower, and the bower owner performed stereotyped movements and vocalizations associated with courtship. Because great bowerbirds are monomorphic, I could not distinguish between displays performed to females and displays performed to other males. Solitary displays occurred when the bower owner performed courtship movements and vocalizations, but no other bird appeared to be present. Painting occurs when bower owners masticate grass stems or fruit and apply the chewed substance to the sticks of the bower structure (Bravery et al. 2006); painting rate is correlated with male mating success (Robson et al. 2005) and with male success as a decoration thief (Wojcieszek et al. 2007) in satin bowerbirds.

Statistical Analyses

I quantified male involvement in decoration theft by determining (1) the number of decorations that a male stole and (2) the number of decorations that were stolen from his own bower, and I converted both measures of stealing behaviour into rates (number stolen or stolen from/days monitored). Like other bowerbird species (Lenz 1994; Wojcieszek et al. 2007), great bowerbirds strongly prefer to steal particular decoration types. In 2003, red wire and green plastic were the only two decoration types stolen more frequently than expected by chance (N. R. Doerr, unpublished data). Thus, I only considered these two decoration types when comparing decoration numbers at bowers before and after standardization. However, when considering the relationships between stealing behaviours, male characteristics and the spatial arrangement of bowers, I calculated stealing rates based on the total number of decorations that a male stole and the total number of decorations stolen from each male; this provides the most detailed record of male involvement in marauding behaviours over the course of the experiment. The total number of decorations at bowers used in these analyses were average numbers quantified over a few days during the experiment: the total number before standardization was estimated using the average of two counts (21–23 July and 12–15 September 2004); the total number after standardization was estimated from the average of three counts (15–16 October, 15–16 November, 5–7 December 2004).

Because of the presence of outliers in the data on rates of stealing, being stolen from and collecting decorations, I primarily used nonparametric statistics in the analysis (Spearman rank correlations, Kendall rank partial correlations). Because I examined the relationship between decoration numbers and male stealing behaviours for two decoration types (red wire and green plastic), I used the false discovery rate (FDR) to correct for multiple tests of the same hypothesis (Benjamini & Hochberg 1995). To determine whether stealing behaviours were better explained by male characteristics (crest size and years of bower ownership) or the spatial arrangement of bowers (nearest-neighbour distance and bower density), I performed a stepwise multiple regression analysis. However, I only chose one spatial characteristic (nearest-neighbour distance) for the analysis because nearest-neighbour distance and bower density were highly correlated (Spearman rank correlation: $r_S = -0.719$, $N = 34$, $P < 0.0001$), and because nearest-neighbour distance had a stronger correlation with male stealing behaviours (see Table 1 below). For the regression analysis, I log-transformed the dependent variables to meet the assumptions of normality and heteroscedacity of the residuals. All tests were two tailed and were performed with SPSS for Windows version 11.5 (SPSS Inc., Chicago, IL, U.S.A.), except Kendall rank partial correlations, in which the significance of each *P* value was determined using published tables (Gibbons 1993).

RESULTS

Effect of Experimental Manipulation on the Distribution of Decorations across Bowers, and Its Relation to Male Stealing Behaviours

The average number of decorations at bowers before the experimental period was highly correlated with the average number at bowers during the experimental period for red wire

Table 1
Relationship between stealing behaviours, male characteristics and the spatial arrangement of bowers

	Rate of stealing	Rate stolen from	Years of ownership (*N*=25)	Crest length (*N*=30)	Nearest-neighbour distance	Bower density
Rate of stealing	—	0.159 (0.370)	0.343 (0.094)	0.205 (0.277)	−0.429 (0.011)	0.323 (0.062)
Rate stolen from		—	−0.493 (0.012)	−0.375 (0.041)	−0.681 (0.0001)	0.506 (0.002)
Years of ownership			—	0.352* (0.108)	0.102 (0.627)	0.000 (1.000)
Crest length				—	0.189 (0.318)	−0.150 (0.428)
Nearest-neighbour distance					—	−0.719 (0.0001)

Bower density = the number of bowers within a 1 km radius of the focal bower. Years of ownership = the minimum number of years that a male owned a bower. Rates are number of decorations/day. Cell values indicate Spearman's r_S; *P* values are in parentheses. $N = 34$ unless otherwise specified.
* $N = 22$.

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(Spearman rank correlation: $r_S = 0.725$, $N = 34$, $P < 0.0001$) and green plastic ($r_S = 0.711$, $N = 34$, $P < 0.0001$; both tests significant after FDR correction; Fig. 1).

There was no relationship between the number of decorations displayed at a male's bower before the experiment and the rate at which that male stole decorations during the experiment (Spearman rank correlation: red wire: $r_S = -0.005$, $N = 34$, $P = 0.976$; green plastic: $r_S = -0.088$, $N = 34$, $P = 0.620$). However, there was a negative correlation between the number of decorations displayed at a male's bower before the experiment and the rate at which decorations were stolen from that male's bower during the experiment (red wire: $r_S = -0.470$, $N = 34$, $P < 0.005$; green plastic: $r_S = -0.571$, $N = 34$, $P < 0.0001$; both tests significant after FDR correction; Fig. 2).

There was a positive correlation between the number of decorations displayed at a male's bower before the experiment and the rate at which that male collected decorations from the environment during the experiment (Spearman rank correlation: red wire: $r_S = 0.695$, $N = 34$, $P < 0.0001$; green plastic: $r_S = 0.800$, $N = 34$, $P < 0.0001$; both tests significant after FDR correction; Fig. 3). Collecting rate was not related to the rate at which males stole decorations (red wire: $r_S = 0.117$, $N = 34$, $P = 0.512$; green plastic: $r_S = -0.059$, $N = 34$, $P = 0.740$). Collecting rate was negatively correlated with the rate at which decorations were stolen from bowers for green plastic ($r_S = -0.445$, $N = 34$, $P < 0.008$) but not for red wire ($r_S = -0.061$, $N = 34$, $P = 0.731$). When controlling for collecting rate, the number of decorations present at a male's bower before the experiment was negatively correlated with the rate at which these decorations were stolen from that male's bower during the experiment (Kendall rank partial correlation: red wire: $\tau = -0.395$, $N = 34$, $P < 0.002$; green plastic: $\tau = -0.287$, $N = 34$, $P < 0.04$; both tests significant after FDR correction). When controlling for the rate at which decorations were stolen from bowers, the number of decorations present at a male's bower before the experiment was positively correlated with collecting rate (red wire: $\tau = 0.532$, $N = 34$, $P < 0.005$; green plastic: $\tau = 0.590$, $N = 34$, $P < 0.005$; both tests significant after FDR correction). The rate at which males collected decorations was unrelated to the availability of these decorations in the environment as determined by transect surveys (Spearman rank correlation: red wire: $r_S = 0.333$, $N = 20$, $P = 0.152$; green plastic: $r_S = -0.205$, $N = 20$, $P = 0.387$).

Relation between Stealing Behaviours, Male Characteristics and Spatial Arrangement of Bowers

The relationships between male stealing behaviours, male characteristics and the spatial arrangement of bowers are presented in Table 1. Male stealing behaviours were not significantly correlated with the weight, tarsus length, wing length or head/bill size of the bower owner (all $P > 0.09$). Collecting rate was not correlated with crest size ($r_S = 0.172$, $N = 30$, $P = 0.362$) or years of bower ownership ($r_S = -0.045$, $N = 25$, $P = 0.830$) when considering all the decorations that males collected from the environment. There was a nonsignificant tendency for both male characteristics to be correlated with collecting rate when only red wires and green plastic pieces were included in the sample (crest size: $r_S = 0.348$, $N = 30$, $P = 0.060$; years of ownership: $r_S = 0.381$, $N = 25$, $P = 0.060$). In general, both crest size and years of ownership were correlated with the numbers of red wires and green

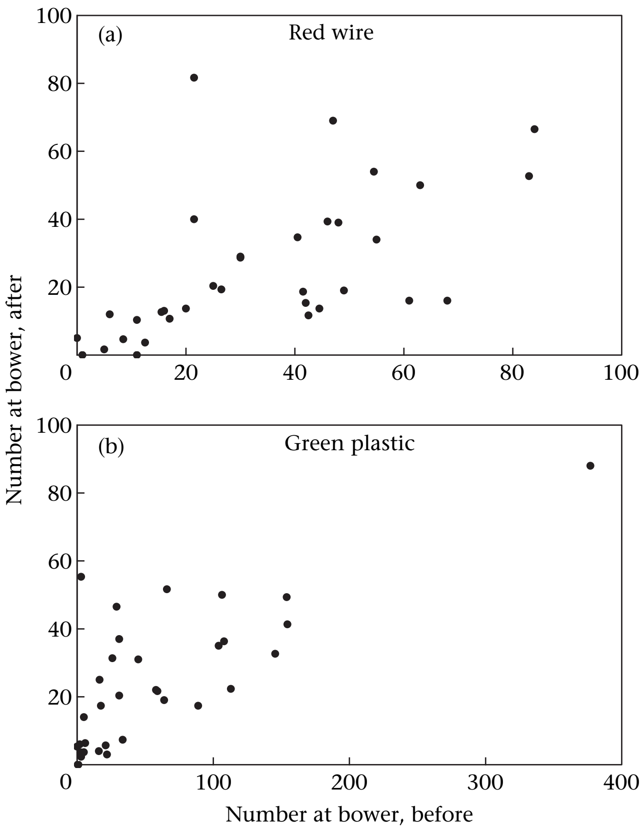

Figure 1. Relationship between the numbers of decorations at bowers before standardization (21 July–11 September) and after standardization (12 September–7 December) for (a) red wire and (b) green plastic.

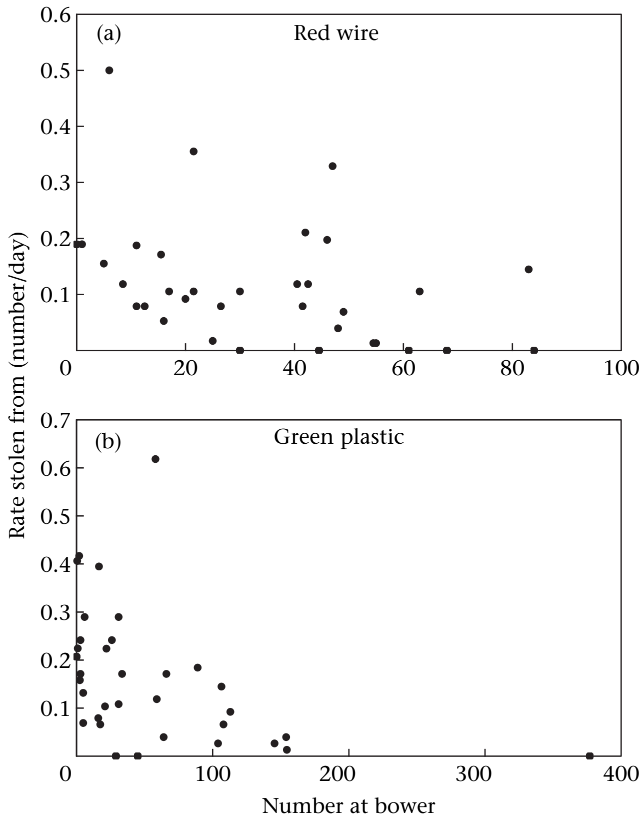

Figure 2. Relationship between the numbers of decorations at bowers before standardization and the rate at which decorations were stolen from bowers after standardization for (a) red wire and (b) green plastic.

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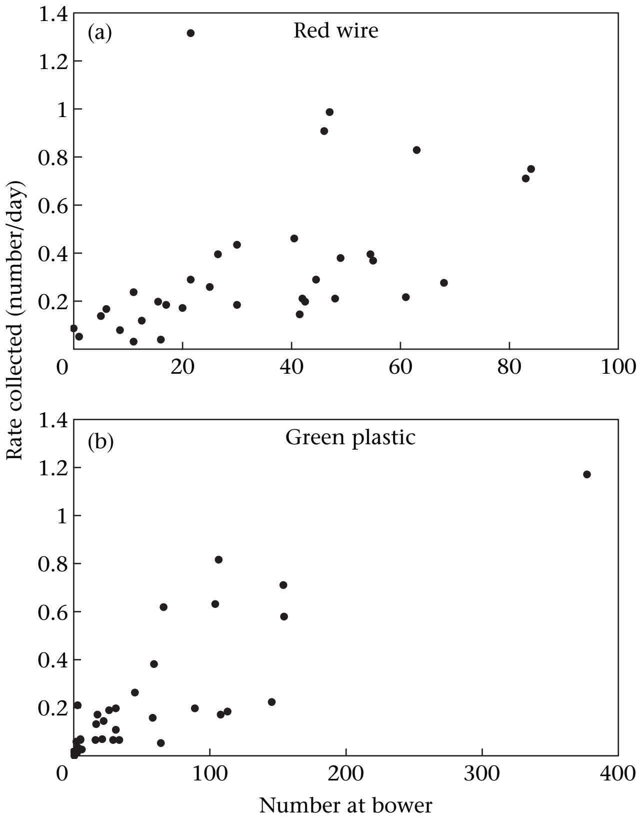

Figure 3. Relationship between the numbers of decorations at bowers before standardization and the rate at which males collected decorations from the environment after standardization for (a) red wire and (b) green plastic.

plastic pieces at bowers before and after the experiment (Table 2). A stepwise multiple regression analysis revealed that nearest-neighbour distance and years of bower ownership both predicted the rate at which decorations were stolen from bowers ($F_{2,19} = 18.066$, $r^2_{adj} = 0.631$, $P < 0.0001$), although nearest-neighbour distance explained more of the variation than did years of bower ownership (nearest-neighbour distance: $\beta_1 = -0.602$; years of bower ownership: $\beta_2 = -0.394$).

Stealing Behaviours and Other Behavioural Variables

There was a positive correlation between the rate at which decorations were stolen from a male's bower and the rate at which his bower was destroyed by other males (Spearman rank correlation: $r_S = 0.735$, $N = 14$, $P < 0.003$). There was no relationship between the rate at which decorations were stolen from bowers and any other behavioural variables: display rate, solitary display rate, painting rate, or time spent at the bower (all $P > 0.30$). None of the behavioural variables was related to the rate at which males stole decorations (all $P > 0.110$).

There was a strong negative correlation between years of bower ownership and the rate at which males displayed to other individuals (Spearman rank correlation: $r_S = -0.818$, $N = 14$, $P < 0.0001$) and the rate at which they displayed solitarily ($r_S = -0.843$, $P < 0.0001$; Fig. 4). The correlation between years of bower ownership and the total amount of time spent at the bower was not quite significant ($r_S = -0.502$, $P = 0.067$). There was no relationship between years of bower ownership and painting rate or destruction rate (both $P > 0.81$), or crest size and any of the behavioural variables (all $P > 0.17$).

Table 2
Relationship between crest size, years of bower ownership and the numbers of decorations at bowers before standardization (21 July–11 September) and after standardization (12 September–7 December)

	Crest size (N=30)		Years of ownership (N=25)	
Red wire, before	0.429	0.018*	0.531	0.006*
Red wire, after	0.442	0.014*	0.480	0.015*
Green plastic, before	0.252	0.178	0.629	0.001*
Green plastic, after	0.562	0.001*	0.520	0.008*

Cell values indicate Spearman's r_S and corresponding P values. *$P < 0.05$ after false discovery rate (FDR) correction.

DISCUSSION

Decoration Numbers and Male Collecting and Stealing Behaviours

My findings suggest that decoration numbers provide females with honest information about male quality in great bowerbirds. When I standardized decoration numbers at bowers such that all males had equal numbers, individual differences in the numbers of decorations at bowers re-emerged, and in a pattern that resembled the original distribution of decorations across bowers. There was a strong correlation between the average numbers of red wires and green plastic pieces at bowers before standardization and the average numbers at bowers during the 11 weeks after standardization. Honest signalling via decoration numbers has been suggested following previous studies of male–male competition in satin (Borgia & Gore 1986; Wojcieszek et al. 2007) and spotted bowerbirds (Madden 2002). However, my study is the first to

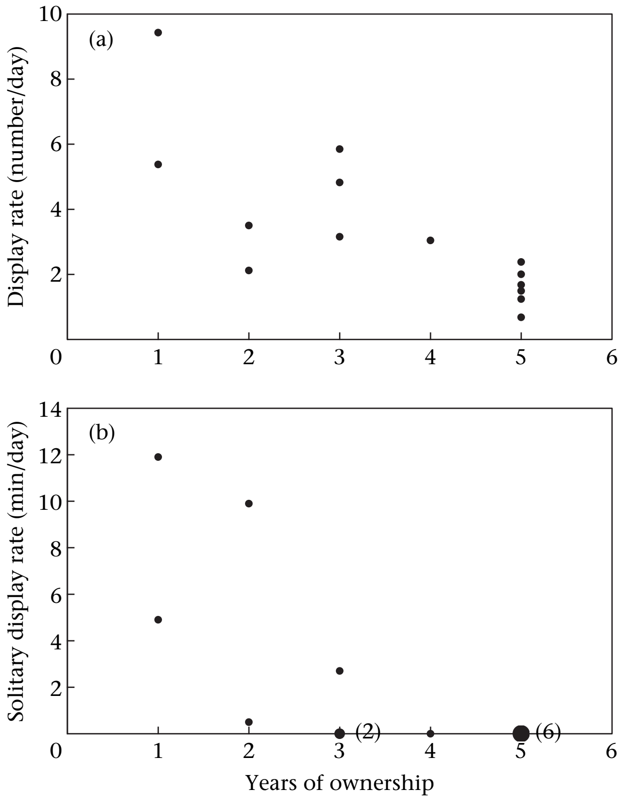

Figure 4. Relationship between years of bower ownership and (a) display rate and (b) solitary display rate. Years of ownership = the minimum number of years that each male had owned a bower. Identical data points are represented by dots of increasing size, and the number of identical data points is indicated to the right of each dot.

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demonstrate that consistent, individual differences in the numbers of decorations at bowers are related to two male behaviours: the ability to defend the bower against theft, and the ability to locate decorations in the environment. Males that had more red wires and green plastic pieces at their bowers before the experiment were less likely to have these decoration types stolen from their bowers during the experiment, and they were more likely to collect these decorations from the environment. Because collecting rate was unrelated to the number of decorations available within a 50 m radius of the bower, it is unlikely that collecting rate was a reflection of the numbers present in the male's surroundings. These results suggest that decoration numbers are an honest and repeatable signal of the male's success at bower defence and decoration search.

Alhough well-decorated bowers were indicative of the male's ability to defend his display site from rivals, they were not an accurate reflection of the male's ability to steal decorations. There was no relationship between the number of decorations displayed at a male's bower before standardization and the rate at which he stole decorations during the experiment. In addition, the rate at which a male stole decorations was not significantly correlated with nuchal crest length or years of bower ownership, but was significantly correlated with the distance to the nearest neighbour, suggesting that stealing ability may be more closely associated with the spatial arrangement of males than with male quality. Because paternity studies in satin bowerbirds demonstrate that females mate exclusively with bower-owning males (Reynolds et al. 2007), and males of most bowerbird species spend the majority of the day guarding the bower (Frith & Frith 2004), this could favour the evolution of mating signals that indicate the male's ability to retain control of a display site. Similar to studies in satin bowerbirds (Borgia 1985a), I found a positive correlation between the rate at which males experienced theft and the rate at which they experienced bower destruction, providing additional evidence that decoration numbers indicate male success at display site defence. Interestingly, male mating success in collared lizards, *Crotaphytus collaris*, is related to the male's ability to guard his territory against rivals, but not to his ability to 'steal' copulations from other territories (Husak et al. 2008), suggesting that the importance of display site defence is not restricted to bowerbirds.

Because previous studies of honest signalling in bowerbirds have focused on male–male competition (Borgia & Gore 1986; Madden 2002; Wojcieszek et al. 2007), the possibility that decoration numbers could indicate the male's success at decoration search has generally been overlooked. Madden & Balmford (2004) suggested that decoration acquisition is unlikely to lead to honest signalling in spotted bowerbirds because neither males nor females prefer decorations that are rare over those that are common. Although red wire and green plastic are not the rarest decorations in the environment, neither decoration is commonly available (N. R. Doerr, unpublished data), so acquiring large numbers may still pose a challenge to males. The ability to locate critical environmental resources may facilitate honest sexual signalling in bird and fish species that incorporate dietary carotenoid pigments into their colour patches (Endler 1980; Senar & Escobar 2002; Karino et al. 2007), and my results suggest that a similar mechanism could occur in bowerbirds.

Previous studies have shown that male satin bowerbirds that owned well-decorated bowers were more likely to experience decoration theft than males that owned poorly decorated bowers (Borgia & Gore 1986; Wojcieszek et al. 2007). These results are in contrast to mine, most likely because previous studies monitored theft under natural conditions, and decorations are not distributed equally among bowers under natural conditions. Because bowerbirds prefer to steal particular decoration types (Lenz 1994; Wojcieszek et al. 2006; N. R. Doerr, unpublished data), males that have many decorations may have more that are attractive to thieves (Borgia & Gore 1986), leading to increased theft of decorations from well-decorated bowers. In addition, thieves can steal up to eight decorations per visit from a victim's bower (Borgia & Gore 1986; N. R. Doerr, unpublished data), so males with well-decorated bowers have the potential to lose more decorations per visit than males with few decorations, leading to a higher apparent rate of theft from well-decorated bowers (Doerr 2009). Because I gave all males an identical set of decorations, I ensured that differences in theft rates were not primarily explained by differences in the availability of decorations at bowers. This experimental protocol may also explain why previous studies found a positive correlation between the numbers of decorations that a male stole and the numbers stolen from him (Borgia & Gore 1986; Wojcieszek et al. 2007), while my study found no relationship.

Similar to the current study, Wojcieszek et al. (2007) standardized the numbers of decorations at bowers of the satin bowerbird and found a positive correlation between the numbers of decorations at bowers before and after standardization. Although the authors did not determine whether this correlation was explained by the male's ability to steal, guard or collect decorations, they did find a nonsignificant tendency for males that naturally displayed large numbers of decorations to experience reduced theft after standardization than before standardization, and they suggested that these 'noncheater' males were more successful at defending their experimental decorations. However, these males also had fewer decorations at their bowers during the experimental treatment, so differences in the availability of decorations between treatments may also explain why they experienced reduced theft. Prior to the experiment, the three noncheaters had a mean $\pm$ SD of approximately 20 ± 6 rosella feathers at their bowers, but each male received only one feather during standardization (Wojcieszek et al. 2007). Because thieves can steal eight feathers per visit (Borgia & Gore 1986), and males prefer to steal feathers over other types of decoration (Borgia & Gore 1986; Wojcieszek et al. 2006), a given bower is likely to lose fewer decorations when it contains one feather than when it contains 20. None the less, these results are consistent with the possibility that decoration numbers indicate the male's ability to defend his display site from rivals.

Stealing Behaviours, Male Characteristics and the Spatial Arrangement of Bowers

The male's ability to prevent theft from his bower was related to two male characteristics that may be of interest to females: nuchal crest length and years of bower ownership. Nuchal crest length is associated with blood testosterone levels (L. Day, unpublished data) and male age (Frith & Frith 2004; K. Eguchi, Y. Yamaguchi, I. Nishiumi, H. Koike & R. Noske, unpublished data). Years of bower ownership is a reflection of male age and experience, and anecdotal evidence suggests that older, more experienced males may be better at defending their bowers (Vellenga 1970; Borgia & Gore 1986). Because these characteristics were also associated with the numbers of red wires and green plastic pieces at bowers, both before and after the manipulation, it is possible that females obtain information about male age or hormonal status by comparing the numbers of decorations at different bowers. Although there was no relationship between crest length, years of bower ownership and collecting rate when considering all the decorations that males collected from the environment, both male characteristics tended to be correlated with collecting rate when only red wires and green plastic pieces were included in the sample (both $P = 0.060$). Thus, both bower defence and decoration search could facilitate the production of honest signals of age and experience. Honest sexual

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signalling in red junglefowl, *Gallus gallus*, and three-spined sticklebacks, *Gasterosteus aculeatus*, may also be influenced by a combination of social and environmental factors (Candolin 2000; Parker & Ligon 2007).

Although males that were unsuccessful at guarding their decorations may have spent less time at their bowers (Morrell & Kokko 2004; Wojcieszek et al. 2007), I did not find support for this possibility. Guarding against decoration theft was unrelated to the amount of time that a male spent at his bower, and there was a nonsignificant tendency ($P < 0.067$) for inexperienced males to spend more time at their bowers than experienced males. Inexperienced males also spent more time displaying, and most displays appeared to be performed to other males; the visitor would alternate between watching the display and manipulating the owner's bower decorations. I was able to confirm that some visitors were male when I saw their colour bands. Some were neighbouring bower owners and others appeared to be younger individuals (based on the degree of speckling on their flanks and their small nuchal crests) that did not own bowers (N. R. Doerr, unpublished data). These results are consistent with the observation that inexperienced males were less successful at guarding their decorations; these males appeared to have difficulty keeping other males, both bower owners and nonbower owners, away from their display sites.

Because male bowerbirds do not provide parental care, it is possible that a female preference for well-decorated bowers results in indirect fitness benefits for her offspring (Borgia et al. 1985). Age-related indicator models suggest that a female preference for older males can result in 'good genes' benefits for her offspring under a number of scenarios (Kokko 1998), and the relationships I observed between decoration numbers, nuchal crest length and years of bower ownership suggest a role for male age. It is also possible that females obtain direct benefits from their mate choice. Inexperienced males were either unwilling or unable to keep other males away from their bowers, so females that mate with inexperienced males could increase their risk of courtship disruption. Courtship disruption has been identified as a cost of mate choice for female satin bowerbirds (Uy et al. 2000), and it reduces female fecundity by delaying nesting in some avian species (Foster 1983). Although courtship disruption is rare in great bowerbirds, it sometimes leads to fights involving the female (N. R. Doerr, unpublished data).

Interestingly, my results suggest that some aspects of decoration theft may be independent of male quality. A stepwise multiple regression analysis revealed that nearest-neighbour distance explained more of the variation in the rate at which decorations were stolen from bowers than did years of bower ownership, although both variables entered the model. Thus, males were more successful at guarding their decorations when their bowers were relatively isolated from others and when their neighbours were competitively inferior. Previous studies have also found a relationship between the frequency of decoration theft and the distance between neighbouring bowers (Borgia & Gore 1986; Madden et al. 2004; Wojcieszek et al. 2007). Because males primarily steal from their near neighbours (Doerr 2009), decoration numbers may indicate a male's quality in relation to one or a few of his neighbours, rather than his overall 'rank' in the population. Females only visit the bowers of a few neighbouring males before selecting one male as a mate (Uy et al. 2000), so they may still gain reliable information about the quality of the males sampled.

In summary, decoration numbers at bowers of the great bowerbird reveal the male's success at preventing decoration theft at his bower, which in turn may indicate male age or experience to females and rival males. Because possession of a territory or display site is a prerequisite to mating in many animal species, it is perhaps not surprising that decoration numbers reflect the male's success at bower defence, although decoration numbers may also be an honest signal of the male's ability to locate resources in the environment. A number of species collect and steal nonbodily ornaments to attract females, including three-spined sticklebacks (Östlund-Nilsson & Holmlund 2003), Lawe's parotia, *Parotia lawesii* (Pruett-Jones & Pruett-Jones 1988), and a Lake Tanganyika cichlid, *Lamprologus callipterus* (Maan & Taborsky 2008), so there may be a general relationship between theft of resources, signal size and male success in defending display sites. In addition, the development of sexually selected traits in many animal species is dependent on access to environmental resources, and repertoire size in songbirds (Nowicki et al. 1998), carotenoid colour patch development in birds and fish (Endler 1980; Hill 1991) and drumming rate in wolf spiders (Kotiaho 2000) are all reflective of the signaller's nutritional background. My results highlight the importance of documenting the processes that males undergo to acquire and retain critical resources, and demonstrate that the male's ability to bear the social costs of resource defence and the environmental costs of resource acquisition can produce honest sexual signals in great bowerbirds.

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