

Stealing rates in the Great Bowerbird (*Ptilonorhynchus nuchalis*): effects of the spatial arrangement of males and availability of decorations

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Abstract. Competitive interactions between males can affect mate-choice decisions of females, so it is important to understand the factors that underlie variation in the frequency and intensity of male–male interactions. In bowerbirds (Ptilonorhynchidae), two hypotheses have been proposed to explain within- and between-species variation in the rate at which males steal each other's decorations. Males may steal more frequently as inter-bower distances decrease because this reduces the time and energy costs of travelling between bowers, or they may steal more frequently when bowers contain relatively few decorations, compared with bowers in other populations or species, because this leads to an increase in the value of decorations to males. I compared stealing rates in two populations of Great Bowerbirds (*Ptilonorhynchus nuchalis*) in Queensland, Australia, in order to assess these hypotheses. Males at one site, Dreghorn, had fewer decorations, higher nearest-neighbour distances (NND), and fewer males within a 1-km radius of their bowers (termed bower density) than males at the Townsville site. Dreghorn males stole decorations at a lower rate and interacted with fewer individuals, though there was no difference between sites in the rate at which males stole decorations from their nearest neighbours. Within sites, stealing rates were not related to decoration numbers, and partial correlations revealed that stealing rates were correlated with bower density, not NND. These results suggest that differences in the spatial arrangement of males, particularly bower density, may explain variation in stealing rates both within and between populations, though alternative explanations, such as differences in resource availability, are also relevant.

Introduction

In many species, the evolution of sexually selected traits has been influenced by both male–male competition and female choice (Berglund *et al.* 1996), and the interactions between these two mechanisms have been the focus of recent study. Male–male competition appears to facilitate accurate mate assessment in some species (Candolin 2000), but competing males may limit a female's ability to mate with preferred males in others (Howard *et al.* 1997; Wong and Candolin 2005). In either scenario, male–male competition has substantial fitness consequences for both sexes, so it is important to understand the factors that underlie variation in the frequency and intensity of male–male interactions.

Bowerbirds (Ptilonorhynchidae) are an ideal system for studies examining within- and between-species variation in male–male competition, and its consequences for female choice. Males of most bowerbird species build and decorate stick structures, called bowers, to attract the females with whom they mate. Males are also highly competitive: they steal each other's decorations and destroy each other's bowers (Marshall 1954; Borgia and Gore 1986). Because males interfere with one another's displays, male–male competition may affect the degree of honesty of the signals assessed by females (Borgia *et al.* 1985; Madden 2002; Wojcieszek *et al.* 2007). In Satin Bowerbirds (*Ptilonorhynchus violaceus*), females

prefer to mate with males that have high numbers of blue rosella (Psittaciformes: Psittacidae) feathers at their bowers (Borgia 1985a; but see Robson *et al.* 2005), and males prefer to steal these decorations from their rivals rather than other types of decoration (Wojcieszek *et al.* 2006). If male quality is correlated with stealing ability, then individual differences in the numbers of decorations at bowers, brought about by differences in male stealing behaviours, may allow females to identify high-quality mates. Though theoretical models suggest that decoration theft and bower destruction are evolutionarily stable strategies in comparison with the alternative strategy of bower guarding (Pruett-Jones and Pruett-Jones 1994), the frequency of decoration theft appears to be highly variable both within and among species (Borgia and Gore 1986; Borgia and Mueller 1992; Hunter and Dwyer 1997; reviewed in Frith and Frith 2004), and this may affect the relationship between male–male competition and signal honesty (Borgia and Mueller 1992).

To date, two hypotheses have been proposed to explain within- and between-species variation in stealing rates. First, differences in stealing rates may be explained by differences in the spatial arrangement of males (Borgia and Gore 1986; Borgia and Mueller 1992). As inter-bower distances decrease, males may interact more frequently because the time and energy costs of travelling between bowers are reduced. An examination of rates

of theft across species generally supports this hypothesis (Borgia and Mueller 1992; Lenz 1994) and several studies have shown that males are more likely to interact with their near neighbours than with any other males in the population (Borgia and Gore 1986; Lenz 1994; Wojcieszek *et al.* 2007). However, only one study has tested this hypothesis by comparing two populations of the same species, and males interacted more frequently in the population that had greater inter-bower distances (Madden 2006).

Variation in stealing rates could also be explained by differences in the value of decorations to males. In populations or species with large numbers of decorations, stealing rates may be lower than in populations or species with small numbers of decorations because the relative contribution of each decoration towards male mating success is reduced when males already have large numbers at their bowers (Hunter and Dwyer 1997). A study testing this hypothesis in two populations of Satin Bowerbirds found that males stole decorations more frequently in the population that contained fewer decorations (Hunter and Dwyer 1997). Likewise, males of a Lake Tanganyika cichlid (*Lamprologus callipterus*) collect snail shells to attract females, and they are less likely to steal each other's shells when these items are abundantly available (Maan and Taborsky 2008). Unfortunately, bowerbird species that have large inter-bower distances also tend to have more decorations at their bowers (Hunter and Dwyer 1997), so it is difficult to use cross-species comparisons to evaluate the relative merit of each hypothesis.

In this study, I compared stealing rates within and between two populations of Great Bowerbirds (*Ptilonorhynchus nuchalis*) in Queensland, Australia, in order to assess whether male–male competition was influenced by the spatial arrangement of males or availability of decorations, or both. Though decoration theft has been recorded in Great Bowerbirds (Borgia 1995), my results provide the first detailed description of stealing behaviour in this species.

Methods

Study species

Great Bowerbirds occur throughout northern Australia and decorate their bowers with a variety of colourful objects, including stones, bones, man-made objects, fruit and leaves. They typically build bowers in June or July, and peak breeding occurs between September and December (Frith *et al.* 1996; N. R. Doerr, pers. obs.).

Study site and search for bowers

Both populations were in northern Queensland, Australia: one in Townsville City (19°19'S, 146°46'E) and the other at Dreghorn Station (20°15'S, 146°42'E) (Fig. 1). Townsville is a mixture of man-made gardens and eucalypt woodland. Bowders were located at James Cook University, the Lavarack Barracks military base, and the suburb of Annandale. Dreghorn Station is a cattle property bordering the Burdekin River. Bowders were located along Six Mile Creek, a dry creek running past the homestead buildings, and along the Burdekin River, which flows year-round. Though the habitat is open eucalypt woodland, the banks of the creek and river are vegetated with many species of fig (*Ficus* spp.), Burdekin Plum (*Pleignium timorense*) and the introduced

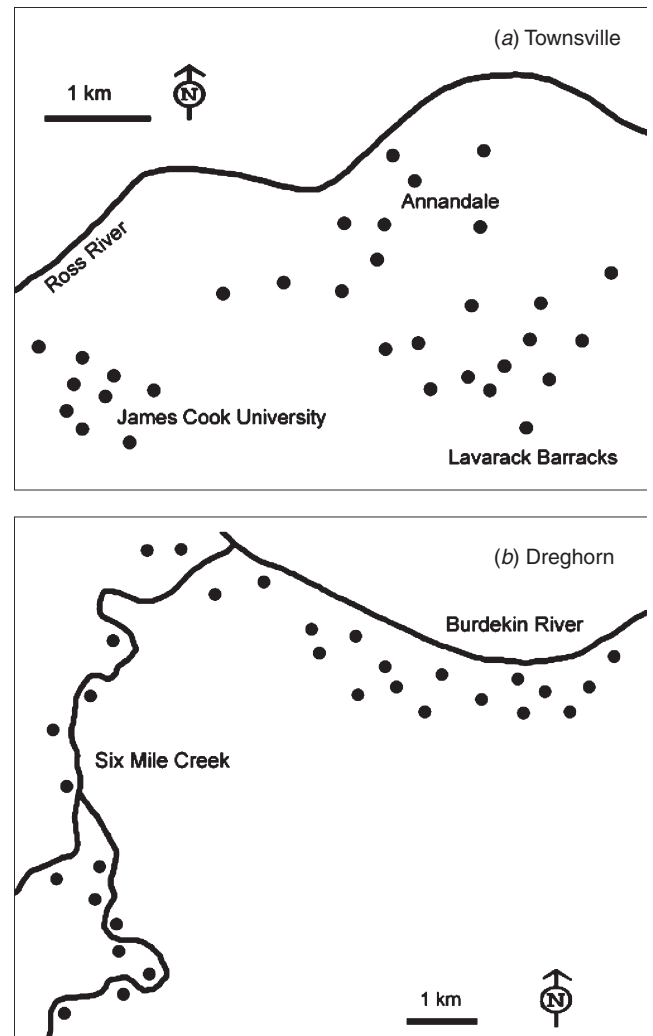


Fig. 1. Map of Townsville (a) and Dreghorn Station (b) study sites. Each bower is indicated by a closed circle.

Chinese Apple (*Ziziphus mauritiana*). Bowerbirds regularly ate fruit from these trees, which may explain why bowders in this population were concentrated along the river and creek, as observed in other populations of this species (Frith and Frith 2004). In Townsville, food, water, and bowders appeared to be more evenly distributed across the landscape (N. R. Doerr, unpubl. data).

I monitored 32 simultaneously active bowders in Townsville from 5 August to 6 December 2003, and 31 simultaneously active bowders at Dreghorn from 3 August to 6 December 2006. Most males in Townsville were colour-banded (27 out of 32), but only two males at Dreghorn were banded. Previous studies have shown that bowders are maintained by a single male during the breeding season, except in the case of rudimentary bowders (Frith and Frith 2004), which are temporary structures that are poorly built and contain few, if any, decorations; these structures are owned by one or more immature males (Vellenga 1970; Maxwell *et al.* 2004). Because I did not include rudimentary bowders in this study, it is likely that bowders at Dreghorn were attended by a single male for

the duration of the study. Bower structures did not differ in any measures of size or symmetry between sites (Doerr 2008).

Great Bowerbirds have been continuously monitored in the Townsville area since 2000, providing information on the location of bowers at James Cook University and Lavarack Barracks. However, 2003 was the first year that males were monitored in Annandale, so I spent over 80 h searching for bowers at this location. I located bowers by listening for male advertisement calls, which allowed me to locate bowers in fenced yards, where they would not otherwise have been detected. In 2004, I located two additional bowers in Annandale, so some Townsville males may have interacted with individuals that I did not monitor. This problem may also have occurred at Dreghorn. Because 2006 was the first year that bowers were monitored at Dreghorn, I spent over 150 h searching for bowers at this site. This does not include the time I spent walking between bowers during monitoring sessions; whenever I thought I heard an advertisement call from a new location, I always searched for the source of the sound. Unlike Townsville, I did not locate any additional bowers at Dreghorn the following breeding season (2007).

Theft monitoring schedule

At both sites, I used a black, waterproof marker to label decorations with a unique symbol signifying the bower where they were located. Bower decorations that could be marked with a pen included natural objects, such as rocks, bones, snail shells, fruit and leaves, as well as man-made objects, such as glass, metal and plastic. Bower decorations that could not be reliably marked were chalk, charcoal and most pieces of animal dung. Decorations that could not be marked accounted for only a small proportion of decorations at bowers (at Townsville, $3 \pm 10\%$ s.d. of decorations; at Dreghorn, $3 \pm 7\%$; Mann–Whitney U test = 510, $P < 0.847$). Every 10–14 days, I visited bowers to record the numbers of stolen decorations and the numbers of new decorations collected from the environment. When I located a stolen decoration, I added the thief's symbol to the decoration. I assumed that decorations without marks were collected from the environment, though it is possible that some were stolen from bowers that I did not monitor. In addition to monitoring bowers for theft, I counted all decorations at bowers at least twice and averaged the results (mean no. of decoration counts: Townsville = 2.6 ± 0.5 s.d., Dreghorn = 2.5 ± 0.6).

Most researchers studying theft of decorations in bowerbirds have visited bowers on a daily basis to monitor theft (Borgia and Gore 1986; Lenz 1994; Wojcieszek *et al.* 2006). I chose not to visit bowers on a daily basis because I was concerned this would cause excessive disturbance to the birds. Averaging across sites, bowers contained a mean (\pm s.d.) of 837 ± 530 decorations, and it took 30–60 min to look through all decorations at each bower. Because I did not visit bowers daily, my estimates of theft are likely to be conservative: I may have failed to record some incidents of theft while absent from bowers. However, males often steal more than one decoration per visit to the victim's bower, so my estimates of theft probably exceed the number of visits in which males stole decorations. Because the monitoring schedule was similar between sites, this should not affect my comparison of stealing rates between the populations. I incorporated males into the monitoring schedule as I located

their bowers, so I calculated the stealing rate for each male by dividing the total number of decorations he stole with the number of days that he had been monitored.

From 5 November to 6 December 2006, I used 14 Dreghorn bowers in an experiment assessing the effects of decoration supplementation on destructive events at bowers (Doerr 2008). During this experiment, I supplemented each of the 14 males with an additional 143 decorations: 125 were red wires, and 18 were red rings, similar in size and shape to the plastic milk tops found at bowers. Both decoration types were frequently stolen by Townsville males in 2003 (N. R. Doerr, unpubl. data). If any of these decorations were stolen from Dreghorn bowers, I returned them to their original owners within two days. Thus, these 14 bowers had a different monitoring schedule during November than the other Dreghorn bowers or the Townsville bowers, which could have led to a higher apparent rate of theft at experimental bowers because the increased monitoring effort may have allowed me to observe stealing and re-stealing events that the more spread-out monitoring schedule would have missed. When comparing stealing rates between sites, I analysed the data with and without the experimental decorations. Including the experimental decorations never altered the significance of the results, and I present both values where relevant. In addition, I used these data to examine whether supplementation affected stealing rates.

I used a handheld GPS unit (Garmin eTrex Vista, Kansas, USA) to determine the location of each bower (accuracy ± 5.1 m), and I calculated the distance between each bower and its nearest neighbour. To quantify bower density, I determined the number of bowers within a 1-km radius of each bower. This value was highly correlated with the average distance between a male and his five nearest neighbours ($r_s = -0.918$, $P < 0.0001$, $n = 63$), an estimate of bower density used in previous studies (Borgia 1985b; Borgia and Gore 1986). Finally, I used an index of dispersion (R) based on Clark and Evans (1954) to examine the spacing of bowers across the study areas. The index of dispersion is a ratio that compares the mean distance to the nearest neighbour observed in the study population with the mean distance to the nearest neighbour expected if individuals were distributed randomly in space. An R value < 1 indicates a clumped distribution, $R = 1$ indicates a random distribution, and $R > 1$ indicates an evenly spaced distribution.

Statistical analysis

When examining the spatial dispersion of bowers, I used a Z test to determine the significance of each R value (Clark and Evans 1954). To test whether the two populations showed different patterns of spatial dispersion, I calculated the variance ratio, F , using formulae described in Clark and Evans (1954), and consulted a table of the F distribution to determine the significance of this value, where the between-group variance was the number of populations minus 1, and the within-group variance was the sum of the sample sizes from both populations minus 2 (Clark and Evans 1954).

For all other analyses, I used non-parametric statistics (Mann–Whitney U test, Kendall's rank partial correlation, Spearman rank correlation corrected for ties) because several distributions were skewed, particularly the rate at which males

stole decorations. All tests were performed with SPSS for Windows version 11.5 (SPSS Inc. 2002), except Kendall's rank partial correlations, in which the significance of each P value was determined using published tables (Gibbons 1993). All tests are two-tailed, and means are \pm s.d.

Results

Inter-bower distances, dispersion, and mean numbers of decorations

The nearest-neighbour distance (NND) was lower, and bower density was higher, in Townsville than at Dreghorn (Table 1). Townsville males had more decorations than Dreghorn males, even when rock, the most common decoration type, was excluded (Table 1).

The dispersion index was 1.49 in Townsville and 1.37 at Dreghorn, indicating that the distance between each bower and its nearest neighbour was more uniform than expected by chance (Townsville: $Z=5.28$, $P<0.0001$; Dreghorn: $Z=3.90$, $P<0.0001$). Dreghorn bowers were not more evenly spaced than Townsville bowers ($F_{1,61}=0.173$, $P<0.5$).

Stealing rates

Over the course of the study, 30 of 32 Townsville males stole at least one decoration, and I recorded 950 incidents of theft at this site. At Dreghorn, 27 of 31 males stole at least one decoration, and I recorded 393 incidents of theft at this site, plus an additional 157 that occurred during the experiment. At both sites, males primarily stole snail shells and man-made objects, whereas rocks and bones were infrequently stolen.

The rate at which males stole decorations was higher in Townsville than it was at Dreghorn, and Townsville males stole decorations from a greater number of individuals (Table 1). When the experimental decorations were included in the Dreghorn sample, the stealing rate was still higher in Townsville, though less so (Table 1). There was no difference between sites in the rate at which males stole decorations from their nearest neighbours (Table 1), even when the experimental decorations were included ($P>0.5$). The 14 Dreghorn males included in the experiment stole decorations at a higher rate during the experiment (0.54 ± 0.59) than under natural conditions (0.17 ± 0.15) (Wilcoxon signed

rank, $z=-2.903$, $P<0.004$), though this result could have occurred because I sampled bowers more frequently during supplementation.

Among all the decorations they stole, Townsville males stole a lower percentage from their nearest neighbours than Dreghorn males, and they also stole a lower percentage from their five nearest neighbours (Table 1). Combining sites, males stole fewer decorations from their nearest neighbour than they stole from all other males in the population combined (Sign test, $P<0.045$, $n=56$). However, males stole more decorations from their five nearest neighbours than they stole from all other males in the population combined (Sign test, $P<0.0001$, $n=57$).

Within study sites, there was a negative correlation between NND and rates of theft in Townsville ($r_s=-0.391$, $P<0.027$, $n=32$) but not at Dreghorn ($r_s=-0.226$, $P<0.223$, $n=31$; Fig. 2a, b). There was a positive correlation between bower density and rates of theft in Townsville ($r_s=0.525$, $P<0.002$, $n=32$) and at Dreghorn ($r_s=0.392$, $P<0.029$, $n=31$; Fig. 2c, d). In Townsville, stealing rates were correlated with bower density when controlling for NND (Kendall's rank partial correlation, $T=0.348$, $P<0.01$), but they were not correlated with NND when controlling for bower density ($T=-0.132$, $P>0.20$).

Males that had more neighbours within a 1-km radius of their bowers stole decorations from a greater number of bowers (Townsville: $r_s=0.414$, $P<0.020$, $n=32$; Dreghorn: $r_s=0.504$, $P<0.005$, $n=31$; Fig. 3). There was no relationship between the number of decorations that males stole and the mean number of decorations at their bowers (Townsville: $r_s=0.090$, $P<0.623$, $n=32$; Dreghorn: $r_s=-0.137$, $P<0.462$, $n=31$).

Other inter-population comparisons

Townsville males collected decorations from the environment at a higher rate than Dreghorn males (Townsville: 4.7 ± 1.7 decorations per day, Dreghorn: 1.1 ± 0.7 decorations per day, Mann-Whitney U test = 950, $P<0.0001$, $n=62$).

Discussion

Stealing rates and the spatial arrangement of males

My results support the hypothesis that the spatial arrangement of males influences the frequency of decoration theft in bowerbirds

Table 1. Site characteristics and stealing rates at Dreghorn Station and Townsville study sites

All means are \pm s.d.

| | Dreghorn ($n=31$) | Townsville ($n=32$) | U | P |
|---|---------------------|-----------------------|-------|--------|
| Nearest-neighbour distance (m) | 557 \pm 157 | 382 \pm 144 | 808 | 0.0001 |
| Bower density ^A | 3.2 \pm 1.5 | 7.1 \pm 2.2 | 910 | 0.0001 |
| Total decorations | 575 \pm 284 | 1090 \pm 591 | 765 | 0.0001 |
| Total decorations, excluding rock ^B | 236 \pm 159 | 597 \pm 361 | 832 | 0.0001 |
| Stealing rate (no. of decorations per day) | 0.15 \pm 0.15 | 0.38 \pm 0.34 | 728 | 0.001 |
| Stealing rate (no. of decorations per day) with experimental decorations ^C | 0.21 \pm 0.26 | 0.38 \pm 0.34 | 673.5 | 0.015 |
| Stealing rate (no. of decorations per day) from nearest neighbour only | 0.07 \pm 0.07 | 0.12 \pm 0.13 | 581 | 0.239 |
| Number of bowers from which decorations stolen | 2.5 \pm 1.8 | 4.9 \pm 2.5 | 771 | 0.0001 |
| Percent stolen from nearest neighbour ^D | 52 \pm 35 | 32 \pm 28 | 540 | 0.030 |
| Percent stolen from five nearest neighbours ^D | 98 \pm 4 | 82 \pm 23 | 648.5 | 0.0001 |

^ABower density is the number of bowers within a 1-km radius of the focal bower.

^BRocks were the most numerous type of decoration at bowers.

^CA subset of Dreghorn bowers were supplemented with decorations during part of the breeding season.

^DOnly males that stole at least one decoration were included in the sample (Dreghorn: $n=27$, Townsville: $n=30$).

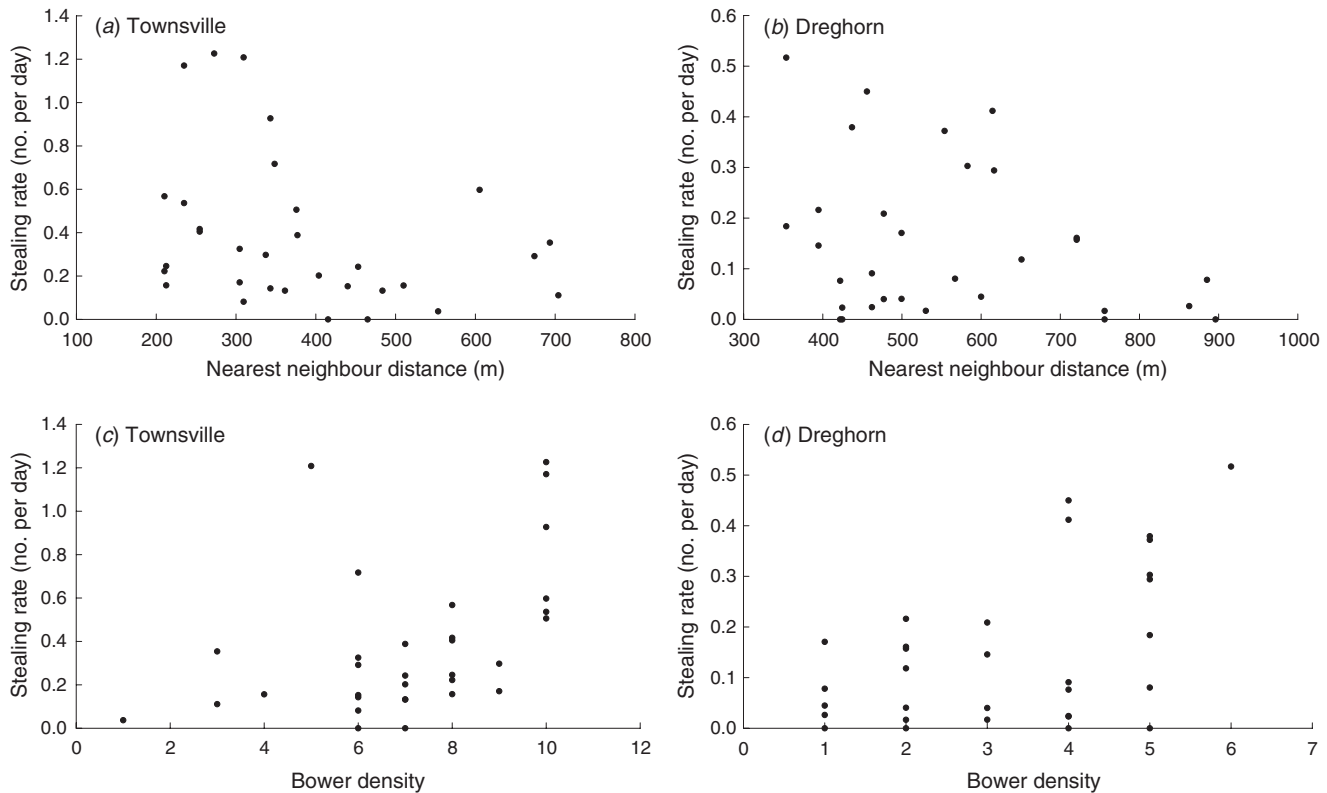


Fig. 2. The relationship between stealing rates and the distance to the nearest neighbour (*a–b*) at Townsville (*a*) and Dregghorn (*b*) study sites; and relationship between stealing rates and bower density (*c–d*) at Townsville (*c*) and Dregghorn (*d*). Bower density is the number of bowers within a 1-km radius of the focal bower.

(Borgia and Gore 1986; Lenz 1994). The number of males within a 1-km radius of the bower, termed ‘bower density,’ was the best predictor of stealing rates both within and between two populations of Great Bowerbirds. In Townsville, stealing rates were positively correlated with bower density and negatively correlated with NND, similar to results obtained in Satin Bowerbirds (Borgia and Gore 1986). However, partial correlations revealed that stealing rates were only correlated with bower density, not NND. Likewise, stealing rates were only correlated with bower density at Dregghorn.

Bower density also appeared to play a more important role than mean NND when considering differences in stealing rates between sites. Though the mean NND was lower – and the overall rate of theft was higher – in Townsville than at Dregghorn, there was no difference between sites in the rate at which males stole decorations from their nearest neighbours, perhaps because mean NND only differed by 175 m between sites. Instead, Townsville males had more than twice as many neighbours within a 1-km radius of their bowers, and they stole decorations from more than twice as many individuals. If there are fixed costs to flying a certain distance, this may have allowed Townsville males to steal more decorations and interact with a greater number of individuals than Dregghorn males. Differences in bower density could also explain why Dregghorn males stole a higher percentage of decorations from their nearest neighbour, and their five nearest neighbours, than Townsville males. Dregghorn males had fewer neighbours within a given radius of their bowers, so the cost of flying to more distant neighbours may have been higher at this

site, leading Dregghorn males to target their nearest neighbours more frequently than Townsville males did. Within sites, males that had more neighbours within a 1-km radius of their bowers stole decorations from a greater number of individuals, further supporting the relationship between male–male competition and bower density.

This is the first study to demonstrate that differences in the spatial arrangement of males may explain inter-population variation in stealing rates. High bower density could increase stealing rates for several reasons in addition to those discussed above. Males that are surrounded by many neighbours may be able to combine foraging and stealing activities into a single trip away from their bowers. Because theft of decorations often occurs in the victim’s absence from its bower (Borgia and Gore 1986), the presence of multiple neighbours may increase the probability that at least one of these individuals will be on a stealing trip while the victim is away from its bower. Indeed, some species have evolved behaviours, such as food caching, that may reduce the occurrence of decoration theft by allowing males to remain at their bowers for longer periods (Pruett-Jones and Pruett-Jones 1985).

Though my results support a role for bower density, I only obtained data from two populations, and several uncontrolled variables could also explain differences in stealing rates between sites, the most obvious of which is climatic changes over time. Because populations were sampled in different years, Townsville and Dregghorn males may have experienced different weather conditions. Studies suggest that males are less attentive to their bowers during drought years when the availability of fruit is low

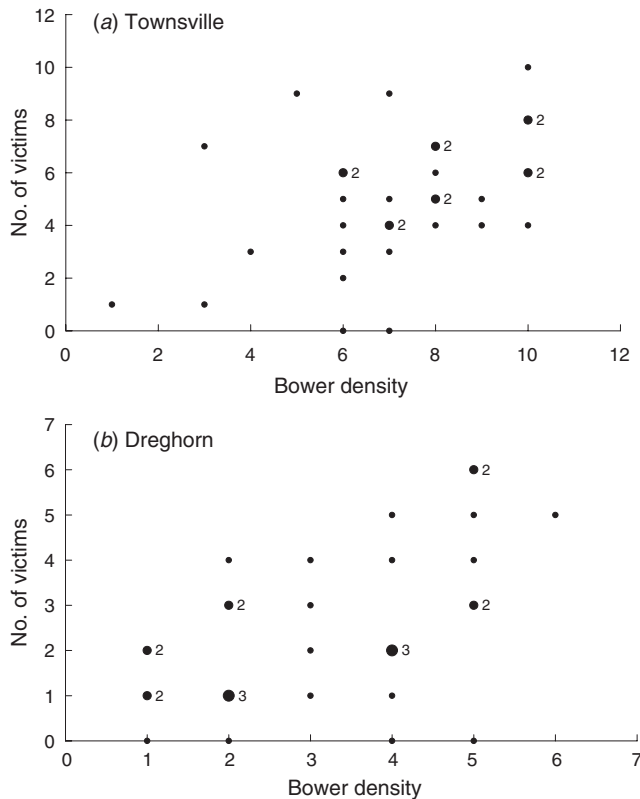


Fig. 3. The relationship between bower density and the number of bowers from which a male steals at Townsville (a) and Dreghorn (b) study sites. Bower density is the number of bowers within a 1-km radius of the focal bower. Identical data points are represented by dots of increasing size, and the number of identical data points is indicated to the right of each dot.

(Frith and Frith 2004). However, the results of the decoration supplementation experiment that I conducted at Dreghorn during November 2006 also occurred in a separate experiment conducted in Townsville during October 2006 (N. R. Doerr, unpubl. data), and stealing rates were still higher in Townsville (Doerr 2008). This reduces the likelihood that between-year differences in climatic conditions explain the results. Nonetheless, the study sites may have differed in the availability of critical resources. Townsville is a suburban environment where food, water and bower decorations may have been more abundant. If Townsville males were in better condition, or required less time and energy to meet their daily foraging needs, they may have been able to increase their investment in male–male competition relative to Dreghorn males. If resource availability and bower density tend to be correlated, experimental studies in which males are provided with supplementary food and water may be needed to tease apart the relationship between stealing rates, availability of resources and bower density. Because my sample size was so small ($n = 2$ sites), a comparison of stealing rates across a larger number of sites may produce a more consistent picture of the factors influencing stealing rates.

Stealing rates and availability of decorations

A different hypothesis suggests that stealing rates should be higher in populations or species with lower numbers of

decorations (Hunter and Dwyer 1997). According to this hypothesis, the relative contribution of each decoration towards male mating success is reduced in populations with large numbers of decorations, and this decreases the value of decorations to thieving males. However, I did not find support for this hypothesis. Dreghorn males had fewer decorations at their bowers than Townsville males, yet they stole decorations at a lower rate. Because Townsville males tended to spend more time at their bowers than Dreghorn males in a related study (Doerr 2008), it is unlikely that the higher stealing rates in Townsville were explained by differences in the amount of time males spent guarding their decorations. In addition, the stealing rate at Dreghorn actually increased when males were supplemented with decorations, though this result could also have occurred because I sampled bowers more frequently during supplementation, allowing me to observe more instances of theft. Within populations, there was no relationship between the numbers of decorations at bowers and the numbers that males stole. Though Hunter and Dwyer's (1997) hypothesis also predicts that a male's investment in theft of decorations may trade off with investment in other forms of male–male competition, such as bower destruction, I found no evidence that destruction rates differed between sites in a related study (Doerr 2008). It appears that males continue to value their decorations even as the numbers at their bowers increase.

These results contrast with a study comparing stealing rates between two populations of the Satin Bowerbird (Hunter and Dwyer 1997). In this study, mean NND did not differ between sites and stealing rates were higher in the population with fewer decorations. My results may have differed for several reasons. First, the availability of decorations may play an important role in male stealing behaviours only when other variables, such as inter-bower distances, are controlled. Owing to the limitations of my study design, I could only examine whether stealing rates were explained by the spatial arrangement of males *or* availability of decorations. Second, Hunter and Dwyer used a different method of calculating stealing rates: they divided the number of decorations stolen by the number of decorations present at bowers. This creates a bias towards rejection of the null hypothesis. Even if all males in both populations stole the same number of decorations, the authors would have found a higher rate of theft in the population with fewer decorations.

Nonetheless, availability of decorations may account for inter-population differences in stealing rates, but in a direction opposite to that predicted by Hunter and Dwyer (1997). Thieves can transport up to eight decorations per visit to the victim's bower (Borgia and Gore 1986), so males with many decorations at their bowers have the potential to lose more decorations per visit than males with few decorations. A study with Satin Bowerbirds in which the numbers of decorations at bowers were experimentally reduced found that rates of theft decreased when there were fewer decorations at bowers (Wojcieszek *et al.* 2007), and my results suggested an increase when Dreghorn bowers were supplemented. Given that Townsville males had more decorations and also stole decorations at a higher rate, I cannot exclude the possibility that availability of decorations contributed to the inter-population differences I observed in stealing rates. However, differences in the availability of decorations cannot explain why Townsville males stole decorations from a greater

number of individuals, nor can it explain why Dreghorn males stole a higher percentage of decorations from their nearest neighbours than Townsville males.

In sum, bower density was the best predictor of stealing rates within and between two populations of Great Bowerbirds, and these results highlight the flexibility of male–male competition as a behavioural strategy in bowerbirds. Because males interacted more frequently when they had more neighbours within a 1-km radius of their bowers, the potential for male–male competition to enhance signal honesty may vary both within and between populations. Future studies are needed to examine how ecological factors affect the spatial arrangement of males, and how this affects the relationship between male–male competition and female choice.

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