



Neighbouring male spotted bowerbirds are not related, but do maraud each other

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Males with elaborate secondary sexual traits can enhance their mating success both by choosing to display at a site that increases the efficacy of their signal and by displaying at a site where the population is structured to provide inclusive fitness benefits via kin selection. Theoretical models and field studies reveal that, across a range of species and especially those with nonresource-based mating systems, males do display with kin. Bowerbirds use a nonresource-based mating system where males show spatial site fidelity and females visit the sites for the purpose of mate choice. However, neighbours can interfere with bower display by marauding (destroying and decoration stealing). Models suggest that local nonaggression pacts provide the best conditional strategy for males, a situation that may be facilitated by kin-mediated inclusive fitness benefits if males displayed together. We used a novel method of calculating relatedness, based on amplified fragment length polymorphism (AFLP), in a population of spotted bowerbirds, *Chlamydera maculata*, and found no evidence of fine-scale genetic structuring of display sites. Furthermore, males did not display next to kin, but instead an owner's neighbours were those most likely to maraud his bower. Marauders did not discriminate between kin and nonkin as their victims. Such theft and destruction may affect the mating success of the targeted bower owner.

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Males of several species display close to relatives (Höglund et al. 1999; Petrie et al. 1999; Shorey et al. 2000). Theoretical models predict that relatives should display together to acquire inclusive fitness benefits (Kokko & Lindström 1996). Females prefer to make their choice from larger aggregations of males, so including even low-quality males in an aggregation increases its attractiveness, with direct benefits for the most successful males and, consequently, indirect benefits to lower-quality kin.

However, males displaying together may hinder as well as help each other. Intrasexual interference may take the immediate form of disruptions of copulations (Théry &

Vehrencamp 1995; Saether et al. 1999; Webster & Robinson 1999). It may also influence sexual success indirectly, for example by causing females to mate away from unusually violent display sites (Lanctot et al. 1998), or by determining the size and structure of aggregations that males form (Westcott 1997). Thus, although theory predicts that kin should display close together, in certain circumstances costs of interference may negate potential benefits.

Male bowerbirds of 17 of the 20 species of the family Ptilonorhynchidae construct and decorate bowers, which act as targets for female choice. Bowes are also targets of intrasexual competition, with males destroying structures and stealing decorations from others in the population (Borgia 1985; Borgia & Mueller 1992; Lenz 1994; Madden 2002). For satin bowerbirds, *Ptilonorhynchus violaceus*, geographically close neighbours are those most likely to maraud each other (Borgia 1985). For other species, including the spotted bowerbird, *Chlamydera maculata*, and Macgregor's bowerbird, *Amblyornis macgregoriae*, such a pattern of exclusively local conflict is less clear

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(Pruett-Jones & Pruett-Jones 1982; Borgia & Mueller 1992). Marauding reduces the subjectively measured quality of the bower, an attribute that relates to the mating success of its owner in a range of bowerbird species (Borgia 1985; Borgia & Mueller 1992; Lenz 1994; Uy & Borgia 2000). Females do not appear to gain benefits by mating at a particular location, other than those provided directly by the male (Borgia 1993; Pruett-Jones & Pruett-Jones 1994). Therefore, bowerbirds of a range of species have been described as having a lek (Borgia 1997), exploded lek (Frith & Frith 1995; Höglund & Alatalo 1995) or nonresource-based mating system (Borgia 1993; Pruett-Jones & Pruett-Jones 1994). Behavioural studies of female sampling methods also suggest similarities to lek like mating systems, with females sampling males by visiting and inspecting bowers that are spatially aggregated, using experience to limit their search tactics (Uy et al. 2000, 2001).

Without the demands of resource defence, male bowerbirds have, at least in theory, many sites where they could potentially display. Despite this apparent freedom, bowers are spatially fixed and the same sites are frequently reused over several years; there is a rigid network of even spacing between members of a population (Frith & Frith 1995, 2000a).

One explanation for this pattern is that suitable environments for maximizing display efficacy are limited. For example, spotted bowerbirds select bushes of particular species with a narrow range of canopy thickness, apparently to increase the efficacy of their signal (Miles & Madden 2002). This finding is analogous to those studies suggesting that males maximize their signal efficacy by choosing or competing for suitable light environments (e.g. Endler & Théry 1996; Andersson et al. 1998; Barry & Hawryshyn 1999; Fleishman & Persons 2001; Heindl & Winkler 2003). However, such explanations fail to account for the regularity of interbower spacing, nor do they prescribe where a male should set up his bower in relation to other males in the population.

In this study, we investigated a complementary explanation for site selection, by considering social factors that affect the location of bowers by male spotted bowerbirds. Specifically, we evaluated the trade-off between the inclusive fitness benefits that displaying near relatives could bring to a male and the possibility of reduced fitness based on the observation that other (neighbouring) males may maraud the bower.

Pruett-Jones & Pruett-Jones (1994) constructed models that showed that the best individual strategy that a male could perform to maximize mating success was to maraud neighbours' bowers. However, neighbouring males who guarded their bowers and did not disrupt each other always did better than those who marauded each other. Such a conditional strategy could be enhanced, or its evolution facilitated, if males who display next to kin also accrue inclusive fitness benefits. Spotted bowerbirds show unusually low levels of marauding (Borgia & Mueller 1992), so this species may provide a case where such a conditional strategy of nonaggression has evolved. Therefore, we might expect to find evidence of fine-scale genetic structuring among the population, with relatives displaying close to each other.

METHODS

Study Site and Species

Birds at Taunton National Park, Queensland, Australia (site details in Miles & Madden 2002), were caught in mist nets from August to November, during the male display and breeding seasons, in 1998, 1999 and 2000. Birds were ringed with unique combinations of coloured bands as well as a metal Australian Bird and Bat Banding Scheme (ABBBS) band. This allowed us to identify individual birds from direct observation at bowers or by motion-activated video cameras set at bowers (Madden 2003). Video equipment allowed us to record marauding events at bowers remotely. These events were typified by violent tugging on parts of the wall until it collapsed. One or two microhaematocrit tubes of blood were collected from most birds (exceptions occurred when birds escaped from the hand) and stored in ethanol in refrigerators or freezers. Bower owners were defined as those birds who regularly frequented, maintained and displayed at a particular bower and who were in attendance at a bower for more than 75% of the time for which we recorded at least one bird present. Molecular sexing indicated that all these birds were males. Bower locations and interbower distances were calculated as in Miles & Madden (2002), with the addition of data collected in the same way in 2000. For analysis of natural marauding and experimental stealing events, bowers were classified as those of either neighbours or nonneighbours. Bowers were separated by a mean \pm SD nearest-neighbour distance of 1059 ± 516 m (Miles & Madden 2002). Therefore, those bowers within 2 km of the focal bower were classified as neighbours, and those beyond were classified as nonneighbours.

Marking Decorations and Retrieval

Human artefacts used as decorations on bowers (including glass, plastic and metal) were marked with the bower identity number using a permanent pen (see also Borgia & Gore 1986) during our three seasonal measurement visits to bowers in 1998 and 1999 (Madden 2003). Such decorations were also marked during a single bower measurement visit in 2000. During these visits and a subsequent bower inspection in August 2001, we recorded all marked human artefacts found on bowers. If they were not originally from the bower, as indicated by their identity number, we added the new number of the thief's bower.

Stealing Experiment

Between 28 May and 28 June 2002, five pieces of broken green glass were placed 1 m in front of the avenue of newly located bowers, primarily to assess whether the bower was in use. These were marked as before with the bower identity number. This procedure was repeated between 28 July and 8 August ($N=14$ active bowers). On subsequent visits to bowers during this period, the locations of these objects were noted. If the glass appeared at another bower we counted this as a theft.

Table 1. The adapter sequences used in the ligation stage of AFLP

Adapter	Adapter sequence (5'–3')
<i>TaqI</i> top strand	GAC GAT GAG TCC TGA C
<i>TaqI</i> bottom strand	CGG TCA GGA CTC AT
<i>EcoRI</i> top strand	CTC GTA GAC TGC GTA CC
<i>EcoRI</i> bottom strand	AAT TGG TAC GCA GTC TAC

AFLP and Primer Selection

For the genetic analysis of relatedness, we originally attempted to clone microsatellite markers. However, the number of positive clones that we were able to obtain was small, and none of the six primer pairs that we designed yielded polymorphic products. Consequently, we turned to amplified fragment length polymorphism (AFLP) methodology (Vos et al. 1995; Mueller & Wolfenbarger 1999) to generate ladders of anonymous, unidominant bands. Such patterns tend to be reproducible and can be used to assess relatedness, even though uncertainties about the mode of inheritance preclude the calculation of relatedness values equivalent to those of Queller & Goodnight (1989) that estimate the extent of identity by descent.

AFLP analysis was carried out on blood samples collected from 21 bower owners and 23 nonowner males. DNA was extracted from blood samples by digestion with Proteinase K followed by treatment overnight with RNase A. The resulting extract was purified by standard phenol–chloroform protocol (Sambrook et al. 1989). To quantify the DNA, the samples were run on a 0.7% agarose gel and the DNA visualized by ethidium bromide staining. Approximately 100–400 ng of DNA were used for AFLP analysis. The AFLP protocol followed was similar to that used by Vos et al. (1995) and Ajmone-Marsan et al. (1997). The DNA was first digested using *TaqI* (5 units in a 10- μ l volume, 2 h at 65°C), followed by *EcoRI* (5 units in a 20- μ l volume, 2 h at 37°C). The *EcoRI* and *TaqI* adapters (Table 1) were then ligated on to the digested DNA using T4 DNA ligase (1 unit in a 50- μ l reaction volume, 3 h at 37°C), generating template DNA for PCR amplification. The ligated mixture was diluted 10 times using Tris–HCl (10 mM) and EDTA (0.1 mM, pH 8).

The PCR amplification consisted of two steps: preamplification and selective amplification. For the preamplification, 5 μ l of the ligated DNA was added to a 50- μ l PCR reaction mix containing Tris–HCl (10 mM, pH 8.3), MgCl₂ (1.5 mM), KCl (50 mM), dATP, dTTP, dCTP and dGTP (0.2 mM of each), *Taq* polymerase (1 unit) and *EcoRI* and *TaqI* primers carrying one selective nucleotide (50 ng of each). The *EcoRI* primer sequence was 5'–GAC TGC GTA CCA ATT CA–3' and the *TaqI* primer sequence was 5'–GAT GAG TCC TGA CCG AC–3'. The reactions were covered with mineral oil (10 μ l). Samples were subjected to 30 preamplification cycles (30 s at 94°C, 60 s at 50°C and 60 s at 72°C) and then diluted with Tris–HCl (10 mM) and EDTA (0.1 mM, pH 8) 10 times.

For the selective amplification, 2.5 μ l of the diluted preamplification solution was added to a 12.5 μ l PCR reaction mix containing Tris–HCl (10 mM, pH 8.3), MgCl₂ (1.5 mM), KCl (50 mM), dATP, dTTP and dGTP (0.2 mM of each), dCTP (0.04 mM), *Taq* polymerase (1 unit), α -³²P-dCTP (0.1 μ Ci), *EcoRI* selective primer (5 ng) and *TaqI* selective primer (30 ng). The reactions were covered with mineral oil (10 μ l). Nine primer combinations were used, yielding 125 loci that could be scored (Table 2). Samples were subjected to 13 selective amplification cycles (30 s at 94°C, 60 s at 65°C, reducing by 0.7°C each cycle, and 60 s at 72°C), followed by a further 23 cycles (30 s at 94°C, 60 s at 56°C and 60 s at 72°C). The products of the selective amplification were mixed with a 0.5 volume of formamide loading dye and denatured (4 min at 94°C), and then 3 μ l of each reaction was loaded and run on a 6% polyacrylamide gel.

Reaction products were visualized by autoradiography. For each primer combination, the samples were visually assessed to determine whether the PCR had been successful. Samples that showed either unusually faint or absent bands at all loci or spuriously strong bands likely to have prevented amplification of DNA at other loci were not scored for that primer combination. Successfully amplified samples were scored for the presence or absence of a band at all loci for which bands were of sufficient strength to be scored reliably and that showed polymorphism between the samples. Any samples that showed an unsuccessful AFLP result for more than three of the nine primer combinations were excluded from the analysis.

Table 2. Primer combinations used in amplified fragment length polymorphism (AFLP) selective amplification

<i>TaqI</i> primer (5'–3')	<i>EcoRI</i> primer (5'–3')	No. of loci scored
GAT GAG TCC TGA CCG A\CAC	GAC TGC GTA CCA ATT C\ACA	13
GAT GAG TCC TGA CCG A\CAG	GAC TGC GTA CCA ATT C\ACG	13
GAT GAG TCC TGA CCG A\CCA	GAC TGC GTA CCA ATT C\AAC	16
GAT GAG TCC TGA CCG A\CTG	GAC TGC GTA CCA ATT C\ATG	19
GAT GAG TCC TGA CCG A\CTC	GAC TGC GTA CCA ATT C\ACA	19
GAT GAG TCC TGA CCG A\CAC	GAC TGC GTA CCA ATT C\AGC	7
GAT GAG TCC TGA CCG A\CGA	GAC TGC GTA CCA ATT C\ACA	8
GAT GAG TCC TGA CCG A\CCA	GAC TGC GTA CCA ATT C\ACA	11
GAT GAG TCC TGA CCG A\CAC	GAC TGC GTA CCA ATT C\AAC	19
Total		125

Using AFLP to Calculate Relatedness

With codominant markers such as microsatellites, relatedness between individuals can be estimated by several alternative methods, of which Queller & Goodnight's (1989) is the most widely used. AFLP markers are assumed to be unidominant, meaning that a band is present or absent, with presence (P) presumably dominant over absence (A). Assuming unidominance, Queller & Goodnight's formula can be adapted by averaging across all possible scenarios, weighting each by its associated probability. When an individual lacks a band, it must be genotype AA, but if an individual carries a band, it may be either PP or AP. If the frequency of band presence in the population is p and the frequency of absence of a band is a , then the probability of a band carrier being PP is $p^2/(p^2 + 2ap)$. Similarly, the probability of a band carrier being AP is $2ap/(p^2 + 2ap)$. These probabilities may then be used to weight each possible genotype combination and hence to calculate relatedness using Queller & Goodnight's formula. For example, if individual 1 carries a band and individual 2 does not, the possible genotype combinations are AA:AP and AA:PP, and these will occur with the probabilities given above.

To explore how our adaptation of the Queller & Goodnight (1989) formula performs in practice, we compared estimates of relatedness with presumed actual levels. This was not possible in the case of spotted bowerbirds, because we found no nests during our study. Instead, in a separate study (R. Pople, unpublished data) blood samples were collected from adult white-winged nightjars, *Caprimulgus candicans*, and their presumed offspring from known nests. We simulated large numbers of AFLP genotypes based on the number of band loci scored in samples from the nightjars, and the frequencies of presence and absence alleles at each of these loci. In each set of simulations, a 'true' relatedness value was set, and then pairs of genotypes with this level of relatedness were generated and the relatedness formula was applied. For comparison, we include empirical values from both nominally unrelated nightjars (pairwise comparisons between adults) and presumed parent-offspring pairs.

Statistical Tests

Mantel tests to compare relationships between spatial and genetic matrices were performed using *zt*, a software tool for simple and partial Mantel tests (Bonnet & Van de Peer 2002). For all analyses, 100 000 iterations were made. All other analyses were carried out using SPSS v. 11 (SPSS, Chicago, U.S.A.) and all tests performed were two tailed. Several bower owners were present in all 3 years ($N=6$), so that analyses for each year are not independent, but statistical methods formally accounting for this could not be applied to the relatively small data set.

Ethical Note

Birds were caught and blood samples were collected under licence from the Australian Bird and Bat Banding

Scheme, Queensland Parks and Wildlife Service and the James Cook University ethics committee. One or two haematocrit tubes of blood were collected from the left brachial vein. All ringed birds were released with no signs of injury, all bower owners were resighted repeatedly at their bowers after catching and several were resighted up to 6 years later. Of the bower owners that died or ceased holding bowers during a breeding season ($N=3$), two were killed by predators and were found dead in their bowers, and one disappeared that had not been captured that season. Of 157 captures, one nonowner bird was attacked in the net by a raptor and died several days later.

RESULTS

Accuracy of Calculating Relatedness Using AFLP

As predicted, relatedness values increased with increasing relatedness (Fig. 1). When Queller & Goodnight's (1989) formula was applied to, for example, microsatellite data, where there were no allele ambiguities, relatedness values between nonrelatives were distributed around zero. With AFLP data, unrelated pairs tended to generate values considerably above zero, the average being a little over 0.5. We found good agreement between the means of the simulated values (0.53) and the observed values (0.51). Simulated first-degree relatives had relatedness values distributed around a mean of 0.78, significantly higher than for nonrelatives. Our empirical values are high (mean = 0.7), but a little lower than predicted. We suggest several possible explanations for this. First, the

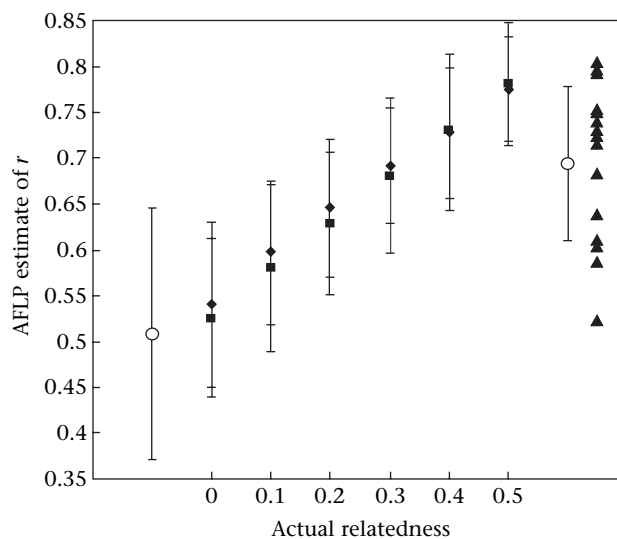


Figure 1. Simulations of mean \pm SD r estimated using AFLP assuming perfect Mendelian inheritance for bowerbirds (■) and nightjars (◆) against actual levels of r . Empirical data for nightjars reveal significant differences in r between presumed first-order relatives ($N=15$) and nonrelatives ($N=100$; ○: empirical relatedness values of nightjars calculated from nominally unrelated adults and presumed parent-offspring pairings; ▲: raw data for presumed parent-offspring pairings).

assumption of perfect Mendelian inheritance of AFLP bands may be false, and/or a proportion of putative loci may not amplify in a way such that reliable scoring is possible. Second, the assumption that the chicks match their mother may be wrong, a possibility that gains tentative support from the high variance in the empirical values, suggesting a mixture of relatedness that might include both first-degree relatives and nonrelatives. Regardless of the reason for this discrepancy, our simulations indicate that, as long as the majority of bands behave reasonably well, genetic relatedness estimates should correlate with true relatedness values. Thus, although the exact slope of the relation may differ from that expected based on the simulations, all our pairs of assumed relatives yielded values higher than the mean of the nonrelatives, which gives us confidence that our method captured an appreciable and useful signal. Over 50% of our AFLP estimates for r of first-order relatives were beyond the 95% CI of estimates for nonrelatives. This result suggests that our novel method had a power of discrimination similar to using eight microsatellites with medium levels of polymorphism (W. Amos, unpublished simulations).

Did Relatives Display Close to Each Other?

We obtained measures of relatedness and corresponding interbower distances for 13 males in 1998, 12 in 1999 and 14 in 2000 (Fig. 2). We found no relation between geographical and genetic distance in any of the 3 years (Mantel tests: 1998: 13×13 , $r = 0.015$, $P = 0.43$; 1999: 12×12 , $r = 0.019$, $P = 0.49$; 2000: 14×14 , $r = 0.085$, $P = 0.32$). The absence of a positive relation suggests that relatives did not display close to each other. The absence of a negative relation suggests that relatives did not actively avoid each other.

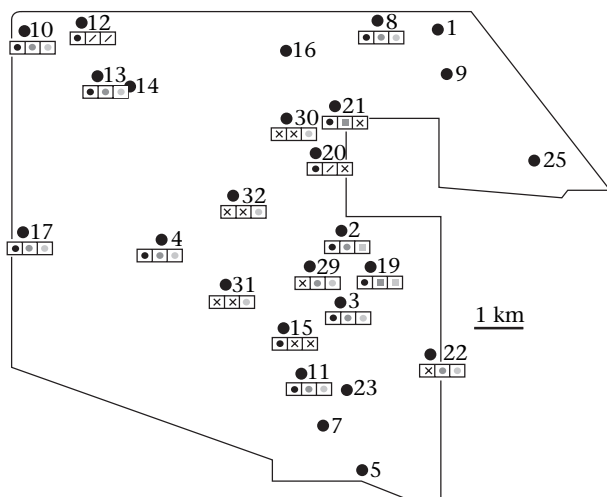


Figure 2. Bowers active over the 3-year study period. Those considered in the Mantel tests for 1998–2000 are coded after the bower number: ●: 1998; ■: 1999 (same owner); □: 2000 (same owner); ■, □: change of owner (genetic information available); /: change of owner (nongenetic information available); ×: bower deserted or not discovered.

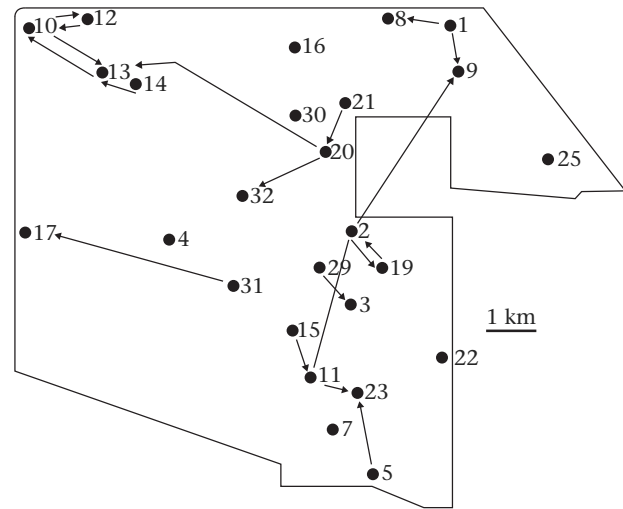


Figure 3. Map of movements of stolen objects between bowers active and monitored in 1998–2001. Bowers are indicated by numbered dots. Arrows indicate movement from the burgled bower to the bower of the thief.

Was the Marauder Likely to be Local?

Observations of natural thefts and destructions

Of the 1447 marked human artefacts used as decorations, we recorded 27 items moved between bowers. These involved 16 bower pair combinations, excluding reciprocal stealing events (Fig. 3). Of these, 13 were stolen from bowers less than 2 km from the thief's bower, and three from bowers more than 2 km apart (mean = 3.56 neighbours within 2 km). Therefore, a mean of 22.44 of the known 26 bowers active over the entire study period were more than 2 km from any focal bower. Stealing was more likely to occur between bowers within 2 km of each other than randomly between any pair of bowers in the study site (goodness-of-fit test: $G_{adj1} = 36.02$, $P < 0.001$).

Destruction of bowers was analysed in a similar manner. Of the 51 cases of destruction recorded over the three seasons, 10 were by unringed birds, 31 were by birds whose identity could not be established because of the rapid nature and violence of the events, and 10 were by identifiable individuals. Of these 10 birds, one destroyed its own bower (cf. Lenz 1994 for regent bowerbirds, *Sericulus chrysocephalus*). Of the remaining nine birds destroying bowers, six were males holding bower less than 2 km from the destroyed bowers, and three were bower-owning males more than 2 km away. These results differed significantly from those expected if birds randomly destroyed bowers (goodness-of-fit test: $G_{adj1} = 12.6$, $P < 0.001$).

Stealing of experimentally placed pieces of glass

Twelve pieces of glass of the 150 offered were stolen from one bower and appeared on another. These thefts involved eight pairings of bowers. In all cases, the glass was stolen by one of the two closest bower owners to the target bower (Fig. 4). Six of the victims had the closest active bower to the thief.

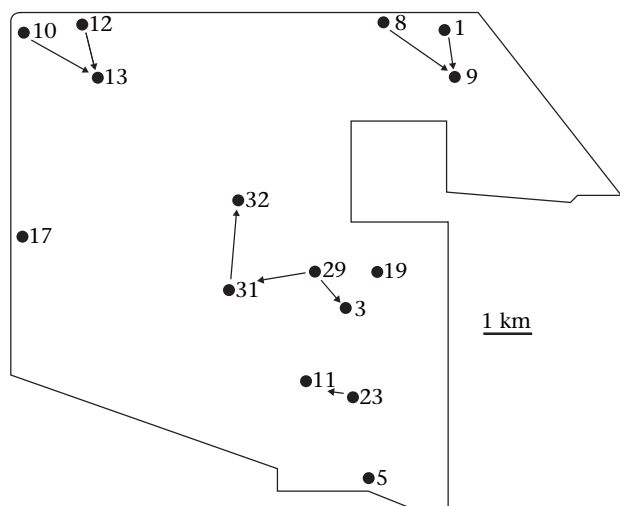


Figure 4. Map of movements of experimentally placed green glass pieces between active and monitored bowers in 2002. Bowlers are indicated by numbered dots. Arrows indicate movement from the burgled bower to the bower of the thief.

How was the Marauder Related to His Victim?

We compared the coefficient of relatedness (COR) between all pairings of bower owners and 10 pairings of thief and victim whose genetic relatedness was known, based on observed movements of stolen objects from 1998 to 2002. Although 14 pairings were available, four of these involved reciprocal stealing, so we used only one instance of reciprocal stealing. The mean genetic relation between thieves and victims did not differ from the mean COR between any other pair of bower owners (Mann–Whitney U test: $U = 535$, $N_{\text{Thief}} = 10$, $N_{\text{Victim}} = 119$, $P = 0.59$). We tested whether thieves targeted nonkin despite spatial constraints, by comparing the COR between the thief and his victim with the COR between the thief and his nearest nonmarauded neighbour. The thief was not less closely related to his victim than to his nonvictimized neighbour (Wilcoxon signed-ranks test: $T = 0.73$, $N = 14$, $P = 0.47$). Finally, we tested whether the thief targeted the bird to which he was most weakly related within the local population of males, by comparing the mean COR between him and his victims with the mean COR between him and the other bower owners within the study population. Coefficients of relatedness between thieves and victims, and thieves and nonvictims, did not differ (Wilcoxon signed-ranks test: $T = 0.46$, $N = 10$, $P = 0.65$), suggesting that thieves were not avoiding marauding relatives.

DISCUSSION

Contrary to some theoretical models concerning where males should display within a population (Kokko & Lindström 1996) and field studies of nonbowerbird species (Höglund et al. 1999; Petrie et al. 1999; Shorey et al. 2000), male spotted bowerbirds at Taunton did not display in local aggregations of relatives. Instead, regular spacing of these males (Miles & Madden 2002) appears to fulfil

predictions that male bowerbirds seek to display away from other males because of the threat of marauding by neighbours (Pruett-Jones & Pruett-Jones 1994).

One explanation for this deviation from predictions from the more general models and observations of male display site selection is that local neighbouring bowerbirds are those most likely to maraud a male's bower, reducing its quality, which affects a male's mating success (Borgia 1985; Lenz 1994; Uy & Borgia 2000). At Taunton, relatedness to neighbouring males appeared to affect neither choice of display sites nor marauding behaviours. Unrelated victims and close kin were not targeted differently; rather, victims were usually close neighbours. Thus, without a high concentration of attractive displays produced by neighbouring kin, males had no opportunity for potential inclusive fitness benefits resulting from more female visits to the area. A lack of kin structure may also have facilitated marauding by these same neighbours.

The identity of the marauder and his geographical location relative to his victim may vary between species or populations of bowerbirds and covary with differences in fine-scale kin structuring within a population. Under the models by Pruett-Jones & Pruett-Jones (1994), local non-aggression pacts, the conditional best strategy for male bowerbirds, could be reinforced by inclusive fitness benefits through kin mating success. Studies have documented the patterns of antagonistic interactions across several species. Borgia (1985) reported that 83–91% of bower destructions carried out by satin bowerbirds focused on near neighbours, defined as those five closest to the focal bower. Male tooth-billed bowerbirds, *Scenopoeetes dentirostris*, appear to maintain a local social hierarchy within immediately adjacent males by stealing leaves (Frith & Frith 1994). Marauding visits made by regent bowerbirds, *Sericulus chrysocephalus*, were generally made by males owning the nearest bower (Lenz 1994). Frith & Frith (2000b) reported an example of a golden bowerbird, *Prionodura newtoniana*, repeatedly stealing decorations from his nearest neighbour. However, anecdotal evidence suggests that neighbouring bowers are not always targeted. For example, a male Macgregor's bowerbird crossed at least six other bowers before marauding (Pruett-Jones & Pruett-Jones 1994), and the only known spotted marauder recorded by Borgia & Mueller (1992) flew 5 km twice within a single day to maraud another bower.

Our results show that spotted bowerbirds, like satin and tooth-billed bowerbirds, preferentially targeted geographically close neighbours for marauding. Although the levels of marauding were low compared with those observed in a range of other species of bowerbirds (Borgia 1995), they followed the general spatial pattern of targeting neighbours, casting doubt on whether kin-mediated inclusive fitness benefits were available to spatial aggregations of males who cooperated. We also investigated why local nonaggression pacts have not evolved by evaluating whether neighbours were genetic relatives. We found no evidence that males display close to kin, so reinforcement of nonaggression pacts by indirect fitness benefits cannot occur. Indeed, males did not appear to recognize kin, targeting them as often as nonkin when marauding.

Our findings do not preclude the possibility of the evolution of nonaggression between neighbours, as predicted by Pruett-Jones & Pruett-Jones (1994). In species or populations of bowerbirds that show low levels of marauding or marauding of nonneighbours, neighbouring males may be closely related. However, several studies have reported high levels of marauding, often targeting close neighbours. This finding suggests that male spotted bowerbirds operate the best individual strategy available, namely, to maraud close neighbours, given the uncertainty of cooperation by local neighbours who are unlikely to be close relatives.

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