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Lekking satin bowerbird males aggregate with relatives to mitigate aggression

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Males in several lekking species aggregate with their relatives to display for females, suggesting that kin selection can affect sexual selection. Several hypotheses have been proposed to explain this behavior, but no general explanation has emerged. In most species with lek mating systems, neighboring males have intense aggressive interactions that can affect the quality of their sexual displays. Here we test the hypothesis that the presence of related neighbors mitigates the negative consequences of this aggression. Male bowerbirds build stick display structures (bowers) that are used by females in mate assessment and are commonly destroyed by males' 2 nearest neighbors. We show that kin aggregate as first or second nearest neighbors, and males direct fewer bower destructions toward kin than equidistant nonkin. Males with more relatives nearby receive fewer bower destructions. These results suggest that the restraining effect of relatedness on aggression favors the close spatial association of related males' display sites. An alternative hypothesis, that related males aggregate to gain copulations from females attracted to successful relatives, was not supported. *Key words:* aggression, bowerbirds, genetic population structure, kin selection, leks, microsatellites, relatedness, sexual selection. *[Behav Ecol 20:410–415 (2009)]*

Non–resource-based (NRB) mating systems, including leks, occur in approximately 6% of bird species (Gill 1995) but are of special interest because they offer the opportunity to study mate choice where material contributions by males are not involved in mate choice (Borgia 1979; Bradbury 1981). Several recent studies have suggested a role for relatedness in affecting the spatial organization of males at breeding leks (e.g., Petrie et al. 1999; Shorey et al. 2000; Regnaut et al. 2006). These studies are noteworthy because, unlike social species where individuals remain in their family group for their whole life (e.g., Emlen and Wrege 1988; Komdeur 1994), males in NRB species do not co-occupy territories with their relatives after fledging. Thus, spatial associations of close kin on display arenas are not likely to be by-products of lifelong social associations (but see Krakauer 2005); rather, they appear to result from an active process of locating kin and choosing to display near them. Because males at neighboring display sites frequently interact (Höglund and Alatalo 1995) relatedness effects on these interactions may have important consequences for males' ability to compete with each other or to attract mates.

Several hypotheses have been proposed to explain how relatedness may affect male display site location (e.g., McDonald and Potts 1994; Kokko and Lindstrom 1996; Saether 2002), but most have not been rigorously tested. Krakauer (2005) showed that in cooperatively displaying wild turkeys, display partners are close relatives, and subordinate partners benefit from cooperation through inclusive fitness by helping their relatives mate. However, this explanation has limited application because males in most NRB species do not engage in highly cooperative displays nor do they form social groups with kin across their lifetime. Also, 2 other studies of cooperatively displaying species did not find that display partners were related (McDonald and Potts 1994; Loiselle et al. 2006).

In species without cooperative display, it is unclear how males might benefit from preferentially positioning themselves near relatives. However, spatial associations of relatives have now been documented in several such species (peacocks, Petrie et al. 1999; black grouse, Höglund et al. 1999; white bearded manakins, Shorey et al. 2000; lesser prairie chickens, Bouzat and Johnson 2004; and capercaillies, Regnaut et al. 2006) but not in others (e.g., sage grouse, Gibson et al. 2005; white-crowned and blue-crowned manakins, Loiselle et al. 2006; spotted bowerbirds, Madden et al. 2004; and great bustards, Martin et al. 2002). Kokko and Lindstrom (1996) proposed that these associations should occur when females prefer larger leks because, when new males have little potential to mate themselves, they should join leks where a relative is the top male, thereby making that relative more attractive and accruing inclusive fitness benefits for themselves. This hypothesis may explain associations of relatives when they occur at the level of one lek versus another, but it is difficult to differentiate this model from philopatry (Höglund et al. 1999), and it does not explain associations among display sites within leks (see Shorey et al. 2000).

A second hypothesis is that males may be less aggressive toward relatives than other nearby males (Hamilton 1964), and spatial associations among relatives can result if males attack related neighbors less often than unrelated ones (Saether 2002). Males at display arenas are competing with each other,

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so reduced aggression is predicted only if individuals have the opportunity to discriminate in favor of kin at the expense of nonkin (Griffin and West 2002). Therefore, reduced aggression due to kinship depends on the presence of individuals of differing relatedness (including both close kin and nonkin) at sites likely to attract aggression. Because aggressive interactions are often important in affecting the quality of sexual display and the location of male's display sites in NRB species (Höglund and Alatalo 1995; Westcott 1997), this hypothesis has potential to be widely applicable across NRB species.

NRB species differ in the degree of aggregation of display sites from tightly clustered leks to widely dispersed display sites (Höglund and Alatalo 1995). All species in which spatial associations among relatives have been observed have traditional lek mating systems with highly aggregated display sites. In at least one species with widely dispersed display sites, the spotted bowerbird, relatives were not found to associate (Madden et al. 2004). Differences in dispersion may explain some of the observed variation in the tendency of relatives to cluster because greater dispersion may decrease the level of interaction among males, reducing the opportunity for social interactions favoring kin at display sites.

Here we study the effects of relatedness on display site location and aggression in satin bowerbirds (*Ptilonorhynchus violaceus*), an NRB species with an exploded lek mating system (Gilliard 1969) in which male display sites are not tightly aggregated but in which males are known to commonly destroy the bowers of males at adjacent display sites (Marshall 1954; Vellenga 1970; Borgia 1985a; Hunter and Dwyer 1997). We test the hypotheses that 1) related males aggregate, 2) there is reduced aggression (bower destruction) among these closely associated relatives, and 3) males benefit from associating with their relatives.

Satin bowerbirds are a valuable model for studying male aggressive interactions because of the importance of aggression to male mating success and our ability to reliably monitor these behaviors. Adult males build bowers on display sites located at least 100 m apart, and neighboring males interact by destroying each others' bowers. Bower destructions are common and have been shown to lower bower quality (Borgia 1985a), which is an important influence in female mate choice (Borgia 1985b). Bower destructions are inversely correlated with female return rates for additional courtships, and 2 experimental studies have shown that destructions reduce male mating success (Borgia G, unpublished data). Individual females visit on average 2.64 (±0.18 standard deviation [SD]) adjacent bowers (Uy et al. 2001), and the vast majority of destructions are directed at males' 2 nearest neighbors (Borgia 1985a). Thus, bower destructions reduce the display quality and attractiveness of neighboring males who are each other's main sexual competitors (Borgia 1985a; Pruett-Jones S and Pruett-Jones M 1994). Selection may favor the aggregation of relatives in this species if related neighbors destroy each others' bowers less often, allowing them to maintain more attractive displays.

MATERIALS AND METHODS

Field methods

We continuously monitored 32 contiguously distributed adult male bowers throughout the mating season of 1997 (November 9 to December 20) at Tooloom National Park, New South Wales, Australia (28°28′S, 152°26′E). Birds were trapped and banded with unique color leg band combinations (Borgia 1995). Blood samples were taken from wing vein punctures and stored in DNA extraction buffer. Behaviors at bowers were recorded using Hi8 video cameras controlled by infrared sensors, positioned at each bower on the study site, and birds were identified on video by their leg bands (Borgia 1995). Interbower distances were calculated from GPS coordinates that were taken in 2001.

Relatedness estimation and classification

DNA was extracted from blood samples (Reynolds et al. 2007) and genotyped at 16 microsatellite loci; 14 loci were developed for satin bowerbirds (Bardeleben et al. 2005; Reynolds et al. 2007), 1 for manakins (Shorey et al. 2000), and 1 for indigobirds (Sefc et al. 2001) (Table 1). Genotypes at 8 loci were analyzed as described previously (Reynolds et al. 2007); newer loci were analyzed using an ABI3130 capillary sequencer (Applied Biosystems, Foster City, CA) and Genemapper software (Applied Biosystems). Population allele frequencies were estimated from a total of 248 birds sampled within the study area. Using GENEPOP 3.1 (Raymond and Rousset 1995), all loci were found to be in Hardy–Weinberg equilibrium and unlinked after Bonferroni corrections. Relatedness coefficients (r) were estimated using SPAGeDi 1.2 (Hardy and Vekemans 2002) following the method of Queller and Goodnight (1989).

Table 1
Characteristics of microsatellite loci

Locus	No. of alleles	Allele size range	H_e[a]	H_o[a]	Amplification protocol[b]
SB11	7	230–244	0.782	0.797	A
SB16.2	17	227–263	0.891	0.923	A
SBC40	7	183–195	0.631	0.641	A
SBC44	12	126–212	0.743	0.743	A
SBC46	5	183–197	0.683	0.706	A
SBC49	8	154–172	0.744	0.794	A
SBC188	5	180–188	0.698	0.655	A
SBC193	11	202–222	0.839	0.851	A
Ind38	9	155–193	0.597	0.602	B
Man7	2	159–163	0.189	0.188	C
AAGG-129	33	191–268	0.942	0.962	D
AAGG-130	16	234–316	0.847	0.735	D
AAGG-167	27	105–224	0.912	0.927	D
AAGG-187	37	105–468	0.941	0.95	D
AAGG-197	13	161–209	0.879	0.904	D
AAGG-209	11	96–138	0.863	0.877	D

[a] Expected (H_e) and observed (H_o) heterozygosities calculated in Genepop (Raymond and Rousset 1995).

[b] Amplification protocols were as follows: (A) as reported in Reynolds et al. (2007). (B) Microsatellite amplification was carried out on an MJ Research PTC-225 (MJ Research, Waltham, MA) thermocycler in a final reaction volume of 25 µl containing 1× buffer solution, 2 mM $MgCl_2$, 0.8 mg/ml bovine serum albumin, 0.2 mM each deoxynucleoside triphosphate (dNTP), 0.2 µM each primer (Sefc et al. 2001), 0.05 units/µl *Taq* polymerase, and 0.8 ng/µl template DNA. Thermocycling profile consisted of 94 °C for 4 min, 35 cycles of 94 °C for 20 s, 65 °C for 20 s, 72 °C for 30 s, and a final extension time at 72 °C for 10 min. (C) Microsatellite amplification was carried out on an MJ Research PTC-225 (MJ Research) thermocycler in a final reaction volume of 25 µl containing 1× buffer solution, 1.5 mM $MgCl_2$, 0.25 mM each dNTP, 0.25 µM each primer (Shorey et al. 2000), 0.04 units/µl *Taq* polymerase, and 1.6 ng/µl template DNA. Thermocycling profile consisted of 94 °C for 3 min, 35 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 30 s, and a final extension time at 72 °C for 7 min. (D) Microsatellite amplification was carried out on a Parallab 350 (Brooks Automation, Chelmsford, MA) thermocycler in a final reaction volume of 4 µl containing 1× buffer solution, 1.5 mM $MgCl_2$, 0.4 mM each dNTP, 0.4 µM each primer (Bardeleben et al. 2005), 0.025 units/µl *Taq* polymerase, and 0.75 ng/µl template DNA. Thermocycling profile consisted of 94 °C for 10 s, 28 cycles of 94 °C for 0 s, 52 °C for 0 s, 72 °C for 15 s, and a final extension time at 72 °C for 60 s.

We expected only close relatives (half-siblings or closer [see Petrie et al. 1999; Komdeur 1994]) to modulate their destruction behavior because inclusive fitness benefits decrease rapidly with more distant relationship (Hamilton 1964). Therefore, we used a cutoff value of r to identify pairs of males whose genetic similarity was consistent with that of close relatives. To pick an appropriate cutoff value of r, we simulated genotypes for 1000 pairs each of 4 relationship types (parent–offspring, full-sibling, half-sibling, and unrelated) using the observed allele frequencies and evaluated the distributions of r estimates for each pair type (Figure 1). All relationship types had r distributions centered on their theoretical values (0 for unrelated pairs, 0.25 for half-siblings, and 0.5 for full-sibling and parent–offspring pairs), and all types had equal variances except for parent–offspring pairs. Our simulations showed that a cutoff value of 0.13, the point of intersection between the distributions of unrelated and half-sibling pairs, simultaneously minimizes both Type I error—the proportion of unrelated pairs misclassified as related—and Type II error—the proportion of related pairs misclassified as unrelated (Blouin et al. 1996). So we defined close relatives as pairs having $r \geq 0.13$; otherwise pairs were considered unrelated.

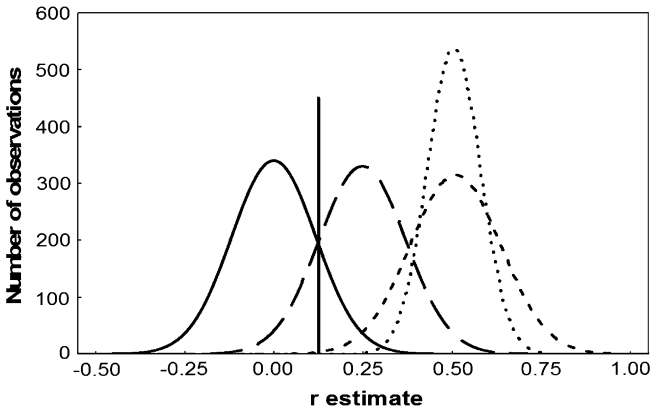

Figure 1
Distributions of relatedness coefficient (r) estimates for 1000 simulated pairs of each of 4 relationship types: unrelated (solid line), half-siblings (dashed line), full-siblings (hatched line), and parent–offspring (dotted line). Pairs with $r \geq 0.13$ (vertical line) were considered close relatives, and pairs with $r < 0.13$ were considered unrelated.

Data analyses

All statistical analyses were performed in Statistica 6.0 (Statsoft Inc., Tulsa, OK) except for the permutation test of bower locations thath was written in SAS 9.1 (SAS Institute, Cary, NC). To compare destructions directed toward related versus unrelated neighbors, we included every male in the study site that 1) had his nearest close relative within 600 m of his own bower and 2) had a nonrelative the same distance away as the nearest close relative (±35 m). If 2 nonrelatives satisfied criterion 2, then we chose the one whose distance from the focal male was most similar to that of the close relative. We limited neighbor distances from the focal male to 600 m because 95% of all destructions performed by focal males occurred within 600 m of their bowers. Among males who destroyed bowers of their second nearest neighbors, the numbers of destructions directed at first and second nearest neighbors did not differ (2-tailed paired t-test: $t_{14} = 0.19$, $P = 0.86$), and the mean difference in distance from the focal male between these 2 neighbors was 68 m, suggesting that a distance difference of 35 m or less should have no effect on the expected number of destructions. We used bower destructions as an indicator of male aggression because they could be most reliably scored from videotapes. Males also steal bower decorations (Marshall 1954; Vellenga 1970; Hunter and Dwyer 1997), and a previous study tracking movement of marked bower decorations showed that bower destructions and decoration stealing are highly correlated and commonly occur on the same visits by males to victims' bowers (Borgia and Gore 1986). All tests for which we had a priori directional predictions were 1-tailed (Gibbons and Pratt 1975).

To test for spatial association of relatives, we ranked each male's neighbors based on distance. Neighbor ranks are not reciprocal; therefore, each male's set of ranked nearest neighbors was considered independently. We then permuted male assignments to the existing bower locations and recalculated the number of close relatives among focal males' 2 nearest neighbors. We compared the observed number of relatives with the null distribution generated from 1000 permutations.

We used Gamma statistics to assess the relationship between the number of destructions given or received and the number of close relatives nearby because destructions were not normally distributed, the relationships are not necessarily linear, and Gamma tests are the most appropriate when there are many ties in the variable rankings (Siegel and Castellan 1988). We excluded 2 males from these analyses and from Figure 2; one because the number of destructions he received is not comparable to other males because he only retained his bower for a small fraction of the mating season. The other excluded male was an outlier who established his bower at a new site in 1996 and received 4 times the number of destructions (71) received by the second most destroyed male in 1997. Ninety-four percent of these destructions were received from his 2 nearest neighbors, who were the closest set of neighbors to any of the 8 males who established new bowers the previous year. The excluded male abandoned his bower site after this onslaught of destructions at the end of the 1997 season. Given the tendency of males not to tolerate neighbors that are closer than a couple hundred meters to their bowers (see Borgia 1985a), we felt that his choice of bower location drove the high observed rate of destruction and justified his exclusion from our analysis.

RESULTS

We evaluated relatedness among displaying male satin bowerbirds to understand the effect of kinship on bower destruction and display site location. The mean nearest neighbor distance

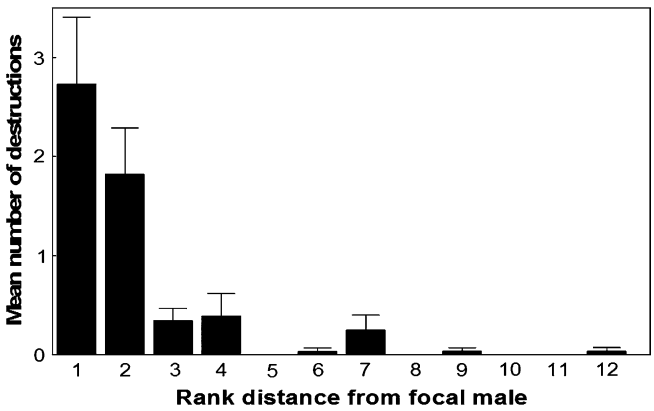

Figure 2
Destructions given to ranked neighbors. Mean (±standard error of the mean) number of bower destructions directed by focal males toward neighbors ranked by distance. No destructions were given beyond the 12th nearest neighbor of a focal male.

was 310 m ± 141 (SD) and, because these distances were not normally distributed, the median nearest neighbor distance was 255 m (range: 135–750 m). Individual bowers were destroyed on average 7.22 ± 13 (SD) times during the mating season, and 77% of bower destructions were directed at males' 2 nearest neighbors (Figure 2). The mean relatedness among all males was −0.005 ± 0.13 (SD) which was not different from zero ($n = 496$, $t = -0.86$, $P = 0.39$). Of the 496 pairwise relationships among the 32 bower-holding males, 73 (15%) pairs were closely related ($r \geq 0.13$) and there was a mean of 4.6 ± 2.9 (SD) close relatives per focal male. Given the high skew in male mating success of this species (Borgia 1985a; Reynolds et al. 2007), this low level of relatedness among resident males in the population suggests that natal dispersal is sufficient to prevent a high concentration of relatives within populations. This low proportion of relatives among competing males leads us to predict that competition among relatives is not likely to erase the benefits of kin selection (West et al. 2002) and that males should be less aggressive toward (give fewer bower destructions to) relatives than nonrelatives.

To test this prediction, we compared the number of destructions executed by focal males on closely related versus unrelated neighbors' bowers. To control for the effect of distance on bower destruction (Borgia 1985a) (Figure 2), we limited this comparison to those males who had both a closely related and an unrelated neighbor within 600 m and at equivalent distances (±35 m). Focal males destroyed the bowers of their closely related neighbors significantly less than those of their unrelated neighbors (Wilcoxon matched pairs test: $T = 4.00$, $n = 8$, $P = 0.045$; Figure 3). The modal number of destructions given to relatives was zero, suggesting that males commonly avoid destroying relatives' bowers. In one exceptional case, the focal male gave 5 destructions to his related neighbor, but these males had the lowest r among related pairs in this analysis ($r = 0.142$), and because they were very close to the cutoff of 0.13, they were the most likely pair among those classed as relatives to be misclassified (see Figure 1). Excluding this pair from our analysis showed an even stronger effect of relatedness on bower destruction (Wilcoxon matched pairs test: $T = 0.00$, $n = 7$, $P = 0.014$). This result supports our prediction that males are less aggressive toward their relatives when we control for interbower distance. Consistent with this result was a significant negative correlation in which males with more relatives nearby (among their 2 nearest neighbors) performed fewer total destructions (Gamma correlation: $Z = -1.73$, $n = 30$, $P = 0.041$).

If males aggregate with relatives because of this reduced aggression, then close relatives should be found disproportionately among males most likely to give destructions. Because the vast majority of bower destructions are directed toward focal males' first and second nearest neighbors (Figure 2), we made the a priori prediction that close relatives would be overrepresented among males' 2 nearest neighbors. The mean relatedness among first and second nearest neighbors was not significantly different from zero (mean ± SD = 0.007 ± 0.14, $t_{63} = 0.05$, $P = 0.48$). Because the proportion of relatives in the population was low, we assessed whether these relatives were randomly distributed among display sites. We compared the number of close relatives observed among the 2 nearest neighbors of each male with a null model in which males were randomly assigned to the existing display sites. We found that close relatives were among focal males' 2 nearest neighbors significantly more often than expected by chance (1000 permutations, $n = 64$ neighbors, $P = 0.001$). The observed number of close relatives among focal males' 2 nearest neighbors (18) was nearly twice the expected number (9.5). The finding that close relatives disproportionately occupy nearby bowers, where destructions are most likely to originate, suggests that relatives associate to mitigate the effects of these bower destructions.

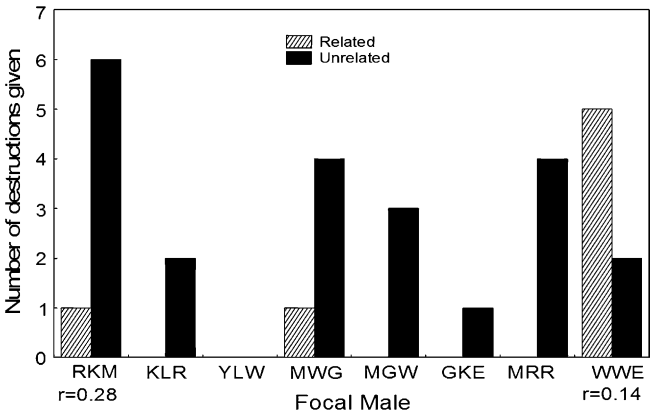

Figure 3
Destructions given by focal males to equidistant neighbors. Closely related neighbors are shown with hatched bars, and unrelated neighbors are shown with filled bars. Focal males are ordered by the relatedness coefficient (r) between themselves and their related neighbor (leftmost focal male had the highest r to his relative, and rightmost focal male had the lowest r to his relative).

If males benefit from displaying near their close relatives, then males with more close relatives nearby should receive fewer total bower destructions than males with fewer close relatives nearby. As predicted, we found a significant negative correlation between the total number of destructions males receive and the number of close relatives among their 2 nearest neighbors (Gamma correlation: $Z = -2.22$, $n = 30$, $P = 0.013$; Figure 4).

DISCUSSION

These results show that relatedness is important in modulating aggressive interactions among aggregated male satin bowerbirds. Males directed fewer bower destructions toward related than equidistant unrelated neighbors, and relatives were overrepresented among males' 2 nearest neighbors, the positions from which bower destructions were most likely to originate. Furthermore, males with more relatives nearby received fewer destructions overall, indicating that aggregating with relatives benefits males by allowing them to maintain more attractive displays.

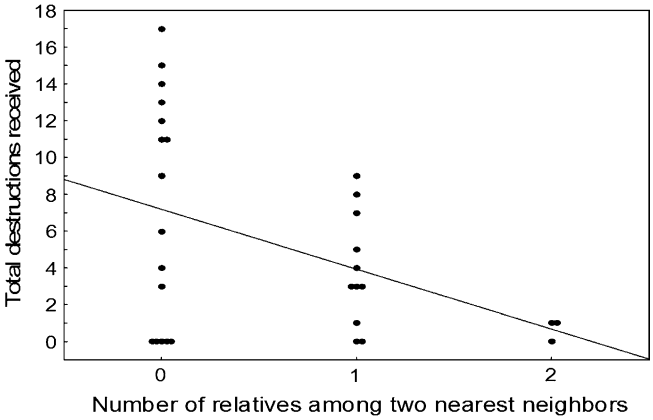

Figure 4
Relationship between the total bower destructions received by males and the number of close relatives among their 2 nearest neighbors.

Bower destruction can have important evolutionary consequences because this behavior directly affects males' ability to attract mates (Borgia 1985a, 1985b). Males may benefit from destroying their neighbors' bowers in 2 ways. First, the destroyer's own display becomes relatively more attractive than the victim's, causing females to prefer the destroying male rather than the victim (Borgia 1985a; Pruett-Jones S and Pruett-Jones M 1994). Second, if the destroyer's relatives are nearby, then females deflected from destroyed bowers may mate with these relatives, providing the destroyer an inclusive fitness benefit. Males should avoid targeting their related neighbors for destruction unless there is a high probability that the deflected females will mate with the destroyer because such destructions will lower the inclusive fitness benefits from that relative. These benefits to destroyers also suggest that nearby relatives of the destroyer may benefit from bower destruction behavior that is modulated by relatedness, through reduced destruction of their own bowers and increased mating opportunities. Together, these effects appear to favor the spatial association of relatives.

Another study has tested for a spatial association of relatives in a bowerbird species, the spotted bowerbird, and did not find aggregation of relatives (Madden et al. 2004). Spotted bowerbirds have much lower levels of bower destruction, one-tenth that observed in satin bowerbirds (Borgia and Mueller 1992; Madden et al. 2004), which may be due to their much more widely dispersed display sites (>1 km apart on average). With very low levels of destruction, spotted bowerbirds would gain little from reduced destructions by having relatives as nearest neighbors, and thus, we would not predict aggregation of relatives in this species.

An alternative explanation for why kin associate is that males gain more mating opportunities from being near their highly successful relatives (Saether 2002). This could occur if a highly successful male has more receptive female visitors than he can accommodate, such that females spill over to the related neighbors who resemble the preferred male. This hypothesis predicts that clustering of kin should be focused around highly successful males. In our study, the distribution of relatives near (within the 2 nearest neighbors) the top 3 males (54, 25, 22 copulations, respectively, 47% of all copulations) did not differ from the distribution of relatives near all other males ($\chi^2_1 = 0.02$, $P = 0.90$), and this result did not change when we considered the top 6 males (13, 12, 11 copulations, respectively, for the fourth through sixth males, 64% of all copulations; $\chi^2_1 = 0.01$, $P = 0.92$) nor when we considered the 4 nearest neighbors of each top male (top 3 males: $\chi^2_1 = 0.23$, $P = 0.63$; top 6 males: $\chi^2_1 = 0.12$, $P = 0.73$). These results do not support the alternative hypothesis that the observed spatial association of relatives is due to a tendency to associate with highly successful relatives.

In this study, we assessed the spatial association of related males by identifying closely related pairs using a cutoff r value and then determining whether these relatives were near neighbors rather than randomly positioned among display sites. Our approach differs from the more often used approach of comparing the mean relatedness of neighboring males to the mean relatedness of the general population. Our approach is more sensitive to the association of relatives when the proportion of close relatives in the population is not high, as may often be true if there is not a high level of philopatry. When we assessed mean relatedness of nearest neighbors, our results were similar to several other studies of species with NRB mating systems (McDonald and Potts 1994; Martin et al. 2002; Madden et al. 2004; Gibson et al. 2005; Loiselle et al. 2006; DuVal 2007) that did not find a significant difference from the population mean. However, mean relatedness fails to capture an overrepresentation of relatives among nearest neighbors when the proportion of relatives in the population is low (15% in this study) because the large number of unrelated pairs contributes to a lower mean relatedness. In the present study, a high proportion of first and second nearest neighbors ($46/64 = 71\%$) were unrelated resulting in a low mean relatedness, obscuring the critical finding that relatives were significantly overrepresented in this group.

How satin bowerbirds recognize their kin is not understood, but it may be achieved through Major Histocompatibility Complex (MHC)-based self-referent phenotype matching (Manning et al. 1992). Males apply a paint to their bower walls, composed of saliva and masticated plant material, which both males and females appear to taste when they visit a bower (Bravery et al. 2006). It is possible that MHC signals can be detected from the saliva in this paint to allow kin recognition.

We have shown that male satin bowerbirds benefit from displaying near relatives through reduced bower destruction by these relatives. As predicted, relatives were overrepresented among males' 2 nearest neighbors, the positions from which the preponderance of bower destructions originated. This supports the hypothesis that relatives aggregate to benefit from nepotistic restraint on bower destruction and suggests an important way in which kin selection influences the operation of sexual selection in NRB species. This effect of kinship on male aggressive behavior is striking because there is no evidence that satin bowerbirds form associations with kin until they become established on display sites, unlike cooperatively breeding species where individuals maintain lifetime associations with kin (Stacey and Bock 1978). Although bower destruction is unique to bowerbirds, other kinds of aggressive interactions that affect male display quality and mating success, such as threat, physical fights, or courtship interruptions, are common among neighboring males in other species with aggregated display sites (Höglund and Alatalo 1995; Westcott 1997). Our results suggest that spatial associations of relatives in these species may also be driven by the mitigating effects of relatedness on aggression.

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