

Male aggression drives spatial association of kin in satin bowerbirds

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INTRODUCTION:

Males in lekking species commonly aggregate with their relatives to display for females¹⁻⁶. Several hypotheses have been proposed to explain this behavior⁷⁻⁹, but no general cause for this kin association has been demonstrated. A previous study found that males enhance their inclusive fitness by displaying cooperatively with kin⁵, but this cannot explain the aggregation of relatives in species where males display individually. In most species with lek-like mating systems, male aggression is important in affecting the quality and location of male sexual displays¹⁰⁻¹¹. Here we test the hypothesis that males with aggregated display sites are less aggressive towards kin¹² and that clustering with relatives mitigates the negative effects of aggression⁹. In bowerbirds (*Ptilonorhynchus violaceus*), males build bowers (stick structures) to attract females and destroy bowers of neighboring males to enhance their own relative attractiveness¹³ (Fig. 1). We intensively monitored behavior at 32 bowers and genetically estimated relatedness¹⁴ to test the following predictions.

PREDICTIONS:

1. Males direct fewer bower destructions towards kin than non-kin.
2. Because destructions are primarily directed at focal males' two nearest neighbors (Fig. 1), relatives should disproportionately occupy these positions to benefit from reduced aggression.
3. Males with more relatives nearby (among two nearest neighbors) should receive fewer destructions overall than males with fewer relatives nearby.

METHODS:

Behavioral observation:

1. Birds were individually marked with leg bands in unique color combinations.
2. Behavior at bowers and was monitored throughout the 1997 mating season using motion-sensitive video cameras positioned at each bower¹⁵.
3. Tapes were reviewed and the identities of males destroying bowers were recorded.

Genetic methods:

1. 16 microsatellite loci¹⁶⁻¹⁸ were scored for 248 birds using PCR and fragment lengths were analyzed on an ABI3130 automated sequencer and Genescan3.1 or GeneMapper software.
2. Allele frequencies, Hardy Weinberg equilibrium and linkage disequilibrium were assessed using Genepop 3.1¹⁹ (mean number of alleles per locus=14 range=2-37; mean expected heterozygosity=0.754, range=0.189-0.942).

Relatedness estimation:

1. Relatedness coefficients (r) were estimated using SPAGEDi 2.0^{14,20}.
2. Pairs with r above 0.13 were classified as close relatives and pairs below 0.13 were classified as unrelated²¹ (see Fig. 2, Box 1). This classification was done because only close relatives are expected to show the predicted modulation of aggressive behaviors¹².

Statistical analyses

1. Destructions directed towards relatives and non-relatives were compared using a Wilcoxon matched pairs test (WMPT).
2. Relationships between destructions given or received versus the number of relatives among focal males two nearest neighbors were assessed using Spearman correlations (r_s) because destructions were not normally distributed.

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Photos: Bower destruction in action

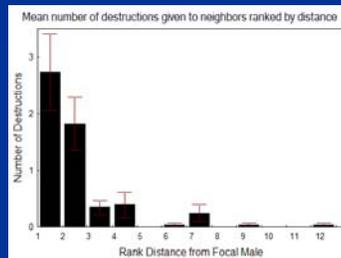


Figure 1: Mean (\pm s.e.m.) destructions given by focal males to ranked nearest neighbors. Males destroy their two nearest neighbors' bowers most often (84% of destructions). This result led to the prediction that relatives should associate within two nearest neighbors if they are seeking to mitigate the major effects of bower destruction.

Figure 2: Distributions of r estimates for 1000 simulated pairs each of unrelated (UN), half-sibling (HS), full-sibling (FS) and parent-offspring (PO) using the observed allele frequencies. We classified pairs with $r > 0.13$ as close relatives (see Box 1).

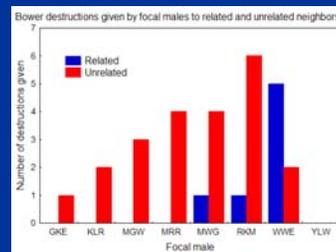
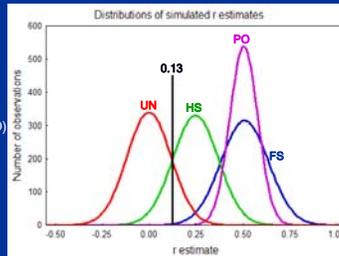


Figure 3: Destructions given by focal males to equidistant closely related (red bars) and unrelated (blue bars) neighbors. Data include all focal males who had both closely related and unrelated neighbors the same distance ($\pm 35m$) away and within 600m of their bower.

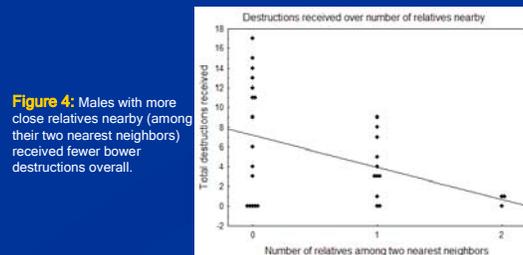


Figure 4: Males with more close relatives nearby (among their two nearest neighbors) received fewer bower destructions overall.

RESULTS AND CONCLUSIONS:

1. Males destroyed close relatives' bowers less often than non-relatives' when we controlled for distance (WMPT: $n=8$, $T=4.00$, $P=0.045$; Fig. 3). This supports the hypothesis that males are less aggressive towards kin than equidistant non-kin. Consistent with this result was a tendency for males with more relatives nearby (among their two nearest neighbors) to perform fewer total destructions ($r_s = -0.24$, $n=30$, $P=0.09$).
2. Close relatives were overrepresented among males' two nearest neighbors versus a null model of random placement of relatives (1000 permutations, $n=64$ neighbors, $p=0.001$). Thus, males cluster with their relatives among bower sites.
3. Males with more close relatives nearby received fewer bower destructions overall ($r_s = -0.315$, $n=30$, $p=0.045$; Fig. 4). Therefore, clustering with relatives mitigates the effect of bower destructions.
4. This is the first study to demonstrate a general mechanism to explain the spatial association of display sights of related males.
5. These results suggest that kin selection plays an important role in sexual selection in bowerbirds and perhaps many other species with aggregated display.

Box 1: Use of relatedness estimates (r) to test behavioral hypotheses

Our analysis differs from other studies in two important ways:

1. *We categorized r estimates.* We did not treat r as a continuous variable, rather we separated close relatives ($r > 0.13$, see Fig. 2) who are expected to show kinship effects from pairs with lower r , who are not expected to respond. Relatedness decreases rapidly with diverging relationship so that kinship effects are expected to be found only among close relatives, and commonly only close kin are recognized as kin. For this reason, we do not expect to find behavioral differences across the range of r estimates, i.e., there is no expectation of differential behavior between pairs of 0 relatedness and those of negative relatedness. By categorizing pairs as those expected to show relatedness effects and those not likely to show them, we expect that previous studies that have not shown kinship effects might uncover them.
2. *We did not use comparisons of mean r .* Mean r may not capture an overrepresentation of relatives in a particular group, especially if relatives are rare in the population, because the majority of unrelated pairs would dilute the mean. For example, in our study, only 15% of bower-holder pairs were related. The mean r among first and second nearest neighbors in our analysis was not significantly different from zero (mean $r = 0.007 \pm 0.14$ s.d., $t_{63} = 0.05$, $P = 0.48$) even though there was a significant structure to display sites as reported above (see result 2).

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