

CHAPTER 5

SOCIAL BEHAVIOR AND ORGANIZATION

ABSTRACT

Parrot social organization is unusual in combining group living with long term monogamy, but it has rarely been studied in the wild. I studied social behavior in a resident flock of wild glossy black-cockatoos (*Calyptorhynchus lathami*) in South Australia. The individuals in the habituated flock of up to 34 birds were recognizable through natural markings. The flock had relatively stable membership, but was not aggressive toward non-members. The most conspicuous social unit was the mated pair, sometimes accompanied a single dependent juvenile. Larger groups roosted together at night, and dispersed into family pairs or trios to feed. All adult pairs were socially monogamous, and stable across seasons and years. Paired birds stayed in close proximity to one another, synchronized their behaviors, oriented toward each other when separated, and showed little attraction to other members of the opposite sex. There was little nesting territoriality. The single juvenile accompanied its parents until the onset of the next breeding season, and was fed and preened by them. Proximity to other family groups was closer during the summer non-breeding season than the winter breeding season. Mated pairs associated preferentially with specific other pairs, but these affiliations were not stable across years. Aggression was infrequent and usually took the form of supplants,

which occurred in both foraging and socializing contexts. Both sexes supplanted same-sex birds disproportionately often. Supplants defined a linear hierarchy that was consistent within but not between years. All paired birds outranked all unpaired birds, and adults outranked subadults. Within mated pairs, females were responsible for almost all aggression, but there was no significant difference between the sexes in dominance ranks. Individuals that nested had higher ranks than those that did not.

INTRODUCTION

Parrots have exceptionally large brains, extensive vocal learning abilities that are not used in interspecific mimicry, and an unusual social system based on permanent pair bonds within mixed-sex groups. The functional significance of these traits is poorly understood, and is likely to remain so without a better understanding of parrots' natural social organization and behavior. Several recent studies of parrots in captivity have revealed complex social behavior based on bonds between specific individuals (e.g., Stamps et al. 1990, Arrowood 1991, Garnetzke-Stollmann & Franck 1991, Baltz & Clark 1994, Pepperberg 1994). However, captive studies often do not reveal the full range of social behavior in large brained and highly mobile vertebrates, and in parrots they have been limited mostly to a few small and easily kept species. Because of the tropical forest habitat and mobility of most parrots, they are notoriously difficult to study in the wild, especially away from the nest (Arrowood & Saunders 1991). Because most species are least social while nesting, we know relatively little about the natural social behavior of most species. The Australian cockatoos have been better studied than most parrots, but generally without a focus on behavior. Behavioral observations have been published on

some species (e.g., Saunders 1974, 1982, Rowley 1990), but there has been no detailed study of social behavior in any member of the cockatoo family.

The current study examined social behavior in the wild in the South Australian glossy black-cockatoo (*Calyptorhynchus lathami halmaturinus*). To my knowledge this is the first detailed study of the behavior of wild parrots away from the nest. Previous research on the glossy black-cockatoo consists of a population survey with notes on ecology and behavior (Joseph 1982), a field study of foraging ecology (Clout 1989), and an analysis of morphological variation and subspeciation (Schodde et al. 1993). In the current study I investigate how glossy black-cockatoo groups are organized, how agonistic and affiliative interactions are structured within groups, and what kinds of social bonds exist.

METHODS

The study was conducted in Lathami Conservation Park on Kangaroo Island, South Australia during Feb. - Dec. 1991 and Sept. 1992 - Aug. 1993. Data were collected using “perch scans” in 1991, and “focal follows” in both 1991 and 1993, as described in Chapter 1. Labels for specific behaviors follow those in Chapter 3, which also provides more detailed descriptions. For brevity I use the term “family” to refer to a mated pair, with their dependent juvenile if they had one. See Chapter 1 for more information on the study site and general methods.

Data Analysis

I designated the breeding season as March - August, and the non-breeding season as September - February (Forshaw 1977, Chapter 1). I used the Systat software package

(Wilkinson 1992) for most statistical analyses. I followed Siegel & Castellan (1988) for significance tests of Spearman correlations, and for Mantel tests (Schnell et al. 1985), I used the “Matsquar” matrix randomization program written by C. Hemelrijk (1990), with 10,000 randomizations per test. Unless otherwise noted, all statistical tests were two-tailed, and chi-square tests were tests of independence on two by two contingency tables.

Analysis of dominance ranks

To examine dominance relations, I counted the number of supplants (Chapter 3) in which each individual was aggressor or target, using records from focal follows, perch scans and *ad libitum* samples. Supplants involving pairs were therefore counted once for each individual. I included only interactions in which all parties were individually identified. Because different individuals were present during the two study periods, I analyzed each separately. Because no existing method was completely satisfactory, I combined two methods to create dominance rankings. The most common approach (Brown 1975) assumes there is a linear hierarchy, and arranges the matrix of supplants so as to minimize the number of reversals (supplants of a dominant by a subordinate individual) and intransitive or circular relationships (e.g., $A > B > C > A$). This approach has the drawback that it does not produce a single best ranking if some dyads were not observed interacting or there were ties (individual A supplanted B as often as B supplanted A). The PeckOrder computer program (J. Hailman, *in litt.*) addresses this problem by producing a ranking based on each individual’s pooled counts of wins and losses. However, this method does not minimize reversals or intransitive relationships, and thus does not produce a ranking that agrees as well as possible with the hypothesis of a linear hierarchy. To minimize reversals and intransitivities while also generating a single dominance ranking, I combined the two methods as follows. I first ranked individuals by the method of Brown (1975), generating one of several possible rankings.

I then resolved any ambiguities using the scores produced by the PeckOrder program. To do this I compared each dyad that was adjacent in the hierarchy or part of an intransitive relationship. If the lower ranked individual had a higher PeckOrder score, and if reversing them was not contrary to Brown's (1975) procedure, I did so. I continued this process until no further changes were possible. Because the supplant matrix was fairly sparse, I only assigned ranks to a subset of individuals that had at least five interactions with other members of the subset. This included 16 individuals in 1991 and 13 in 1993.

Measures of association levels and association preferences

Because monogamous pairs were very coherent units, it was feasible to use group composition data to measure association levels between pairs as well as between individuals. By any single measure of affiliation, association levels between some sets of pairs would be higher than others merely through chance or sampling error. I therefore measured association five different ways, using three data sources. I used data from 1991 to define temporary groups in five different ways, as follows: *Foraging tree*: all individuals foraging in the same sheoak tree during an ad lib observation. *Focal tree*: the focal individual and all other individuals perched in the same tree. *Focal nearest neighbor*: the focal individual and its nearest neighbor, excluding family members. *Perch tree*: all individuals perching in the same eucalypt at a time point sample during a perch scan. *Perch nearest neighbor*: each individual present in a eucalypt at a time point sample during a perch scan, together with its nearest non-family neighbor. The data from 1993 did not include perch scans or ad lib foraging observations, and *Focal tree* observations rarely included more than two pairs, so for 1993 I only analyzed *Focal nearest neighbor* groups.

To estimate the proportion of time any two pairs spent together in a given type of group I used the "simple ratio" index (Cairns & Schwager 1987), which has the advantage

of being a statistically unbiased estimator (Ginsberg & Young 1992). When, as in this study, all groups are assumed to be independent, this index is calculated the number of groups containing both A and B, divided by the number of groups containing either. I modified this index for use with pairs rather than individuals by scoring a pair as present if at least one member was present. In the vast majority of cases, both members of a pair were present if one was.

To measure association preferences, I used the ratio of observed to expected association level, or “preference quotient” (Chapter 8). For the first four type of groups listed above I used the GROUPS program (Chapter 8) to generate expected values of the association index, and p values for observed levels under the null hypothesis of random association. For the *Perch nearest neighbor* groups I measured association preference differently, both in order to make it independent of the *Perch tree* measure, and to make it independent of possible differences in home ranges. I measured the observed association level between two pairs by counting the total number of times that a member of one pair had a member of the other pair as its nearest non-family neighbor. I then calculated expected association levels *given the observed compositions of perching groups*, as follows. If the nearest non-family neighbor is chosen randomly from the individuals present in the tree, the expected number of times that members of pair A would have members of pair B as their neighbor in a group of size N is: $n_a * (n_b / (N - n_a))$, where n_a and n_b are the number of members of pairs A and B present in the tree, respectively, and $(n_b / (N - n_a))$ is the probability that an A bird will have a B bird as nearest neighbor by chance. Summing across all groups gave the total number of nearest-neighbor links expected by chance between two pairs. Again, I measured association preference as the ratio of observed to expected association level.

RESULTS

Movement and Grouping Patterns

The birds within the study area formed a resident flock with fairly stable membership. Of the 27 known individuals present in 1991, 12 were also among the 21 present in 1993. All resident individuals associated with one another, but not usually at the same time. Single birds were rarely encountered far enough away from other birds to be out of hearing range, and the largest flocks included up to 34 birds. There was no evidence of territorial defense, as unfamiliar birds appeared occasionally and were not subject to aggression by local residents. The most conspicuous social unit was the mated pair, accompanied by in a few cases a single dependent juvenile (one pair in each year). Among all adults individually identified during the study, there were 19 males and 14 females, or 1.4 males per female. All adult females were paired, and no all-male or all-subadult flocks were observed.

The cockatoos spent essentially all of their time in two types of trees, which constituted two distinct micro-habitats. They foraged in mostly pure stands of drooping sheoak, *Allocasuarina verticillata*), a small bushy tree less than 10 meters high. During other activities, including socializing, resting, and preening, they usually perched in much larger and more open *Eucalyptus* trees (mainly sugar gum *E. cladocalyx* and blue gum *E. leucoxyton*). Focal subjects were feeding during 80.2% of time points in drooping sheoaks, and only 2.4% in eucalypts. Members of more than one family often shared eucalypts, but rarely drooping sheoak trees (39.4% vs. 7.9% of focal time points).

Daily Activity Pattern and Time Budget

The cockatoos roosted at night in the tops of tall sugar gum trees (*Eucalyptus cladocalyx*). They tended to roost in the same stand of trees repeatedly, and in the study area they usually roosted year round in the same stand of about 1/4 hectare of sugar gums. They became active soon after sunrise, perching in the tops of eucalypts, preening, calling, and flying about. They then dispersed into smaller groups of variable composition as they moved into drooping sheoak trees to forage. After a morning foraging period they spent mid-day perching quietly, sleeping, and preening, usually in eucalypts, and returned to foraging in the afternoon. The mid-day break in foraging activity was most pronounced during the summer non-breeding season (Fig. 5.1). Toward the end of the afternoon foraging period the cockatoos became more active and vocal, and often congregated to drink at habitual sites along a stream before moving toward the roosting area. Interactions between unpaired birds were most frequent between the end of foraging and the start of roosting. As darkness fell family parties gradually moved together into tree canopies to roost for the night. During this daily cycle of activity, larger groups gradually dispersed during the morning and reunited during the afternoon, but families remained together throughout the day (Fig. 5.2).

The cockatoos spent most of their daylight hours foraging. To estimate the amount of time spent foraging without biases from uneven sampling effort, I calculated the proportion of time spent foraging for each hour of the day from focal time points, and summed these over the full day. Paired birds without nests spent an average of 6.4 hours per day foraging during the winter breeding season, and 7.6 hours during the summer non-breeding season. After foraging, the next most common activity was perching quietly (Table 5.1).

Table 5.1. Estimated proportion of time spent in different activities while not nesting. Based on 1678 focal time points on 25 individuals. The data include both sexes in both seasons, but exclude birds with active nests.

<u>Behavior</u>	<u>Percentage of time</u>
Foraging	59.5%
Perching quietly	34.0%
Sleeping position	2.6%
Autopreening	2.0%
Allopreening	1.4%
Flying	0.4%

Sex Differences in Activity Levels

To examine activity levels, I calculated each paired bird's frequency of movement in each season by pooling the following six behaviors from focal all-occurrence samples: walk toward/away, fly toward/away, and enter/leave tree. Within pairs during the breeding season, males moved 49% more often on average than their mates (Fig. 5.3; $N = 11$ pairs, Wilcoxon signed ranks test, $Z = 2.29$, $p = 0.02$). Females were slightly more active than males during the non-breeding season, but the difference was not significant. Both sexes were more active during the autumn-winter breeding season, but this difference only reached statistical significance for males (Mann-Whitney U test, $N = 22$, $p = 0.001$ for males, $p = 0.76$ for females).

Nesting Behavior and Parental Care

In both years, most mated pairs did not fledge young. In 1991 our observations did not cover the nesting period thoroughly, but only one of 11 pairs had a dependent juvenile afterward. In 1993 only three of 9 pairs started nests. They all failed, but one pair re-nested in a different hollow, probably successfully. Active nests were observed from 19 March through 28 August. Nesting pairs aggressively excluded other cockatoos from only a small area of a few meters around the nest hollow, and other individuals sometimes perched in the nest tree without any agonistic interactions. Only females entered tree hollows, either while prospecting for nest sites or during nesting. Early in the nesting cycle females spent little time outside the nest hollow, but later began to forage during the middle of the day. Males also changed their daily routine while their mate was foraging, foraging mostly in the middle of the day and staying near the nest in the morning and evening (Fig. 5.4).

One nesting male was observed during focal follows away from the nest on four days for a total of 16 hours. He foraged during 86% of time points, and had very little interaction with other cockatoos. He never shared a tree, or approached another individual to closer than 80 bird lengths (about 38 meters). He also gave no bow displays, kwee-chuck calls, or other displays.

No family group was ever observed with more than one juvenile. Until the onset of the following nesting season, juveniles were fed and preened by both parents, took partly eaten seed cones from both parents, often perched in physical contact during the day, and always roosted in contact at night. Although I did not observe the separation process closely, aggression by parents toward their year-old juveniles seemed to be involved in ending this period of dependency. Males may associate more loosely with

their parents after becoming independent, as some adult pairs were frequently followed by a subadult male, which they routinely allowed to share their foraging trees.

Mated Pairs

Pair bonds were present throughout the year, and none ended during the study (N = 9 known heterosexual pairs in 1991 and 11 in 1993). All pairs were mutually exclusive, and unambiguously distinct from other relationships in terms of proximity, behavioral synchrony, and specific behaviors.

Pair formation

Two females in stable pair bonds with adult males had little or none of the yellow head color characteristic of adults. Both were slow and clumsy at foraging, begged from their mates more often than other females did, and took partly eaten seed cones from their mate as juveniles do from their parents (Chapter 3). In contrast, no males with the tail barring characteristic of sub-adults were ever seen paired with a female. The process of pair formation was relatively infrequent because of the low rate of reproduction. It was also difficult to follow because birds without stable pair bonds were more transient and had fewer distinguishing markings than other individuals. However, on five occasions young females with little or no yellow on the head were observed being followed by two to four males, who showed frequent aggression to each other. Most severe fights seemed to occur in these contexts (e.g., chase, tandem flight, strike with wing, grapple fight; Chapter 3).

Characteristics of pair bonds

Excluding periods when females were incubating or brooding, paired birds' nearest neighbors were almost always their mate (98.7% of focal time points, $N = 1552$). Pair mates were usually within two body lengths, while the nearest non-family member was never closer than two body lengths, and usually more than 20 (Fig. 5.5). Mated pairs without active nests shared the same tree in 90.0% of focal time points, but shared their tree with non-family members only 19.4% of the time ($N = 1008$ focal time points). Pairs usually synchronized their activities. When I divided activity by whether birds were eating, perching, or flying, pair mates were engaged in the same activity in 90.1% of focal time points when the female was not on a nest. Several social behaviors were entirely restricted to within mated pairs and families, including allopreening, allofeeding, taking partly eaten seed cones, perching and roosting in contact, and exchanging soft calls frequently (see also Chapter 3).

When pair members were more than a body length apart, both sexes oriented toward their mate more as the distance between them increased (Fig. 5.6). Overall, males spent slightly more time oriented toward their mate than females did (48% vs. 42%, chi-square = 7.0, $p < .01$). This polarity was consistent in both sheoaks and eucalypts. There was no effect of season on the frequency with which either sex oriented toward their mate (chi-square test, $p > 0.05$). However, during the breeding season males oriented toward their mate more often when non-family members (which always included adult males) were present in the tree than when they were not (Fig. 5.7). In contrast, the presence of non-family members did not affect male orientation during the non-breeding season, or female orientation in either season.

Conflict within pairs

Aggression within mated pairs was limited to mild forms, and almost entirely to the breeding season. All but one of 46 observations of within-pair aggression (including spread-wing display, supplant, lunge, and fence with bill) occurred during the breeding season. Within-pair aggression was not restricted to nesting pairs, however. In focal follows during the breeding season, nesting pairs had slightly higher rates of within-pair aggression than non-nesting pairs (0.59 vs. 0.37 acts per hour), but this difference was not statistically significant ($N = 32$ focal follows, Mann-Whitney $U = 64.5$, $p = 0.23$). Females directed much more aggression at their mates than vice versa during focal follows (29 vs. 1 lunges, 2 vs. 0 supplants, 4 vs. 0 fence with bill, 0 vs. 3 spread wing displays; binomial test on pooled counts, $p < 0.001$).

Extra-pair sexual activity

Among paired birds there was very little evidence of extra-pair sexual activity or interest, and some evidence of avoidance. No extra-pair copulations were observed. Paired birds showed no sex difference in distance to their nearest non-family neighbor, either pooled across seasons or broken down by season (Wilcoxon matched-pairs signed ranks test, $N = 314$ total time points, $p > 0.45$ for each). However, during the breeding season paired birds of both sexes tended to avoid individuals of the same sex. When each member of a pair had a different nearest non-family neighbor, each tended to have a same-sex neighbor (chi-square = 14.4, $p < 0.005$). When both pair members had the same female neighbor, the female pair member was closer than the male to the neighbor ($N = 30$, Wilcoxon $Z = 2.01$, $p = 0.045$). When both had the same male neighbor, the male pair member tended to be closer but the result was not significant, probably due to small sample size ($N = 10$, $p = 0.12$).

Same-Sex Pairs

One male-male pair was present in each year: an adult male paired with a subadult male in 1991, and a pair of adult males in 1993. They engaged in all of the commonly observed manifestations of pair bonds, including maintaining close proximity, feeding in the same tree most of the time, perching in contact, allopreening, exchanging vocalizations frequently, and roosting together. They were not seen to copulate or take seed cones from one another, but the same is true of most heterosexual pairs. Although I did not collect enough data for quantitative comparisons, homosexual male pairs gave the impression of being as strongly bonded as heterosexual pairs.

Associations Between Pairs

Patterns of association preference

I analyzed association preferences between different pairs in 1991 based on four different measures of spatial proximity between pairs: *Focal tree*, *Focal nearest neighbor*, *Perch tree*, and *Foraging tree* (see Methods section). The number of pairs for which data were available for these measures ranged from seven to 11. I used the GROUPS program (Chapter 8) to test whether each dyad associated at a level significantly different from expected under random group composition. Each measure of proximity showed significantly non-random levels of association among some sets of pairs, ranging from one of 21 dyads for *Foraging tree* to 14 of 45 dyads for *Focal tree*.

To assess whether these different proximity measures revealed congruent patterns of affinity between different pairs, I compared the matrix of preference quotients generated from each measure. I also used a fifth proximity measure, *Perch nearest neighbor*, that was explicitly calculated to be independent of *Perch tree* (see Methods). I conducted pairwise comparisons of the preference quotient matrices using Mantel tests.

Of the 10 possible pairwise comparisons among five measures, all showed positive correlations, seven with p values below 0.10, and three below 0.05.

I also examined *Focal nearest neighbor* preference quotients from 1993. Of the 36 possible dyads among nine mated pairs, observed association levels deviated from expected at below the 0.05 probability level for 19 of 36 dyads (as compared with the 3.6 dyads expected by chance).

Stability of association preferences

There were five mated pairs with sufficient data for analysis in both 1991 and 1993. To examine the stability of association preferences over time, I used a Mantel test to examine whether the matrices of preference quotients among these five pairs were similar in the two years. The *Focal nearest neighbor* preferences from 1991 were negatively correlated with the *Focal nearest neighbor* preferences from 1993. I also averaged the preference quotients from all five measures of proximity in 1991 to produce a composite measure of association preference, and these values were also negatively correlated with the 1993 data. Neither correlation was statistically significant.

Relationship between proximity and rates of aggression

To examine whether rates of aggression were correlated with social affinity as reflected by proximity, I first used data from perch scans to estimate the rate of aggressive acts for each dyad of mated pairs in 1991. I tallied the total number of wingspread displays, supplants, and lunges, for each dyad. I then estimated how much time the two pairs spent together by counting the number of time points in which at least one member of each pair was together in the same tree. Finally, I divided the number of aggressive acts by the amount of time together to estimate the rate of aggression between the two mated pairs. I used a Mantel test to compare the matrix of aggression rates with the

matrix of composite affinity indices. The two were negatively correlated, but not significantly so.

Seasonal Changes in Association Between Families

Distances between different family units were substantially higher during the breeding season, even when pairs with active nests were excluded. Paired birds without nests shared eucalyptus trees with non-family members much less frequently during the breeding than non-breeding season (27.5% vs. 63.3% of focal time points, chi-square = 34.3, $p < 0.005$). They also stopped sharing drooping sheoak trees with non-family members almost entirely during the breeding season (0.6% vs. 16.9% of time points during breeding season, chi-square = 52.3, $p < 0.005$). Moreover, nearest non-family neighbors were several times farther away during the breeding versus the non-breeding season (Fig. 5.8).

The characteristics of nearest non-family neighbors also changed seasonally. For paired birds of both sexes, the nearest non-family neighbor was usually a paired bird during the non-breeding season, but during the breeding season was often an adult male unaccompanied by a mate (Fig. 5.9). As far as I am aware these were unpaired males, but I could not always rule out the possibility that they had a mate tending a nest. The seasonal difference in the frequency of unaccompanied males as neighbors was significant for both sexes (chi-square > 37, $p < 0.005$).

Aggression and Dominance

During focal follows, paired birds were involved in supplants at an average rate of 0.06 per hour. The breakdown of supplants by age/sex category is summarized in Table 5.2. Coordinated supplants by mated pairs were usually directed at other pairs (52%),

while those by individuals were usually directed at other individuals (80%) (chi-square = 12.2, $p < 0.005$). Coordinated pairs never supplanted subadults or juveniles, females supplanted pairs more often than males did (30 of 42 = 71%), and juveniles supplanted only other juveniles. Among paired birds, each sex supplanted same-sex individuals about twice as often as opposite-sex individuals (66% same-sex for females, 67% for males, chi-square = 8.25, $p < 0.005$). After excluding within-pair supplants, the bias for same-sex supplants was evident in each season (non-breeding: 71%, chi-square = 6.31, $p < 0.025$; breeding: 81%, chi-square = 13.51, $p < 0.005$).

Changes in the contexts of supplants suggest that their roles may vary seasonally. During the non-breeding season most supplants (51%) occurred in the sheoak trees where the cockatoos fed, but during the breeding season most (76%) occurred in eucalypts where they socialized (chi-square = 14.3, $p < 0.005$). Moreover, unpaired males were supplanted more often by paired males during the breeding season, and by paired females during the non-breeding season (chi-square = 7.58, $p < 0.01$). Subadult males in particular were supplanted much more often during the breeding season than the non-breeding season (25 vs. 3 observations).

Dominance relationships were very consistent within years, but not between them. Within years, reversals accounted for only four supplants out of 242, or 1.7%. These occurred in three events, one of which was a coordinated supplant by a pair. To examine the stability of dominance relations between years, I examined the seven individuals that had enough interactions to be ranked in both 1991 and 1993. Their relative rankings in the two years were not significantly correlated (Spearman rank correlation, $R_s = 0.25$, $N = 7$, one tailed $p > 0.25$). I therefore treated the two years as statistically independent in further analyses.

The hierarchy was linear in each year, and very structured by age and sex class. The matrices of supplants were fairly sparse, with only 54% of dyad-years (106/198) observed in supplant interactions, and this makes an apparently linear hierarchy more likely to arise by chance (Appleby 1983). However, all but one of the 105 dominance relations observed were transitive (no non-transitive dyads occurred in 1991, and only one in 1993). All adults were dominant to all subadults and juveniles, and all paired birds ranked above all unpaired birds. Among paired adults, females had slightly higher dominance ranks than males, but this did not reach significance (data pooled across years, (N = 28 individual-years, $t = 0.36$, $p = 0.72$). However, all of 11 supplants within pairs were by females.

Table 5.2. Number of supplants, broken down by age/sex category. Tallies include data from focal follows, perch scans, and ad libitum observations.

<u>Aggressor:</u>	<u>Target:</u>						Total
	Pair	Paired female	Paired male	Unpaired male	Subadult male	Juvenile	
Coordinated pair	13	1	5	4	0	0	23
Paired female	30	35	18	19	12	1	115
Paired male	12	10	20	30	11	0	83
Unpaired male	0	0	0	0	2	1	3
Subadult male	0	0	1	1	0	2	4
Juvenile	0	0	0	0	0	2	2
Total	55	46	44	54	25	6	230

Responses to temporary dominance reversals

To investigate whether the cockatoos were aware of their established dominance relationships with other individuals, I examined their reactions to temporary dominance reversals during the 30 minutes following the original supplant. Temporary reversals were defined as supplants in the opposite direction of most of those observed within the dyad. In each of the three interactions involving temporary dominance reversals, the victim was a paired male perched far enough away from his mate to be supplanted separately. In each case, within 30 minutes of being supplanted the dominant bird in turn supplanted the aggressor, sometimes repeatedly. In contrast, when a dominant bird was the aggressor the roles were never reversed within 30 minutes, or on the same day.

Dominance Rank and Nesting

The subset of individuals to whom I initially assigned dominance ranks included only one pair that nested. However, by relaxing my criteria to require four rather than five interactions, I was able to assign dominance ranks to all three females and two of the three males that nested in 1993. Of the 15 individuals with dominance ranks, the two highest ranking were nesting females, and the third nesting female was in the upper half. Overall, individuals that nested had significantly higher ranks than those that did not (Mann-Whitney $U = 9$, $p = 0.05$).

DISCUSSION

Comparative Cockatoo Socio-ecology

Glossy black-cockatoos are unusual in being highly specialized on the seeds of *Allocasuarina* trees as their food source (Chapter 4). There is little evidence that they feed on anything else, and in each part of their range they feed almost entirely on a single *Allocasuarina* species (Forshaw 1981 p. 84). This degree of feeding specialization is unusual not only in cockatoos, but in birds in general. In contrast, most members of the cockatoo family are more generalist foragers on seeds, fruit, and insects (Forshaw 1977).

The glossy black-cockatoo's unusual feeding specialization probably accounts for many differences in social organization from its closest relatives. The main ecological factors influencing group living in general, including flocking in birds, are believed to be predation pressure and food distribution (Alexander 1974, Pulliam & Millikan 1982, Mangel 1990). Predation pressure has been suggested as a dominant influence on flocking in parrots (Westcott & Cockburn 1988), and the response of glossy black-cockatoos to large raptors is consistent with such a role (Chapter 3). However, even if predator protection creates a strong benefit to flocking, the increased feeding competition in larger groups could still limit flock size. Glossy black-cockatoos do not form the large flocks that are so conspicuous in other cockatoos such as galahs, corellas, and sulphur-crested cockatoos (Forshaw 1977, Chapter 9), probably because their food supply is less concentrated. Drooping sheoak woodland on Kangaroo Island in May-June contained an estimated 26.5 grams of seed per square meter (Chapter 2). However, because other

cockatoos have less easily quantifiable food sources, there are no comparable estimates of food density for other species.

Glossy black-cockatoo flocks are of comparable size to those of other black-cockatoos (*Calyptorhynchus spp.*), but are more sedentary (Forshaw 1977, Chapter 9). This is probably because this species' foraging ecology reduces both the need and the ability to travel long distances. Drooping sheoaks hold their seeds for several years, and thus provide a relatively constant food supply, both seasonally and in terms of predictability between years. This would reduce the need for large movements. Moreover, glossy black-cockatoos may be less capable of long flights than their congeners because *Allocasuarina* seeds are a reliable food source, but not a rich one. Glossy black-cockatoos spent 60% of their daylight hours extracting seeds in the current study. Clout (1989) reported an even higher proportion of 88% for by *C. l. lathami* foraging on *Allocasuarina littoralis* in New South Wales, but this was probably an overestimate because he specifically sought feeding birds to study their foraging behavior. Clearly, though, most of the cockatoos' time is required for foraging. Handling time tightly constrains the rate at which they can feed (Chapter 4), and as a result both time and energy are probably limiting factors no matter how abundant the food supply is. This would tend to limit the ability to travel long distances. Local knowledge may also be an important advantage, because tree quality varies both regionally (Chapter 2), and between individual trees (Chapter 4). These factors would also tend to limit the ability to aggregate into large flocks, which must travel more because they deplete local resources more quickly.

Glossy black-cockatoos nest during autumn and winter, instead of spring and summer like most birds, including the other cockatoos (Forshaw 1977). This too is probably an adaptation to their feeding ecology. Both the calculations in Chapter 4, and the fact that only one egg is laid suggest that the species has a very tight energy budget

during reproduction. Food is most plentiful for the South Australian population when drooping sheoak seed cones first ripen in July-August (Pepper 1993), and seeds are probably easiest to extract from new cones as well (Clout 1989). Thus the timing of nesting is such that chicks fledge when the food supply is most plentiful.

Despite the differences caused by their unique ecology, social organization in glossy black-cockatoos is similar in most ways to what we know about other members of the black-cockatoo genus. Glossy black-cockatoos are unique in always laying a single egg, but other species fledge only one or two young, and share long periods of parental care of up to a full year. Thus the small nuclear family is the basic social unit in all the black-cockatoos (Forshaw 1977). The tendency of subadult male glossy black-cockatoos to consistently follow certain adult pairs suggests that attachment to the parents may sometimes last longer than one year. This pattern was confirmed for the Carnaby's cockatoo (*Calyptorhynchus funereus latirostris*) in two cases. In at least one of these, the immature bird was a male (Saunders 1979).

Glossy black-cockatoo social organization is affected by the presence of excess males. Unpaired males were attracted to mated pairs, especially during the breeding season, almost certainly because all females were paired. Single males were as close to paired males as females, but this was probably because paired males persistently interposed themselves between their mate and any nearby single males. Despite their apparent attraction to mated pairs during the breeding season, unpaired males were kept at a distance by the frequent supplants directed at them by paired birds, and especially paired males. The biased adult sex ratio presumably resulted from higher female mortality rates. Other cockatoo species also have male-biased sex ratios, but none as extreme as that found in the current study and in Chapter 2. Many birds suffer higher rates of predation

while tending nests, and because females do all brooding and incubation in glossy black-cockatoos, nesting mortality might account for the biased sex ratio.

Seasonal Changes in Behavior and Social Organization

Males were much more active during the breeding season than the non-breeding season. During the breeding season they moved more often, and also foraged faster and for more hours per day than females (Chapter 4). Studies of other parrots have not compared activity rates between seasons. However, captive studies found males to be more active than females in budgerigars (Trillmich 1976), and also in Carnaby's cockatoos during the breeding season (Saunders 1979). This may be related to a metabolic differences; male European kestrels (*Falco tinnunculus*) are more active than females and have a higher metabolic rate after adjusting for body size (Masman et al. 1988). Male glossy black-cockatoos might increase their metabolic rate relative to females during the breeding season because females need less energy to incubate and brood than males need to forage for themselves, their mate and their nestling.

Changes in the diurnal pattern of foraging, both seasonally and with nesting status, probably function in thermoregulation. Cockatoos foraging in hot weather often show signs of heat stress, including panting and wing opening (Chapter 3). The longer midday pause in foraging during the summer (non-breeding season) would reduce heat stress. A similar pattern occurs in the congeneric Carnaby's cockatoo (Saunders 1979). In contrast, nesting females probably restrict their foraging to mid-day because that is the warmest part of the day in winter, and thus the only safe time to stop incubating. The average daily maximum temperatures in nearby Kingscote are at their lowest in June-August (14-15° C), and these are also the wettest months of the year (Burrows 1979). Nesting males alter their foraging patterns as well, perhaps in order to accompany their mates.

Within flocks, families were farther apart in the breeding season than the non-breeding season. This probably reflected the same factors that cause seasonal fluctuations in flock size. Flocks are smallest near the start of the breeding season, and largest near the end of it (Chapter 9). Because most focal data were collected relatively early in each season, lower within-flock proximity in the breeding season corresponds to the period when flocks tend to be small, and higher proximity in the non-breeding season corresponds to the period when flocks are large.

Seasonal changes in gregariousness are often related to nesting activity. Many bird species live in groups outside the breeding season, but disperse during the breeding season to defend exclusive territories. Glossy black-cockatoos do not fit this pattern well, however, as pairs often nest near one another (i.e., within 100 meters), and sometimes even in the same tree (Sindel & Lynn 1989 p. 213; Chapter 2). Moreover, I found no evidence that nesting *per se* reduces gregariousness. Nesting birds actually maintain greater proximity to other pairs than do non-nesting birds during the breeding season (Chapter 6).

In this species, seasonal changes in gregariousness may be better explained by changes in the availability of food. The new crop of drooping sheoak seed cones matures in July and August (Pepper 1993, pers. obs.), and these are the months in which flock sizes rise most sharply (Chapter 9). It is also significant that during the breeding season different families perched together in eucalypts at 27% of the non-breeding season rate, but shared food trees at only 2% of the non-breeding season rate. This suggests that feeding competition may be the driving force behind seasonal changes in within-flock sociality as well as flock size.

Characteristics of Pair Bonds

Mated pairs were very behaviorally distinct from other dyads, despite a paucity of behaviors associated specifically with courtship and mating (Chapter 3). They were also characterized by behavioral symmetry and a striking lack of interest in other members of the opposite sex. Pair bonds were also quite stable, both between seasons and years. Accurate estimates of pair bond duration would require longer study of a larger population, but I observed a total of 20 pair-years without any divorce, suggesting that the divorce rate is quite low. Both the symmetrical nature and the stability of pair bonds suggest that they provide benefits to both sexes. The functional significance of long term pair bonds is addressed further in Chapter 6. Close proximity within pairs is typical of cockatoos, as well as many other parrots, but not of the smaller Australian species in the tribe Platycercini (Smith 1975). Very stable pair bonds lasting years or even lifetimes are also typical of other parrot species, particularly cockatoos (Forshaw 1977). Their symmetric or “egalitarian” quality has been noted in some other parrots as well (Arrowood & Saunders 1991).

A range of behaviors seemed to be involved in maintaining pair bonds. Physical contact and mutual grooming are often hypothesized to be important pair-bonding mechanisms, and are prominent in glossy black-cockatoo pairs. Allofeeding is obviously important in parental care, but continues year round and probably functions in pair bond maintenance as well (Chapter 3). Mated pairs maintain contact both by increasing their visual monitoring with increasing distance, and by exchanging “contact” calls while foraging and before flying (Chapter 3). These mechanisms allow pairs to closely synchronize their activities, which facilitates staying in close proximity.

Both sexes may also protect the pair bond by “guarding” their mate from same-sex competitors. The same-sex pair member was usually closest to the pair’s nearest neighbor, suggesting that each sex tended to interpose itself between the mate and nearby

opposite-sex birds. Mutual guarding is also implied by the fact that both sexes directed supplants at same-sex individuals disproportionately often. Mate guarding by females has been described in other species in which the pair bond represents an important resource for the female as well as the male (Kilpimaa et al. 1995). Paired males supplanted unpaired males from near their mates especially often, and this appeared to be effective in keeping them at a distance. This could be interpreted as mate guarding, but it might also serve to protect the female from harassment by other males.

Females appeared to dominate their mates in aggressive interactions. However, within-pair dominance is probably not comparable to interactions outside of families, because pair members do not compete for access to resources. Aggression within pairs was restricted almost entirely to the breeding season, and usually occurred when females reacted to their mate directing allopreening, bow displays or kwee-chuck calls at them (Chapter 3). Observations of unpaired males masturbating suggest that the male sex drive is quite strong during the breeding season (Chapter 3), and most female aggression appears to result from unequal interest in sexual activity. This greater sexual interest by males suggests that the risk of cuckoldry is not insignificant, despite females' apparent lack of interest in other males.

Association Preferences Between Different Pairs

Different pairs associated with each other in significantly non-random patterns. This is apparently not attributable to differences in the extent of range overlaps. Because the "Perch nearest neighbor" measure reflected the tendency for particular individuals to perch together after they were already in the same tree, it would not be affected by differences in pairs' ranging patterns, yet it was positively correlated with all of the other measures.

Although they were consistent within years, association preferences between pairs were very unstable between years in this study. This result can only be generalized very tentatively because of the few pairs examined, and the fact that only two time periods were compared. However, it suggests that association preferences between the pairs in a flock may not be determined primarily by genetic relatedness.

Comparisons with other species

Glossy black-cockatoos show consistent patterns of association outside of mated pairs and their dependent young. It is not clear how unusual this is among birds, because it has not been a frequent focus of avian research. I am not aware of any relevant evidence on other parrot species in the wild. The clearest examples of consistent association between nuclear families in other orders are in “communal” species that defend joint territories year-round, such as acorn woodpeckers (*Melanerpes formicivorus*) and noisy minors (*Manorina melanocephala*) (Brown 1987). Among species with more open social organization, sanderlings (*Calidris alba*) live in groups of fluid composition, but do not show association preferences for particular conspecifics (Myers 1983). The clearest example of stable bonds between different pairs within freely mixing groups occurs in the black vulture (*Coragyps atratus*). “Coalitions” of several nuclear families occur together consistently at roosts and carcasses, and apparently cooperate to compete over food (Rabenold 1986). Association levels are moderately correlated with genetic relatedness (Parker et al. 1995). A similar correlation between association in roosts and genetic relatedness was reported for green woodhoopoes (*Phoeniculus purpureus*) (Du Plessis 1993).

The functional significance of association preferences between pairs

If some mated pairs have other pairs as consistent associates, they might benefit either through mutual tolerance, or through cooperation in resource competition. I did not

find that frequent associates experienced lower rates of aggression, as might be expected under a mutual tolerance hypothesis. However, preferred associates did share foraging trees more often than other non-family members. This suggests that preferred associates might gain better access to favored feeding trees by defending them cooperatively. A similar advantage in feeding competition has been proposed to explain association preferences between genetically related nuclear families in black vultures (Parker et al. 1995). In glossy black-cockatoos, birds other than the initial pairs often became involved in severe fights (Chapter 5), suggesting that agonistic support between families could influence dominance and access to resources. Such fights were rare and difficult to collect data on, however, and I was not able to test this idea.

Aggression and Dominance

Aggressive interactions were rare, with the average individual engaging in no conflicts at all on a typical day. Most aggression was in the form of threats or supplants, rather than actual physical conflict. Most severe conflicts involved adult males fighting over young females that were not yet paired (Chapter 3). Despite the fact that supplants were relatively infrequent, a strongly linear dominance hierarchy was present in each year. The existence of a linear hierarchy despite the low rate of interactions suggests that the cockatoos may have a good memory for the outcomes of past agonistic encounters, or may learn about dominance by watching interactions (e.g., Freeman 1987). Linear dominance hierarchies have been reported previously in captive parrots (e.g., Kavanau 1987, Garnetzke-Stollmann & Franck 1991), but not in the wild. Saunders (1979 p. 202) specifically noted that Carnaby's cockatoos formed dominance hierarchies in captivity but not in the wild.

In contrast to the consistency within study periods, the dominance hierarchy changed substantially between years. This is difficult to interpret with only two time

periods to compare, and it is unclear how typical such year-to-year changes are or what causes them. The change was apparently not due to the hierarchy dissolving and being re-established each year, as dominance relationships were stable across seasons. It could have been related to changes in flock membership between the two years.

Although females did not have significantly higher dominance ranks than males, this could be because females confer their dominance status on their mates by supporting them in conflicts. Females were dominant to their mates, and only males suffered temporary dominance reversals when separated from their mates. Females are reportedly dominant to all males in the closely related Carnaby's cockatoo (Saunders 1979). In contrast, males are apparently dominant in another cockatoo, the galah (Rowley 1990). Females are usually dominant in the Psittaculini, a tropical Old World tribe of parrots, but neither sex dominates in Australian species of the tribe Platycercini (Smith 1975).

Dominance rank was correlated with nesting, probably because higher ranking birds have better access to needed resources, and are therefore more likely to reproduce. Alternatively, the correlation could have arisen because nesting pairs were more highly motivated in agonistic encounters. However, there was little nesting territoriality, few supplants occurred near nests, and individuals' dominance status did not appear to change when they established a nest. It is also possible that dominance and nesting were correlated only because both are influenced by a common underlying factor such as age or overall vigor. However, it seems likely that dominance directly affects nesting success. Many supplants involved contests over food trees, which vary substantially in their quality (Chapter 4), suggesting that dominance affects access to quality food resources (Clout 1989, Chapter 3). Moreover, the cockatoos are apparently energetically constrained while nesting, so that nutrition may be crucial to nesting success (Chapter 4).

Nest hollows may also be a limiting resource in this population (Chapters 2, 9, and 11), and dominance status is probably important in acquiring and defending a nest hollow.

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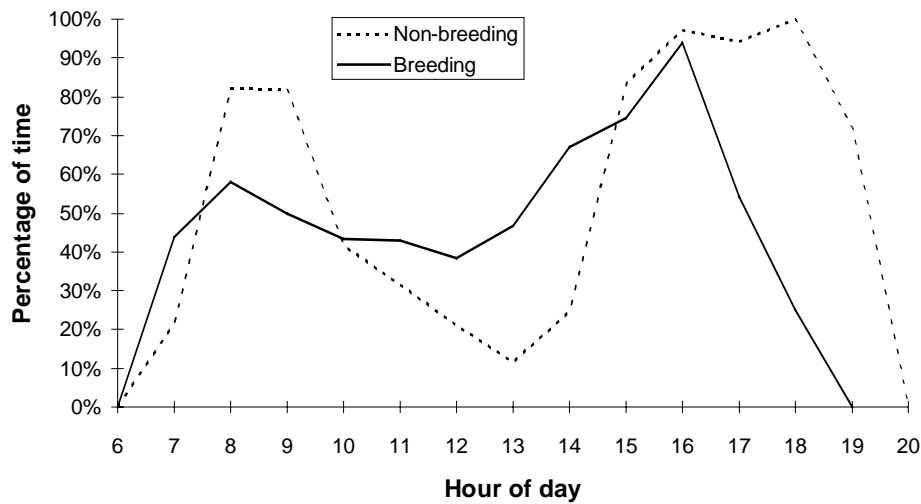


Figure 5.1. Amount of time spent foraging as a function of time of day and season, with nesting birds excluded. Calculated as the proportion of focal time points in which subject was foraging in each one-hour time block. Data are from 26 individuals, with a mean of 65 time points per individual.

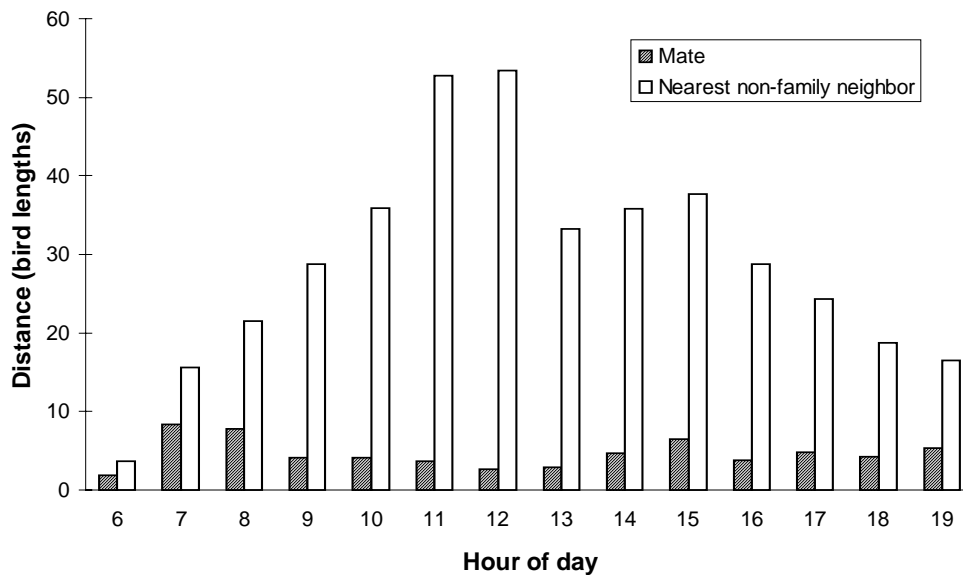


Figure 5.2. Average distance to mate and to nearest non-family member as a function of time of day. Data are from focal follows on 12 pairs, with a mean of 96 time points per pair.

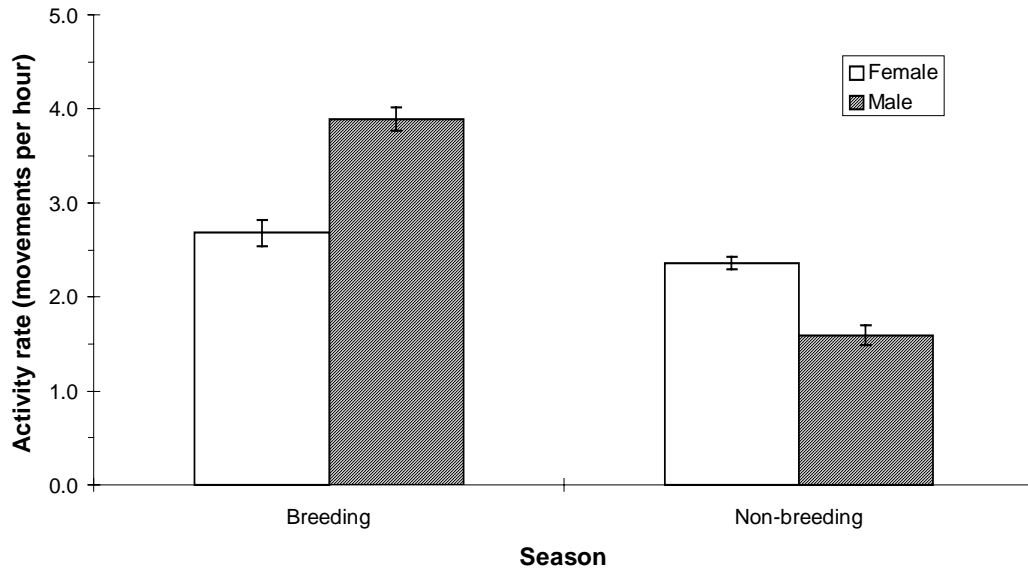


Figure 5.3. Movement rates as a function of sex and season. N = 11 individuals for each column. Bars show standard error of the mean across individuals.

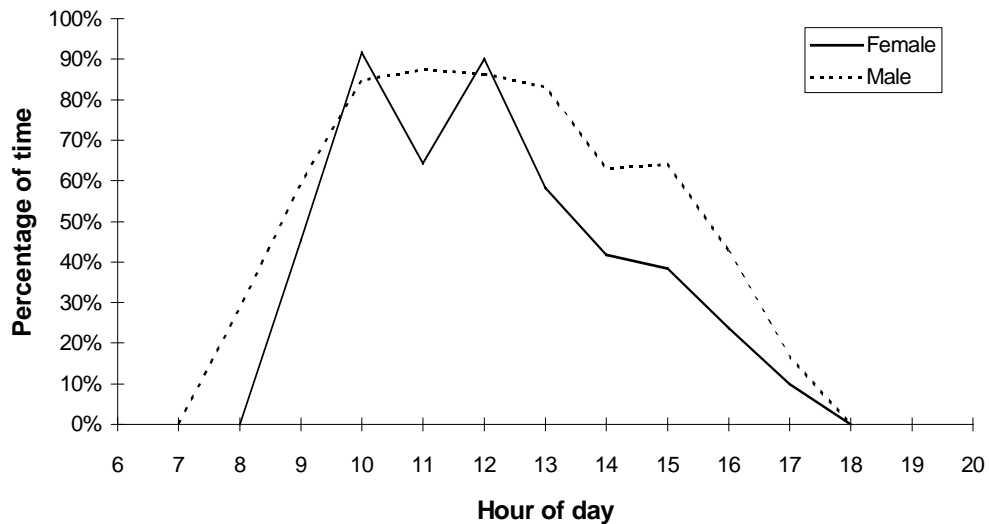


Figure 5.4. Proportion of time outside nest hollow that nesting pairs spent foraging, by time of day. Based on focal follows of two pairs, with a mean of 107 time points per individual. For comparison with non-nesting birds, see Figure 5.1.

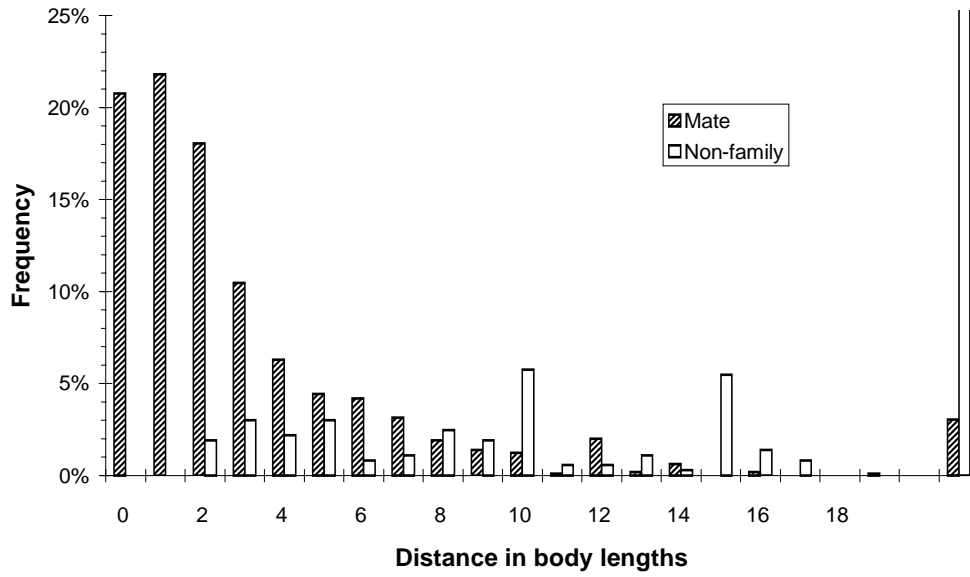


Figure 5.5. Frequency distribution of distances within pairs, and between paired individuals and their nearest non-family neighbor. The far right bar extends to 69%. Based on 13 pairs, N = 544 focal time points in which non-family neighbor was within 100 body lengths, N = 1146 for distance to mate.

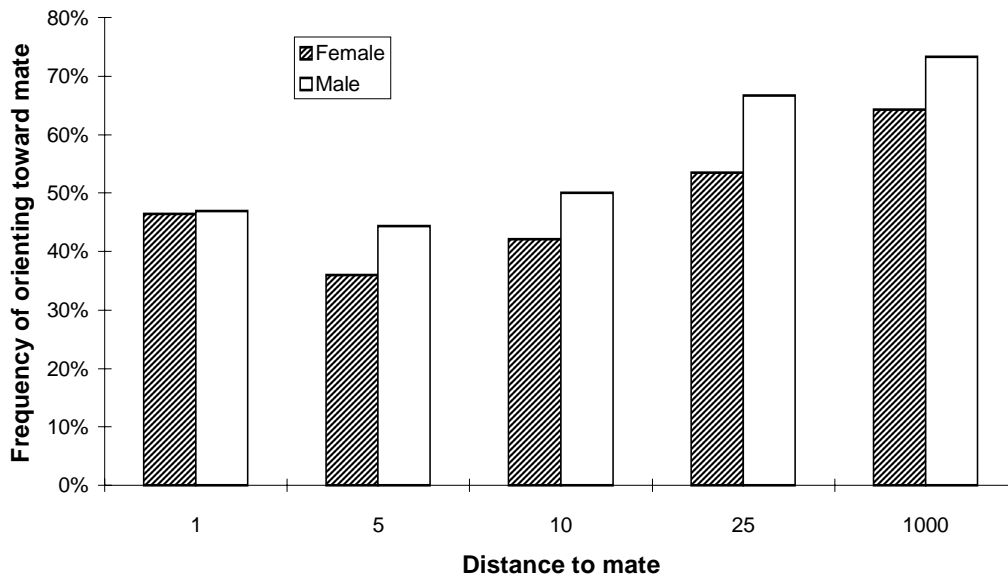


Figure 5.6. Proportion of time spent oriented toward mate as a function of sex and distance to mate. N = 1105 focal time points from 13 pairs.

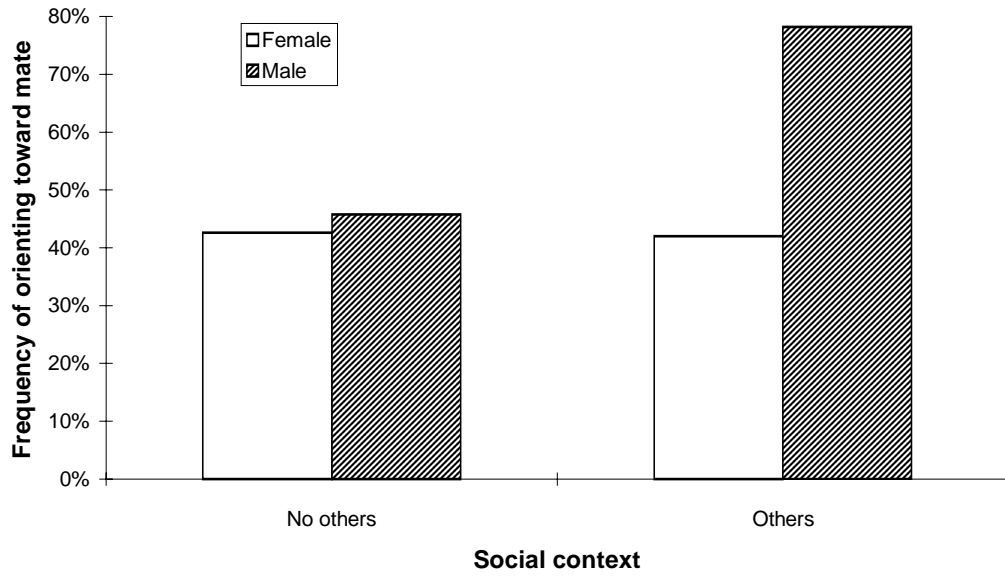


Figure 5.7. Frequency of orienting toward mate as a function of the presence of non-family birds in the same tree. Breeding season. Orientation toward the mate was significantly more frequent for males with non-family members present than for each of the other three conditions, $p < 0.002$ for each.

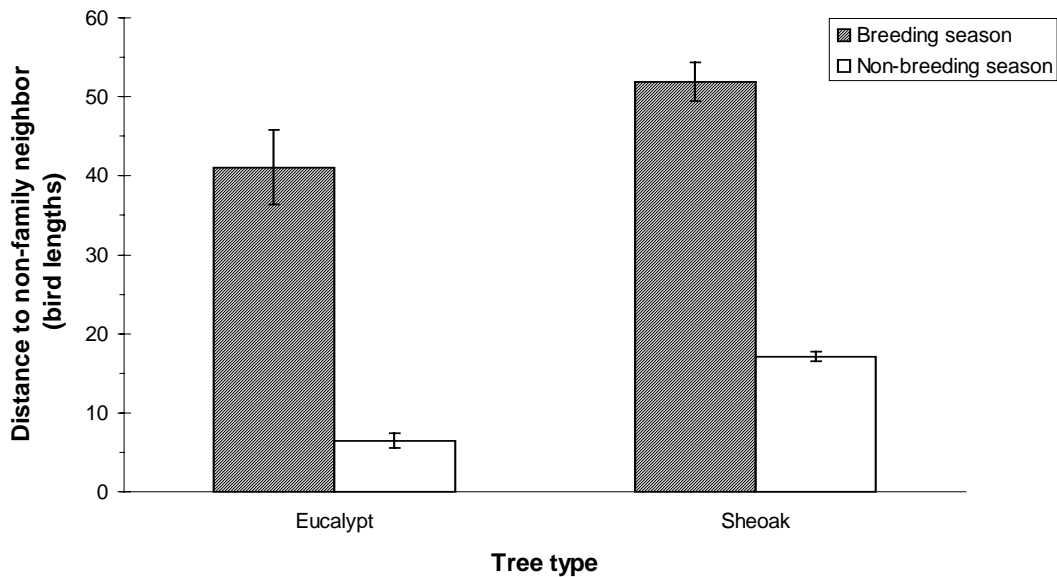


Figure 5.8. Seasonal changes in distance from mated pairs to their nearest non-family neighbors. Bars show standard errors. Based on 452 focal time points on 12 pairs without active nests, with distances truncated to 100 bird lengths. Seasonal differences are significant in both tree types (Mann-Whitney U test, $p < 0.001$ for each tree type).

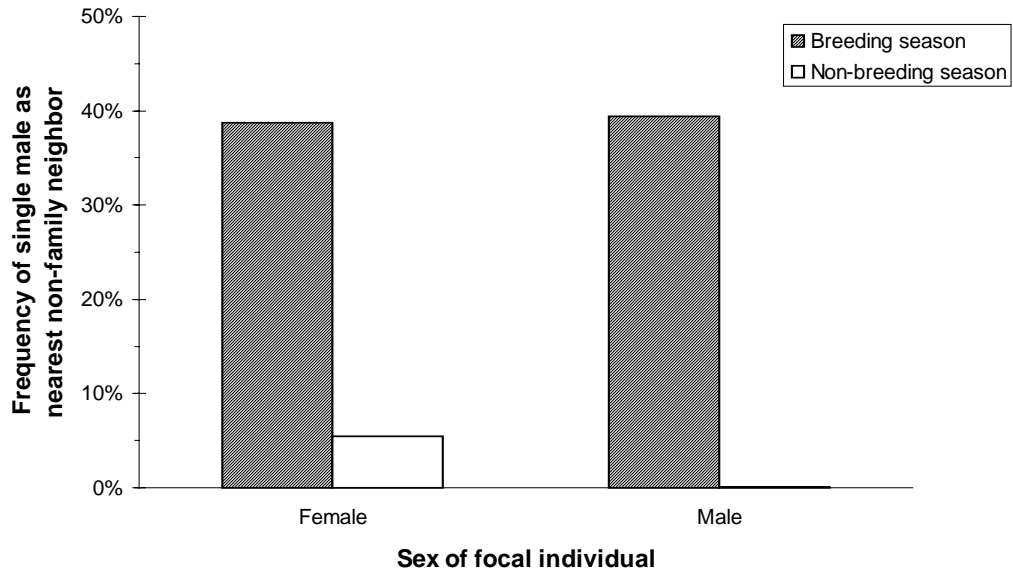


Figure 5.9. Frequency of unaccompanied males as nearest non-family neighbors of paired birds. All other nearest non-family neighbors were either paired birds or dependent juveniles. N = 969 time points from focal follows on 12 pairs.

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