

CHAPTER 6

THE FUNCTIONAL SIGNIFICANCE OF LONG TERM PAIR BONDS

ABSTRACT

One of the most striking features of social organization in many parrot species is the existence of strong year-round pair bonds within larger groups. Unlike those in most other birds, parrot pair bonds do not appear to function only in coordinating parental care. I tested several alternative hypotheses for the function of pair bonds among habituated wild glossy black-cockatoos (*Calyptorhynchus lathami*) in South Australia. The evidence supported the hypothesis that monogamous pairs function year round as social alliances in within-group resource competition with conspecifics. In contrast, the observed patterns of behaviors were not consistent with the hypothesis of a strictly reproductive role for the pair bond, or with an explanation based on extended mate guarding by males. The limited data available on social behavior in other species suggest that perennial pair bonds may serve a similar function in other parrots, and possibly in other birds as well.

INTRODUCTION

In most socially monogamous birds, pair bonds form only during the breeding season and clearly function primarily in coordinating parental care. In contrast, “perennial monogamy”, or year-round pair bonding, occurs in at least a dozen avian families, including cockatoos and other parrots (Psittaciformes) (Oring 1982). Monogamy in general, and perennial monogamy in particular, has received less theoretical attention than other mating systems (Wittenberger & Tilson 1980, Mock & Fujioka 1990). There is no accepted general explanation for the evolution of perennial monogamy, and it has probably evolved for different reasons in different taxa. Here I examine the function of perennial social monogamy in one species. The term “pair bond” has been used by some researchers to refer to persistent association patterns, and by others to refer to an emotional attachment (reviewed in Gubernick 1994). In this paper I adopt the former definition.

Parrots are at an extreme in the spectrum of monogamous mating systems. Mated pairs in most species persist year round, are maintained for years or even lifetimes within larger mixed-sex groups, and engage in affiliative behaviors at unusually high frequencies (Forshaw 1989, Arrowood 1991). These unusual features raise the question of why parrot pair bonds evolved the way they did, and how they function in natural social behavior. Parrot social behavior has rarely been studied outside of the breeding season, especially in the wild.

In the current study, I examine the function of pair bonds in an Australian parrot, the glossy black-cockatoo (*Calyptorhynchus lathami*), in the wild. This species forages almost exclusively on the trees of drooping sheoak trees (*Allocasuarina verticillata*). The cockatoos are not territorial, but individual trees vary substantially in their nutritional

quality, and they compete for access to high quality trees (Clout 1989, Chapters 4 & 5). Like most cockatoos, mated pairs stay together for many years. They stay in close proximity year round, perch and roost in contact, synchronize their activities, and engage in allofeeding, mutual preening, and frequent vocal exchanges (Chapter 5). I used behavioral observations of known, habituated wild individuals to test three hypotheses for the function of pair bonds in glossy black-cockatoos.

Hypothesis 1: Pair bonds function only in coordinating reproductive activities. This is the classic explanation for seasonal avian pair bonds, but it might apply to some cases of perennial monogamy as well. Oring (1982) suggested that the need for parental care beyond the breeding season might have lead to perennial pair bonds in swans and geese (Anserini). In white-tailed black-cockatoos (*Calyptorhynchus funereus*), juveniles accompany their parents until the onset of the following breeding season, and Rowley (1983) suggested that extended parental care is responsible for perennial pair bonds in this species. Juveniles also accompany their parents through the non-breeding season in the congeneric glossy black-cockatoo, and are fed and preened by them (Chapter 5). Thus extended parental care may result in perennial pair bonds in this species as well. I therefore tested the hypothesis that mated pairs remain together only to coordinate nesting and parental care.

Hypothesis 2: Apparent “pair bonds” actually result from mate guarding by males rather than mutual attraction. Monogamy in non-territorial species is generally thought to evolve when males can profitably defend exclusive access to only a single female. In this scenario, females are monogamous simply because the cost of accepting a male’s continual presence is less than the cost of resistance. When the sex ratio is male biased and competition for females is therefore intense, males may begin guarding well before the breeding season (Lack 1968, Wittenberger & Tilson 1980). The sex ratio is strongly male-biased in glossy black-cockatoos (Chapters 2, 5), and males do guard their mates

(Chapter 5). Thus perennial monogamy in this species could result from year-round mate-guarding by males.

Hypothesis 3: Monogamous pairs function as social alliances in within-group competition for resources. Individuals of many species form “alliances” that cooperate to compete more effectively with other group members (reviewed in Harcourt & de Wall 1992). Such alliances are usually, but not always, between genetic relatives. Oring (1982) suggested that perennial bonds might provide pairs with “unknown benefits” during the nonbreeding season, but the nature of these benefits has not been proposed. In glossy black-cockatoos, mated pairs cooperate in agonistic encounters over preferred food trees, and are able to supplant unpaired birds (Chapter 5). I hypothesize that by cooperating as social alliances year-round, glossy black-cockatoo pairs can better compete with other flock members over food and other limiting resources.

METHODS

The study was conducted on habituated cockatoos in Latham Conservation Park on Kangaroo Island, South Australia during Feb. - Dec. 1991 and Sept. 1992 - Aug. 1993. Birds were identified by sex and age category, and in most cases by individual, based on their plumage characteristics and other natural markings (Chapter 1). For brevity I use the term “pair” to refer to a monogamously pair-bonded heterosexual pair, and the term “family” to refer to a pair, with their dependent juvenile if they had one. Labels for specific behaviors follow Chapter 3, which provides more detailed descriptions. Data were collected using “perch scans” in 1991, and “focal follows” and *ad libitum* observations in both 1991 and 1993. See Chapter 1 for more information on the study site and observational methods.

To compare breeding and non-breeding seasons, I designated the breeding season as March - August, and the non-breeding season as September - February (Forshaw 1989, Chapter 1). For some analyses I divided the data based on whether the subjects were in eucalypts (*Eucalyptus spp.*), where they engaged mostly in resting and socializing, or in drooping sheoaks (*Allocasuarina verticillata*), where they engaged mostly in foraging. I followed Siegel & Castellan (1988) for significance tests of Spearman correlations, and used the Systat software package (Wilkinson 1992) for other statistical analyses. Unless otherwise noted, chi-square tests were tests of independence on two by two contingency tables with one degree of freedom, and all other tests were two-tailed.

I calculated dominance ranks based on observations of supplants during both focal follows and *ad libitum* observations. I ranked individuals using the algorithm of Brown (1975), with ambiguous relationships assigned using the PeckOrder program (J. Hailman, in lit.). See Chapter 5 for further details on the ranking procedure.

RESULTS

Hypothesis 1: Pair Bonds Function Only In Nesting and Parental Care

If pair bonds function primarily in the contexts of nesting and parental care, they should be associated with those activities. This leads to two predictions: 1) pair bonds should be stronger during the breeding season than the non-breeding season, and 2) during the breeding season pair bonds should be stronger among nesting pairs than non-nesting pairs. In addition to measuring proximity, I consider pairs' exclusivity and behavioral synchrony as aspects of the relationship that would be expected to co-vary with pair bond strength.

Were pair bonds stronger during the breeding season?

To test the first prediction, I compared pair proximity between seasons using focal time point data. To examine the effect of time of year independently of the activities of nesting and parental care, I included only focal follows on pairs without active nests or dependent juveniles. Contrary to the predicted pattern, proximity to the mate was lower during the breeding season than the non-breeding season in both sheoaks and eucalypts, although neither trend was statistically significant (Fig. 6.1). The exclusiveness of the pair bond, as indicated by the proportion of focal time points in which the nearest neighbor was the mate, did not differ significantly by season for either sex (chi-square < 1.6 , $p > 0.1$ for each). Also contrary to the prediction, pairs were slightly less synchronized in their activities during the breeding season. With activities divided into eating, perching, and flying, pair mates shared the same activity 89% of the time during the breeding season, and 95% of the time during the non-breeding season ($N = 640$, chi-square = 5.83, $p < 0.025$).

Were pair bonds stronger among nesting pairs than non-nesting pairs?

To test the second prediction, I compared pairs with and without active nests during the breeding season. This comparison was possible because in each year most pairs did not nest. I used focal time point data, excluding periods when the female was on the nest. Contrary to the prediction, birds with active nests stayed farther from their mates than did non-nesting birds, both while feeding and while perching (Fig. 6.2). Nesting pairs also had less, rather than more exclusive pair bonds, as indicated by the proportion of focal time points in which the nearest neighbor was the mate (85% vs. 99%, $N = 611$, chi-square = 49.1, $p < 0.005$). Nesting pairs were also less synchronized in their behavior than non-nesting pairs, but this was probably due to the different demands of nesting for the two sexes, as only females incubate.

Hypothesis 2: “Pair Bonds” Result From Mate Guarding by Males

If proximity within mated pairs results from mate guarding by males, males should be responsible for most of the movements that maintain proximity within pairs. To test this prediction, I used focal all-occurrence data to examine the frequency with which members of each sex moved toward and away from their mate. I tested three pairs of behaviors separately: Fly toward/Fly away, Walk toward/Walk away, and Initiate contact/End contact. I also tested the three behaviors pooled into a single tally. Sample sizes are shown in Table 6.1, and the results are illustrated in Fig. 6.3. None of the behaviors showed a significant difference between the sexes, either pooled across seasons or tested separately by season (chi-square, $p > 0.05$ for each).

Table 6.1. Sample sizes of movements by paired birds toward and away from mate. From focal all-occurrence data.

	Fly	Walk	Contact	Total
Breeding	306	280	34	620
Nonbreeding	45	167	20	232
Total	351	447	54	852

Hypothesis 3: Mated Pairs Function as Social Alliances

Cooperation in defensive behaviors

When paired birds were supplanted, they almost invariably flew directly to their mate (Chapter 5). This suggests that paired birds might stay near their mate in order to ward off potential aggression from other individuals. To test this idea I used focal time point data to examine whether the presence of non-family members perching in the same eucalypt affected how close pair members stayed to each other. To reduce the possible confounding effect of mate-guarding, I excluded cases in which the non-family birds included unpaired males. Mated pairs stayed significantly closer together when non-family members were present versus absent (mean = 1.0 versus 6.1 body lengths, $N = 86$ focal time points, Mann-Whitney $U = 1256$, $p < 0.005$). They also perched closer together as the number of other pairs in the tree increased (Fig. 6.4). Pair members also spent more time perching in contact with each other when non-family members were in the same eucalypt with them (33% vs. 18% of time points, $N = 334$, chi-square = 10.6, $p < 0.005$). This effect was strongest during the non-breeding season (Fig. 6.5).

A correlation between the presence of non-family members and greater proximity to the mate does not demonstrate a direct causal connection. To address this question I used focal all-occurrence data to examine the responses of paired birds to the arrivals and departures of non-family members. I scored the first movement toward or away from the partner within 20 minutes of a non-family member joining or leaving the pair's tree, including: Fly toward/Fly away, Walk toward/Walk away, and Initiate contact/End contact. Pair members did adjust their proximity as a direct response to arrivals and departures of non-family members. Seven of eight movements after arrivals were toward the mate, while four of four movements following departures were away from the mate (Fisher exact test, one-tailed $p = 0.005$). There was no significant sex difference in the

response: females were responsible for five of seven moves toward and three of five moves away from the mate (Fisher exact test, one-tailed $p = 0.50$).

If paired birds approach their mates as a means to ward off potential aggression from other individuals, the extent of this behavior should reflect the pair's dominance rank and thus its vulnerability. To test this prediction, I calculated each pair's average proximity to the mate in eucalypts, both with and without non-family members present. (Non-family members were rarely present in drooping sheoaks.) The difference in average proximity under these two conditions indicated how strongly the pair reacted to the presence of non-family members. Because pairs changed ranks between years, I analyzed each year separately. In each year, low ranking pairs showed a stronger tendency to increase proximity in the presence of non-family members than high ranking pairs. This trend reached significance in 1991 with data on seven pairs (Spearman correlation, $R_s = 0.714$, $p = 0.05$, one tailed), but not in 1993 with observations on only four pairs ($R_s = 0.40$, $p > 0.25$).

Lower ranking pairs also tended to maintain both closer physical proximity and more visual contact with each other than higher ranking pairs. These trends did not reach significance in either year with six and seven pairs respectively, but both were true in both years. (Physical proximity based on mean within-pair distance in focal time points, $R_s = 0.31$ and 0.25 in 1991 and 1993 respectively. Visual contact based on proportion of focal time points oriented toward partner, pooling male and female for each pair, $R_s = 0.25$ and 0.07 , respectively.)

Cooperation in aggressive behaviors

Mated pairs often coordinated their supplants and other aggressive behavior (Chapter 5). If coordinated supplants are more effective than attempts by solitary individuals, paired birds might be expected to use them disproportionately often against

more formidable targets. To test this prediction, I examined all interactions in which paired birds supplanted non-mates. The targets of coordinated supplants had higher ranks relative to the aggressor than did targets of solitary supplants (mean rank difference = 3.8 vs. 5.9, $N = 202$, Mann-Whitney $U = 5132$, $p = 0.002$). This was partly because coordinated supplants were never directed at subadults or juveniles, which had the lowest ranks. However, when I included only supplants of paired adults, aggressors still used coordinated supplants against higher ranking opponents than they used solitary supplants against (mean rank difference = 3.8 vs. 5.6, $N = 179$, Mann-Whitney $U = 4261$, $p = 0.005$). Moreover, paired birds used coordinated supplants against united pairs more frequently than against solitary individuals (30.2% vs. 10.2% of supplants, $N = 102$, chi-square = 6.61, $p < 0.025$).

Pair bonds and dominance status

If pair bonds are important in determining the outcomes of aggressive encounters, dominance status should be related to pairing status. Consistent with this prediction, all paired birds ranked above all unpaired males (no unpaired females were present during the study). Moreover, aggression was completely uni-directional. In 53 supplants between paired and unpaired adults, the paired birds were the aggressors in every case, even though only four interactions were actually coordinated supplants by both pair members.

Among paired birds, individuals' dominance ranks were highly correlated with those of their mates (Fig. 6.6). Six pairs in each year were observed in enough interactions to be assigned dominance ranks, including three that appeared in both years. Treating pair-years as independent data points, the Spearman correlation was 0.85 ($N = 12$, $p < 0.001$). Each year also showed a significant correlation separately ($N = 6$, $p < 0.05$ for each). In fact, the actual correlation between the ranks of mated pairs may be higher than these figures indicate. The assigned dominance ranks were only estimates

because not all dyads were observed interacting. If it was assumed that all mated pairs shared adjacent ranks, the hierarchies for each year could be rearranged accordingly without introducing any reversals or non-transitive relationships, with the exception of one pair in 1991.

DISCUSSION

Previous Explanations for Avian Pair Bonds

Most suggestions in the literature for the functions of perennial monogamy in birds are based on special ecological circumstances that do not apply to glossy black-cockatoos. For example, if nesting must be completed quickly, being paired before the breeding season starts could save valuable time. This may apply to migratory species that nest at very high latitudes (Rowley 1983), or to opportunistic breeders such as budgerigars (*Melopsittacus undulatus*), which nest in arid areas after unpredictable rainfall (Trillmich 1976). In contrast, glossy black-cockatoos have a long and predictable breeding season (Chapter 5). Some tropical species hold permanent feeding territories that cannot be defended by a single bird, and apparent pair bonds may arise from attachment to a territory rather than a mate *per se* (Oring 1982, Mock & Fujioka 1990). Glossy black-cockatoos do not hold feeding territories, however, nor do they defend permanent nesting sites (Chapter 5). Another hypothesis is that migratory species maintain pair bonds year-round to enable them to relocate their mate each breeding season, because retaining the same partner increases reproductive success. However, there is little evidence that a permanent pair bond is necessary for pair members to relocate each other, even among migratory species (Rowley 1983). Particularly in sedentary species such as the glossy black-cockatoo, permanent pair bonds are probably

unnecessary to re-locate the previous year's mate each breeding season (Mock & Fujioka 1990).

My observations on glossy black-cockatoos did not support the first two hypotheses I tested. The characteristics of pair bonds were not consistent with a purely reproductive function, because they did not increase in strength either during the breeding season, or among nesting pairs as compared to non-nesting pairs during the breeding season. Both exclusive proximity to the mate and behavioral synchrony within pairs were also at least as pronounced in the non-breeding season as in the breeding season, and among non-nesting as nesting pairs during the breeding season. A desirable additional test would be to compare pair bonds during the nonbreeding season between pairs with and without dependent juveniles. This was not possible in the current study because too few pairs successfully fledged young.

Mate guarding by males also did not appear to be a primary factor in maintaining pair bonds. The two sexes were equally responsible for maintaining proximity to their mates in general, as well as in response to the arrival of other individuals. Thus unlike in ring doves (*Streptopelia risoria*) and some other birds (Lumpkin et al. 1982), the relationship between mated glossy black-cockatoos is meaningfully described as a mutual social bond, rather than simply as proximity resulting from mate guarding by males.

Clearly, cooperative parental care is extensive in this species, and mate guarding also occurs (Chapter 5). These factors probably influence the nature of the pair relationship, but they are not sufficient to explain the observed patterns of proximity within glossy black-cockatoo pairs. Moreover, any hypotheses that do not involve extensive cooperation within mated pairs fail to explain the frequent and relatively symmetrical displays of affiliative behavior that are so striking in glossy black-cockatoos and other parrots (Arrowood & Saunders 1991).

Mated Pairs as Social Alliances in Glossy Black-Cockatoos

Several lines of evidence support the hypothesis that mated pairs function as social alliances in resource competition. Paired birds were more likely to coordinate their aggressive behavior when their opponents were more formidable, either because of high dominance rank or because they were a united pair. Pair bonds were also important in defensive contexts, as proximity to the mate appeared to ward off potential aggression. Paired birds that are supplanted while apart immediately join their mates (Chapter 5), and this tactic appeared to be effective. While separated from their mate, paired birds were often supplanted by single individuals, but when close enough together to present a united front they were usually supplanted only by coordinated pairs. Paired birds also adjusted proximity to their mate preemptively to meet varying levels of threat from conspecifics. Pairs moved closer together when non-family members joined their tree, and maintained closer average proximity if they were lower ranking and thus subject to more frequent aggression. This behavior was not due to male mate-guarding, as it was exhibited equally by both sexes and was stronger during the non-breeding season (Fig. 6.5). Scott (1980) reported similar tactics in mated pairs of Bewick's swans (*Cygnus columbianus*), which apparently inhibit aggression from conspecifics by staying closer to the mate when conspecifics are nearby.

Several other features of glossy black-cockatoo social structure suggest that pair bonds are important to dominance status. Paired birds shared similar dominance ranks, probably because they consistently supported each other in agonistic encounters. Consistent agonistic support is known to confer adjacent dominant ranks in some mammalian species (e.g., spotted hyenas *Crocuta crocuta*, Frank 1986; old world monkeys, Chapais 1992). Among birds, a similar phenomenon occurs in Bewick's swans (Scott 1980), and jackdaws (*Corvus monedula*, Wechsler 1988). An alternative explanation for this pattern is that the cockatoos might mate assortatively based on their

dominance ranks. This seems unlikely though, because pair bonds are very stable, while dominance ranks vary between years (Chapter 5).

The fact that all paired birds were dominant to all unpaired birds also suggests that pair bonds are essential for achieving dominance. In principle, the same pattern could result if dominance led to pairing, rather than vice versa. However, this seems unlikely because I never observed an unpaired adult supplant a paired adult, suggesting that it is impossible to dominate any paired bird without the aid of a mate. More escalated forms of aggression, including physical fights, were infrequent and difficult to collect data on, but are probably crucial to dominance status. The fact that paired birds almost always joined fights that their mate was involved in (Chapter 5) suggests that pair bonds are important in escalated conflicts as well as supplanting interactions.

The increased dominance status that pairs achieve by cooperating is probably most important in gaining access to high quality food trees. This determines how efficiently they can forage, which is crucial because extracting enough food requires most of the cockatoos' time (Chapter 4). Access to quality trees may also be an important benefit that pairs provide for their juveniles, which accompany their parents and feed with them during their first year (Chapter 5). Nonetheless, the results of this study show that the presence of juveniles is not a necessary condition for pairs to maintain close proximity and cooperative aggression. Suitable nesting hollows may also be a limiting resource for this species, but nest hollow competition does not appear to be a principal factor in the maintenance of pair alliances. Unlike galahs (*Eolophus roseicapillus*) (Rowley 1990), glossy black-cockatoos do not defend nest hollows outside of the breeding season, yet pair alliances persist year round.

Mated Pairs as Social Alliances in Other Parrots

Do mated pairs function as social alliances in other parrots? Waltman & Beissinger (1992) suggested that parrot pairs must cooperate to compete for nest hollows, and that this may account for the high degree of pair cohesion in many species. However, captive studies have shown that in various species mated pairs cooperate extensively in intraspecific competition not just over nest hollows, but over dominance and resource access in general. In spectacled parrotlets (*Forpus conspicillatus*), “Pair mates cooperate in agonistic situations. As long as they stay close together they hold the same rank-order position. ... Pairs were always higher ranking than single adults.” (Garnetzke-Stollmann & Franck 1991). Paired birds are also dominant over all unpaired birds in the white-fronted amazon (*Amazona albifrons*) (Levinson 1980). Lorikeet (*Trichoglossus spp.*) pair-mates “cooperate fully... during agonistic interactions with other individuals and pairs”, and their coordinated displays “function as cooperative aggressive demonstrations directed at rivals” (Serpell 1981). Similarly, coordinated duets, which apparently serve other functions in non-parrot species, function as cooperative threats against conspecifics in canary-winged parakeets (*Brotogeris versicolurus*, Arrowood 1988).

There is also some experimental evidence that pair bonds are crucial to dominance status in captive parrots. When two pairs of white-tailed black-cockatoos were caged together they quickly formed a hierarchy with females dominant to males, and members of one pair dominant over the other within the sexes. When the dominant female was removed, the dominant male dropped to the bottom of the hierarchy, while removing the dominant male did not affect the dominant female’s status (Saunders 1979). Similarly, Garnetzke-Stollmann & Franck (1991) found that spectacled parrotlets of both sexes often suffered an immediate and dramatic drop within the hierarchy when they lost their mate.

Are Homosexual Pair Bonds in Parrots Adaptive?

If pair bonds are important as social alliances, this might explain parrots' puzzling tendency to form reproductively inappropriate pair bonds. Many parrot species, including cockatoos, form homosexual pair bonds in captivity (e.g., lovebirds *Agapornis spp.*, Dilger 1960; orange-fronted parakeet *Aratinga canicularis*, Hardy 1963; budgerigar, Brockway 1964; orange-chinned parakeet *Brotogeris jugularis*, Power 1967; lorikeets *Trichoglossus spp.*, Serpell 1981; canary-winged parakeet, Arrowood 1988; galah, Rogers & McCulloch 1981, Rowley 1990 p. 60). Previous workers have suggested that cockatoos may form homosexual pair bonds in the wild (Rogers & McCulloch 1981), and indeed glossy black-cockatoos do (Chapter 5).

Although this behavior could be a maladaptive behavioral "error", another interpretation is possible. In other animals, genetic relatives are typically preferred as allies, both because they provide an inclusive fitness "bonus", and because alliances among relatives may be more stable and efficient (Harcourt 1989). However, when relatives are unavailable, unrelated individuals are sometimes accepted as allies (e.g.; lions *Panthera leo*, Packer & Pusey 1982; vervet monkeys *Cercopithecus aethiops*, Cheney & Seyfarth 1987; cheetahs *Acinonyx jubatus*, Caro 1994 pp. 235-8). A social alliance with a reproductive partner is analogous, in that investing in the mate can increase the donor's inclusive fitness (Ligon 1983, Alexander 1987 p. 70). The reproductive partner is therefore the best alliance partner. However, if a reproductive partner is not available and alliances are crucial for resource acquisition, other individuals might be accepted. Facultative homosexual bonds may thus be adaptive responses to a lack of suitable opposite-sex alliance partners. If these same-sex alliances improve their members' dominance ranks and access to resources, they might increase the probability both of surviving, and of eventually acquiring a reproductive partner. Female homosexual pair bonds in several species of gulls (*Larus spp.*) may also be adaptive, but

in this case because they facilitate parental care rather than competition against conspecifics (Oring 1982).

Social Alliances and the Evolution of Intelligence

If parrots routinely use social alliances in competition with conspecifics, this may have implications for the evolution of intelligence and brain size. Brains are metabolically expensive, and the fact that they are much larger relative to body size in some species than others suggests that cognitive demands vary considerably between taxa (Jerison 1973, 1985). A number of researchers have suggested that the unusually large brains of mammals such as primates and cetaceans may be an evolutionary response to the cognitive demands of complex social interactions, in particular the use of coalitions and alliances within larger social groups (Byrne & Whiten 1988, Harcourt & de Waal 1992, Byrne 1994).

Parrots have the largest brains relative to their body size of any birds (Pearson 1972, pp. 596, 605). They also show evidence in captivity of cognitive abilities exceeding those demonstrated in most other animals (Moore 1992, Heyes 1993, Pepperberg 1993). There has been little evidence until now for what selective pressures might have favored these unusual traits, or what functions they serve in the wild. If pair bonds in most parrots take on the novel role of year-round alliances in resource competition within groups, then the hypotheses previously used to explain the extremes in mammalian brain size may apply equally well to parrots.

Monogamous Pairs as Social Alliances in Other Species

Mated pairs may cooperate to compete for resources within flocks in non-parrot bird species as well, but this appears to be relatively rare. Most apparent examples are from the geese and swans (Anserini). The members of perennially monogamous pairs

support one another in agonistic encounters, and apparently as a result, dominate unpaired birds in several species (greater white-fronted geese *Anser albifrons*, Boyd 1953; Canada geese *Branta canadensis*, Raveling 1970; Bewick's swans, Scott 1980; barnacle geese *Branta leucopsis*, Black & Owen 1989; snow geese *Chen caerulescens*, Gregoire & Ankney 1990). Given this parallel function of pair bonds in geese and swans, it is worth noting that homosexual pairs have also been reported in Canada geese (Collias and John 1959), and in black swans (*Cygnus atratus*, Braithwaite 1970). Perennially monogamous jackdaws also coordinate aggression with their mates, and win a higher proportion of contests against dominant birds when their mate supports them (Wechsler 1988).

The presence of the mate improves access to food resources in a few seasonally bonded species as well, but cooperation is much less well-developed in these species (e.g., black-capped chickadees, *Parus atricapillus*, Orr & Verbeek 1984; pigeons, *Columba livia*, Lefebvre & Henderson 1986). Pair bonds are most likely to be important as social alliances in perennially monogamous and long lived species with high confidence of paternity and extended parental care. In such species mated pairs share many opportunities for cooperative nepotistic effort. For this reason they are primed for alliance formation in the same way as genetic relatives, because their reproductive interests overlap substantially (Alexander 1987 p. 70).

Potential Tests of the “Mated Pair as Social Alliance” Hypothesis

The hypothesis of pair bonds as social alliances leads to several predictions beyond those tested here. One is that pair bonds should be more prominent when resource competition is more intense. This prediction would be easier to test in glossy black-cockatoos than most species, because their extreme foraging specialization makes it feasible to measure the quantity and quality of available food (Chapters 2 and 4).

Competition for nest hollows could also be experimentally manipulated by adding nest boxes (e.g., Chapter 11).

A second prediction is that paired individuals should have higher foraging success when with their mate than when they forage alone. This would usually be difficult to test in glossy black-cockatoos without capturing and holding mates, because pairs so rarely forage separately. However, it could be tested during the nestling stage when males forage both alone and with their mates (Chapter 5). Foraging success can be measured fairly accurately by combining observed feeding rates with measures of seed quantity and quality per cone (Chapter 4).

Finally, a central prediction is that dominance status should change sharply with the gain or loss of a mate. I was not able to observe these events in the field, but the prediction could be tested through either observational or experimental studies in the field or lab (e.g., Saunders 1979, Garnetzke-Stollmann & Franck 1991).

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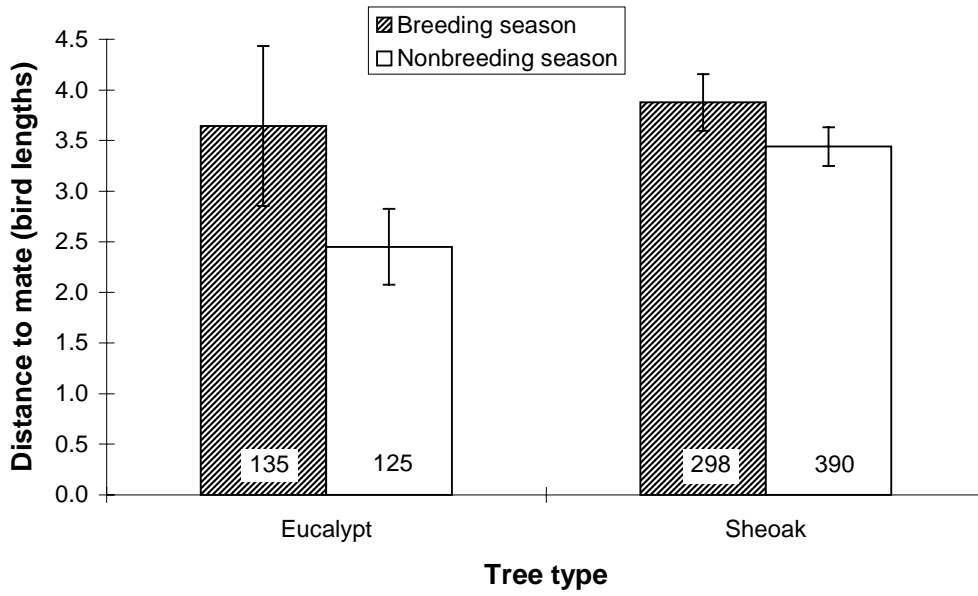


Figure 6.1. Seasonal differences in proximity to the mate in perching trees (eucalypts) and feeding trees (drooping sheoaks). Bars show standard errors, and samples sizes are shown at the base of each column. The difference was marginally significant in eucalypts (Mann-Whitney $U = 9569$, $p = 0.059$), but not in drooping sheoaks ($p = 0.79$).

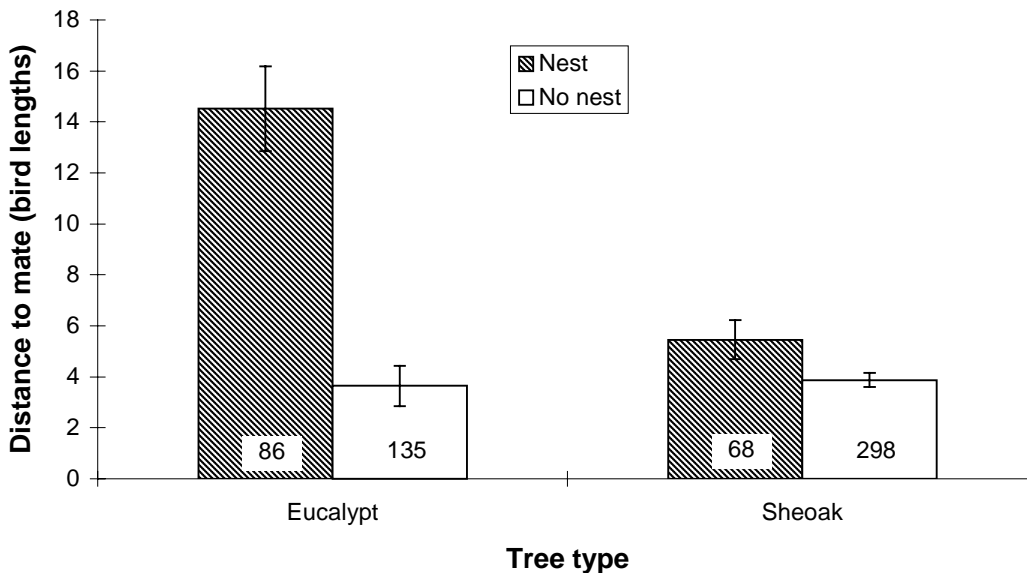


Figure 6.2. Differences in proximity to the mate during the breeding season in pairs with versus without active nests. The difference was highly significant in both tree types (eucalypts: Mann-Whitney $U = 2221$, $p < 0.005$; drooping sheoaks: $U = 6376$, $p < 0.005$).

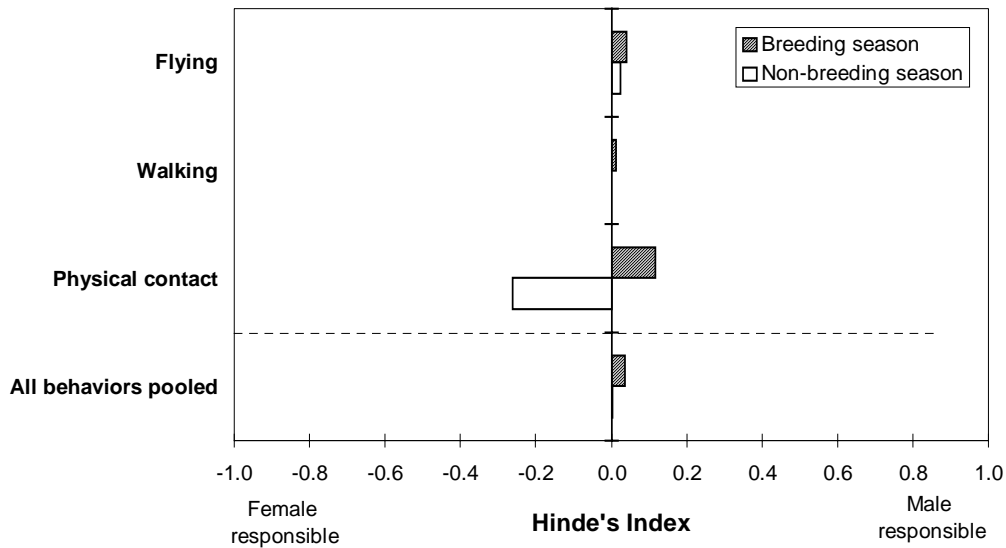


Figure 6.3. Sex differences in the maintenance of proximity to the mate. Hinde's index = $T_M/(T_M+T_F) - A_M/(A_M+A_F)$, where T_M and T_F are the number of times that males and females respectively moved toward their mate, and A_M and A_F are the number of times that each sex moved away (Martin & Bateson 1993, p. 79). The index ranges from -1 (females totally responsible for maintaining proximity) to +1 (males totally responsible). A value of 0 indicates that both sexes were equally responsible for maintaining proximity.

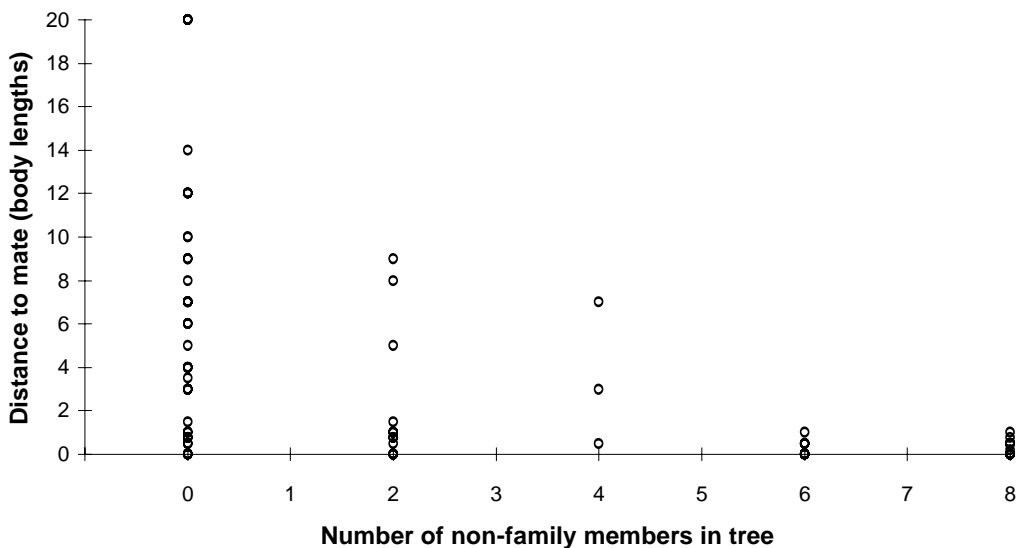


Figure 6.4. Distance between the members of mated pairs as a function of the number of non-family individuals perched in the same eucalypt. Cases involving unaccompanied males were excluded to avoid confounding effect of mate guarding. Spearman rank correlation, $N = 86$, $R_s = -0.62$, $p < 0.001$.

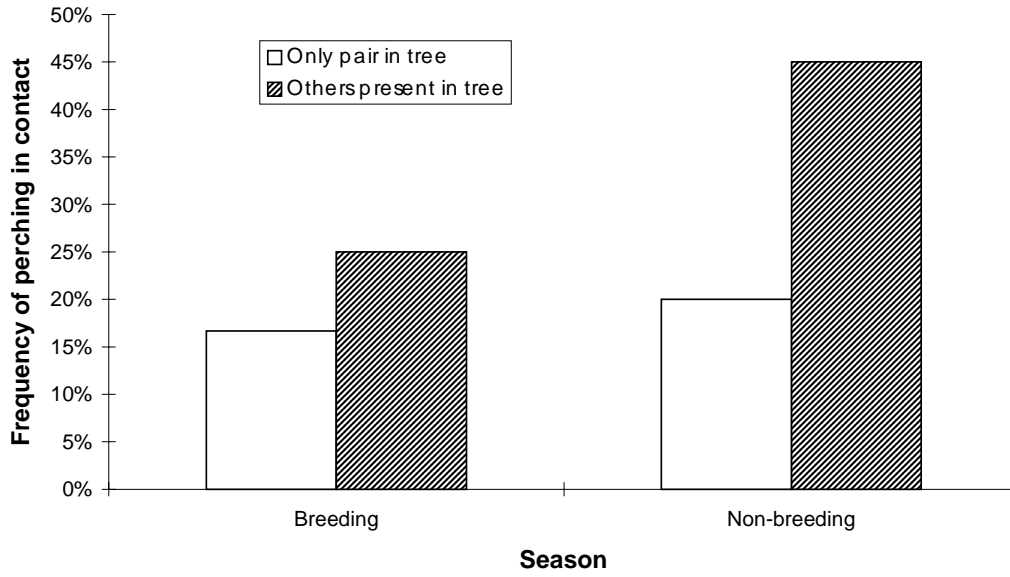


Figure 6.5. Effect of the presence of other individuals on the frequency with which mated pairs perched in contact.

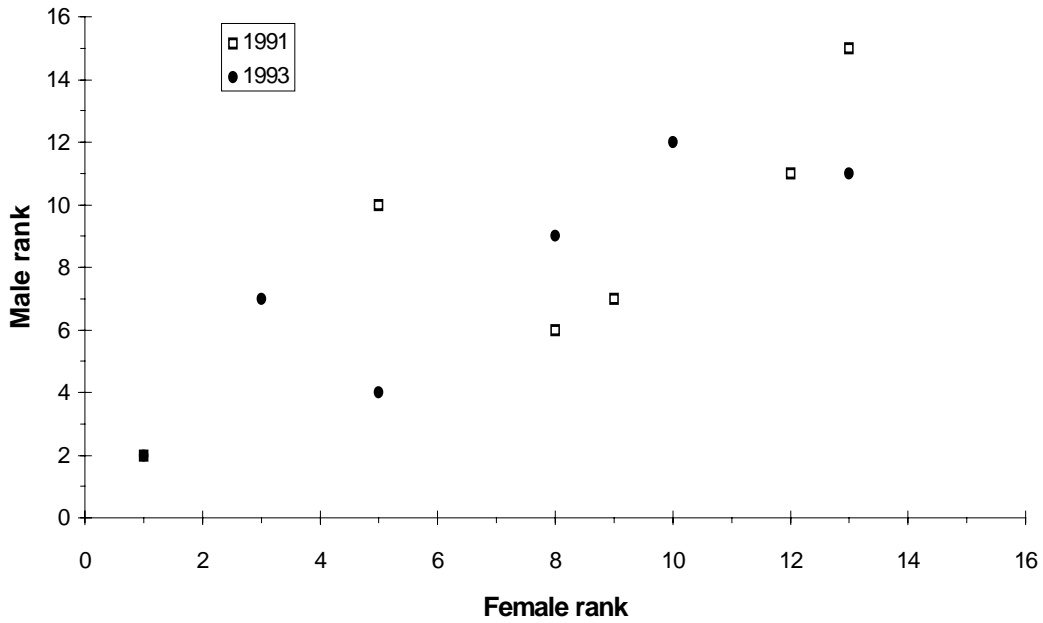


Figure 6.6. Relationship between the dominance ranks of paired birds and their mates. Each data point represents one mated pair in one year.

REFERENCES

- Alexander, R.D. 1987. *The Biology of Moral Systems*. Aldine de Gruyter, New York.
- Arrowood, P.C. 1988. Duetting, pair bonding, and agonistic display in parakeet pairs. *Behaviour* 106(1-2):129-157.
- Arrowood, P.C. 1991. Male-male, female-female, and male-female interactions within captive canary-winged parakeet *Brotogeris v. versicolurus* flocks. Pp. 666-672 in: *Acta XX Congressus Internationalis Ornithologici*. Christchurch. New Zealand Ornithological Congress.
- Arrowood, P.C. and D.A. Saunders. 1991. Concluding remarks: Symposium on the ecology and social behaviour of parrots and parakeets. Pp. 697-698 in: *Acta XX Congressus Internationalis Ornithologici*. Christchurch. New Zealand Ornithological Congress.
- Black, J.M. and M. Owen. 1989. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Anim. Behav.* 37: 199-209.
- Boyd, H. 1953. On encounters between wild white-fronted geese in winter flocks. *Behaviour* 37: 291-319.
- Braithwaite, L.W. 1970. The black swan. *Australian Natural History* 16:379-79.
- Brockway, B.F. 1964. Ethological studies of the budgerigar: Reproductive behavior. *Behaviour* 22:193-222.
- Byrne, R.W. 1994. The evolution of intelligence. In: Slater, P.J.B. and Halliday, T.R., eds. *Behaviour and Evolution*. Cambridge University Press, Cambridge.
- Byrne, R.W. & Whiten, A. 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Oxford: Oxford University Press.
- Cairns, S.J. and S.J. Schwager. 1987. A comparison of association indices. *Anim. Behav.* 35:1454-1469.
- Caro, T.M. 1994. *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species*. University of Chicago Press, Chicago.

- Chapais, B. 1992. The role of alliances in social inheritance of rank among female primates. In: *Coalitions and Alliances in Humans and Other Animals*. A.H. Harcourt and F.B.M. de Waal, eds. Oxford University Press, Oxford. Pp. 29-60.
- Cheney, D. and R. Seyfarth. 1987. The influence of intergroup competition on the survival and reproduction of female vervet monkeys. *Behav. Ecol. Sociobiol.* 21:375-86.
- Clutton-Brock, T.H. 1989. Mammalian mating systems. *Proc. R. Soc. Lond. B* 236:339-372
- Collias, N. and L. John. 1959. Social behavior and breeding success in Canada Geese (*Branta canadensis*) confined under semi-natural conditions. *Auk* 76:478-509.
- Dilger, W.C. 1960. The comparative ethology of the African genus *Agapornis*. *Z. Tierpsychol.*, 17:649-85.
- Forshaw, J.M. 1989. *Parrots of the World*. 3rd edition. Lansdowne, Melbourne.
- Frank, L.G. 1986. Social organization of the spotted hyaena (*Crocuta crocuta*). II. Dominance and reproduction. *Anim. Behav.* 34:1510-27.
- Garnetzke-Stollmann, K. and D. Franck. 1991. Socialisation tactics of the spectacled parrotlet (*Forpus conspicillatus*). *Behaviour* 119 (1-2): 1-29.
- Ginsberg J.R. and T.P. Young. 1992. Measuring associations between individuals or groups in behavioural studies. *Anim. Behav.* 44:377-9.
- Gregoire, P.E. and C.D. Ankney. 1990. Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. *Auk* 107: 550-560.
- Gubernick, D.J. 1994. Biparental care and male-female relations in mammals. In: *Infanticide and Parental Care*. S. Parmigiani and F.S. vom Saal, eds. Harwood Academic Publishers, Chur, Switzerland. Pp. 427-464.
- Harcourt, A.H. 1989. Social influences on competitive ability: alliances and their consequences. In: *Comparative Socioecology*, V. Standen and R.A. Foley, eds. Pp. 223-42. Blackwell, Oxford.
- Harcourt, A.H. and F.B.M. de Waal, eds. 1992. *Coalitions and alliances in humans and other animals*. Oxford University Press, Oxford.
- Hardy, J.W. 1963. Epigamic and reproductive behavior of the orange-fronted parakeet. *Condor* 65:169-99.
- Heyes, C.M. 1993. Imitation, culture and cognition. *Anim. Behav.* 46:999-1010.
- Jerison, H.J. 1973. *Evolution of the Brain and Intelligence*. Academic Press, NY.

- Jerison, H.J. 1985. Animal intelligence as encephalisation. In: Animal Intelligence (L. Weiskrantz, ed.), pp. 21-35. Clarendon Press, Oxford.
- Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.
- Lefebvre, L. and D. Henderson. 1986. Resource defense and priority of access to food by the mate in pigeons. Canadian Journal of Zoology 64:1889-92.
- Levinson, S. 1980. The social behavior of the white-fronted amazon (*Amazona albifrons*). In: Conservation of New World Parrots, R.F. Pasquier, ed. Pp. 403-417.
- Ligon, J.D. 1983. Cooperation and reciprocity in avian social systems. American Naturalist 121: 366-84.
- Lumpkin, S., K. Kessel, P.G. Zenone, and C.J. Erickson. 1982. Proximity between the sexes in ring doves: social bond or surveillance? Anim. Behav. 30:506-13.
- Martin, P. and P. Bateson. 1993. Measuring Behavior: An Introductory Guide. 2nd edn. Cambridge University Press, Cambridge.
- Mock, D.W. and M. Fujioka. 1990. Monogamy and long-term pair bonding in vertebrates. Trends Ecol. Evol. 5(2): 39-43.
- Moore, B.R. 1992. Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. Behaviour 122(3-4):231-263
- Oring, L. 1982. Avian mating systems. In: Avian Biology, Vol. VI. Ed by Farner, King, and Parkes. Academic Press, NY.
- Orr, C.D. and N.A.M. Verbeek. 1984. Female demands: some fitness implications in chickadee flocks. Can. J. Zool. 62: 2550-2552.
- Packer, C. and A. Pusey. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? Nature 296:740-42.
- Pearson, R. 1972. The Avian Brain. Academic Press, NY.
- Pepperberg, I.M. 1993. Cognition and communication in an African grey parrot (*Psittacus erithacus*): Studies on a nonhuman, nonprimate, nonmammalian subject. In: H.L. Roitblat, L.M. Herman, and P.E. Nachtigall, eds. Language and Communication: Comparative Perspectives. Lawrence Erlbaum Associates, New Jersey.
- Power, D.M. 1967. Epigamic and reproductive behaviour of orange-chinned parakeets in captivity. Condor 69:28-41.

- Raveling, D.G. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. *Behaviour* 37: 291-317.
- Rogers, L.J. and McCulloch, H. 1981. Pair-bonding in the galah *Cacatua roseicapilla*. *Bird Behaviour* 3:80-92.
- Rowley, I. 1983. Re-mating in birds. In: *Mate Choice*. P. Bateson ed. Cambridge Univ. Press, Cambridge.
- Rowley, I. 1990. Behavioural Ecology of the Galah *Eolophus roseicapillus* in the Wheatbelt of Western Australia. Surrey Beatty & Sons, Chipping Norton NSW.
- Saunders, D.A. 1974. The function of displays in the breeding of the white-tailed black cockatoo. *Emu* 74:43-46.
- Saunders, D.A. 1979. The biology of the short-billed form of the white-tailed black cockatoo *Calyptorhynchus funereus latirostris* Carnaby. Ph.D. Thesis, University of Western Australia.
- Scott, D.K. 1980. Functional aspects of the pair bond in winter in bewick's swans (*Cygnus columbianus bewickii*). *Behavioral Ecology and Sociobiology* 7:323-327.
- Serpell, J.A. 1981. Duets, greetings, and triumph ceremonies analogous displays in the parrot genus *Trichoglossus*. *Z. Tierpsychol.* 55:268-83.
- Siegel, S. and N.J. Castellan Jr. 1988. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.
- Trillmich, F. 1976. Spatial proximity and mate-specific behaviour in a flock of budgerigars (*Melopsittacus undulatus*; Aves, Psittacidae). *Z. Tierpsychol.* 41:307-331.
- Waltman, J.R. and S.R. Beissinger. 1992. Breeding behavior of the green-rumped parrotlet. *Wilson Bull.* 104(1):65-84.
- Wechsler, B. 1988. Dominance relationships in jackdaws (*Corvus monedula*). *Behaviour* 106(3-4):252-64
- Wilkinson, L. 1992. *SYSTAT for Windows: Statistics, Version 5 Edition*. SYSTAT, Inc., Evanston Ill.
- Wittenberger, J.F. and R.L. Tilson. 1980. The evolution of monogamy: hypotheses and evidence. *Annual Review of Ecology and Systematics* 11:197-232.