

AGONISTIC INTERACTIONS OF NESTING AND NONBREEDING MACAWS

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Abstract. Agonistic interactions of nesting and nonbreeding Blue-and-yellow Macaws (*Ara ararauna*) were observed in the Manu Biosphere Reserve, Peru, during the nestling phase of the nest cycle in 1988 and 1989. Three nesting pairs of macaws were identified by facial line and tail patterns, and agonistic behavior was categorized as high-intensity or low-intensity interactions. Nesting pairs associated strongly with cavities and perch trees within the nest area, and frequently chased nonbreeding conspecifics from an area of up to 100 m from the nest. In one case, loss of control of the nest cavity and perch trees by a lone nesting macaw to a nonbreeding pair led to infanticide and abandonment of the nest. Agonistic interactions were predominantly intraspecific, and 79% of agonistic interactions by nesting macaws were directed at nonbreeding conspecifics. The frequency of agonistic interactions increased significantly with day of the nesting cycle, being greatest toward the end of the nestling period. Nonbreeding macaws spent significantly more time in trees at the edge of the nest area than in trees within the nest area, and significantly less time within the nest area when nesting pairs were present than when absent. In both years, only 36% of the available cavities within the nest area were utilized by Blue-and-yellow Macaws, though some cavities were utilized by smaller macaw species. Intraspecific interference competition of nesting macaws may exclude potential breeders from investigating cavities, effectively limiting availability where nest sites are clumped in distribution.

Key words: *Ara ararauna*, *cavity nesting*, *intraspecific competition*, *Manu Biosphere Reserve*, *Peru*, *Psittacidae*, *rainforest*.

Interacciones Agonísticas entre Guacamayas Reproductivas y No Reproductivas

Resumen. Se llevaron a cabo observaciones de las interacciones agonísticas entre parejas reproductivas y no reproductivas de la guacamaya *Ara ararauna* en la Reserva de la Biosfera de Manu en Perú, durante la fase de crianza de los pollos en 1988 y 1989. Se identificaron tres parejas de guacamayas por medio del patrón de líneas en su rostro y por la forma de desgaste de la cola, y el comportamiento agonístico fue caracterizado como interacciones de alta y de baja intensidad. Las parejas nidificantes presentaron una fuerte asociación con las cavidades y los árboles de percha dentro del área de anidación, y frecuentemente persiguieron a individuos coespecíficos no reproductivos hasta 100 m fuera del nido. En un caso, una guacamaya reproductiva solitaria perdió posesión de su nido y del árbol de percha frente a una pareja no reproductiva, resultando en el infanticidio de una cría por la pareja no reproductiva, y en el abandono del nido. Las interacciones agonísticas fueron predominantemente de tipo intraespecífico, con el 79% de las interacciones agonísticas por parte de las parejas nidificantes dirigidas a coespecíficos no reproductivos. La frecuencia de las interacciones agonísticas incrementó significativamente con el día del ciclo de anidación, siendo mayor hacia finales del periodo de crianza de los pollos. Las guacamayas no reproductivas pasaron significativamente más tiempo en los árboles alrededor del área de anidación comparando que en los árboles dentro del área de anidación, y permanecieron significativamente menos tiempo dentro del área de anidación cuando las parejas reproductivas estaban presentes que cuando estaban ausentes. En 1988 y 1989, sólo el 36% de las cavidades disponibles fueron utilizadas por *A. ararauna*, aunque algunas fueron utilizadas por otras especies de guacamayas más pequeñas. La interferencia por competencia intraespecífica de las guacamayas reproductivas podría excluir a reproductores potenciales de las cavidades, limitando así la disponibilidad de cavidades en áreas en donde los sitios de anidación se encuentran agrupados.

INTRODUCTION

Availability of nest sites is one of the main factors limiting breeding density for many cavity-nesting birds (von Haartman 1957, Newton 1994). Nest-site availability may be a stronger limiting factor in tropical than temperate forests due to a low density of tree cavities combined with a greater number of hole-nesting species in tropical forests (Gibbs et al. 1993).

The limited breeding opportunities hypothesis (Beissinger and Waltman 1991, Martin 1993, Beissinger 1996) predicts that strong competition for nest sites should be exhibited where nesting opportunities are limited (Waltman and Beissinger 1992, Beissinger 1996, Beissinger et al. 1998). The varying quality of natural cavities (Nilsson 1984) may also result in intraspecific competition for the best nest sites (Gustafsson 1988). This may take the form of interference competition, where direct contact or confrontation occurs over the defense of a resource (Maurer 1984, Minot and Perrins 1986, Gustafsson 1988), and can result in destruction of the nest contents (Bellesisles and Picman 1986, Quinn and Holroyd 1989, Pribil and Picman 1991).

Territoriality and interference competition of nesting pairs may effectively limit the availability of nest sites by excluding potential breeders from occupying nest sites within the defended territory (Krebs 1971, Village 1983, Gauthier and Smith 1987). Hence the aggressive behavior of nesting pairs may be a proximate factor regulating breeding density (Watson and Moss 1970), particularly where nest sites are clumped in distribution.

Most psittacines are secondary cavity nesters, being dependent on the availability of existing hollows (Forshaw 1989). Nest-site availability is considered to be a limiting factor for many psittacines (Saunders et al. 1982, Snyder et al. 1987, Iñigo-Elias 1996), and various species exhibit agonistic interactions over nest sites (Saunders 1982, Snyder et al. 1987, Waltman and Beissinger 1992). However, the extent to which the available resource of cavities is being utilized, or whether the nesting pairs regulate breeding density by excluding potential breeders from available cavities, is unknown.

Parrots are one of the most threatened avian families (Bennett and Owens 1997), and exhibit low reproductive rates making wild populations

vulnerable to decline under pressures of habitat destruction and capture for trade. Information on the factors that limit breeding density in wild populations is necessary to develop effective strategies for conservation and management of threatened species (Renton 2000). This paper analyzes agonistic interactions and interference competition of nesting Blue-and-yellow Macaws (*Ara ararauna*) to determine whether nesting pairs exclude nonbreeding conspecifics from the area.

METHODS

STUDY AREA

The study was conducted in the tropical moist forest of the Manu Biosphere Reserve, southeastern Peru, along the 6-km-wide floodplain of the Rio Manu between 71°02'W, 12°14'S and 71°38'W, 11°55'S. Average annual rainfall is just over 2000 mm, with 87% of the annual rainfall occurring during the rainy season from October to April. The dry season extends from June to October. Temperatures throughout the year fluctuate by only 4–6°C around a mean of 25°C (Terborgh 1983).

Blue-and-yellow Macaw nests were observed at a *Mauritia* palm swamp approximately 3 km long and 100 m wide. The central area of the swamp contained dense concentrations of live *Mauritia* palms. Macaw nests were located in a seasonally inundated area at the eastern edge of the palm swamp, which comprised free-standing dead *Mauritia* palms, occasional isolated trees such as *Calycophyllum* sp., *Ficus trigona*, and *F. insipida*, and a ground layer of 3-m-tall *Heliconia*.

Observations were made from an east-facing canopy platform, 15 m high in a *Ficus trigona*, providing a view over the 100 × 200 m nesting area. The main trees and dead palms within the nest area were identified by compass bearing from the observation platform. Trees were distinguished from dead palms by the prefix A followed by the compass bearing (Fig. 1).

Observations on nesting macaws were conducted from January to April in 1988 and 1989, during the nestling phase of the nesting cycle. In both years there were three active Blue-and-yellow Macaw nests at the site with, in addition, one Chestnut-fronted Macaw (*Ara severa*) nest in 1988, and one Red-bellied Macaw (*Orthopsittaca manilata*) nest in 1989. Observations

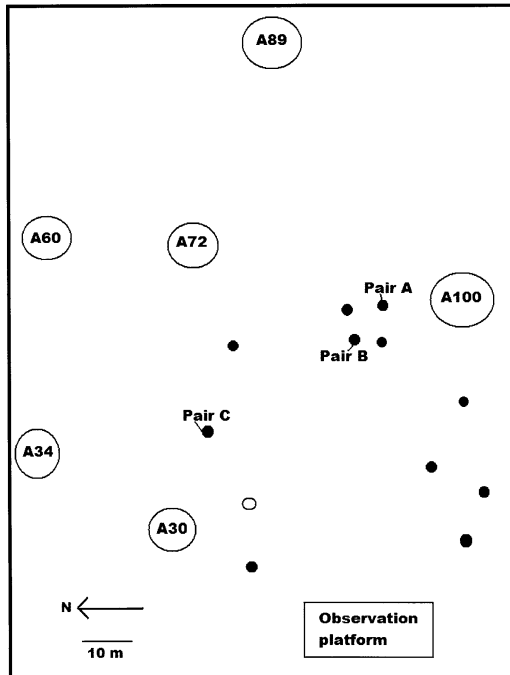


FIGURE 1. Diagram of the Blue-and-yellow Macaw study site in 1989 indicating positions of dead *Mauritea* palms with cavities (filled circles); live *Mauritea* palm (small unfilled circle); trees (large unfilled circles; all except A72 were used by macaws); and nest sites labeled with the name of the nesting pair.

from the tree platform were conducted from sunrise at 05:30 to sunset at 18:15 (EST), with a total 229 hr of observation from 11 March to 20 April 1988, and 267 hr of observation from 23 January to 27 March 1989.

IDENTIFICATION OF NESTING PAIRS

Nesting pairs were identified by facial line patterns, using a Questar (New Hope, Pennsylvania) field model telescope with a 32-mm eyepiece. The facial pattern in the Blue-and-yellow Macaw consists of three lines of small, black feathers. The auricular area of the face where the three lines terminate was the area of greatest variation, and the key area for identification of individuals. The sex of nesting pairs could only be determined when individuals identified by facial patterns were observed mating.

Tail patterns of individuals were determined by the pattern of feather breakage on the longer segments of the tail feathers (Renton 1994). Individuals could be identified rapidly by tail patterns using Zeiss (Chester, Virginia) 10×40

binoculars at distances of 150–200 m, and even when viewed in silhouette. Therefore identification of individuals by tail patterns proved the most efficient method for these observations. Data were recorded on the inter- and intraspecific agonistic behavior of nesting macaws. Non-breeding macaws were distinguished by their bright plumage, in contrast with the dowdy plumage of nesting macaws as a result of frequent activity in the nest cavity.

AGONISTIC INTERACTIONS

The types of agonistic interactions exhibited by nesting macaws were characterized during the observations conducted in 1988. In 1989, data were collected to evaluate the frequency of interactions, and determine whether nest pairs excluded nonbreeding pairs from the area. Agonistic interactions by nesting macaws were divided into high-intensity and low-intensity interactions (Saunders 1974, Levinson 1982). Vocal or visual displays were classified as low-intensity interactions, and included wing displays and the approach-withdraw interaction. The wing display involved the macaw raising both wings in an arc above the body, revealing the bright yellow underwing. This was usually accompanied by a characteristic *kraak kraak* vocalization. In the approach-withdraw, the resident bird flew or hopped to the perch of an intruding bird, which responded by withdrawing to a different branch or leaving the tree (Saunders 1974).

Interactions involving a greater expenditure of energy or some degree of risk through physical contact were classified as high-intensity interactions. These included aerial chases, bill-lunges, physical contact of bills and feet, and midair contact. In aerial chases one pair flies after another, occasionally swooping toward the fleeing pair. A bill-lunge was defined as one bird lunging toward another and displaying its bill. Finally, physical contact occurred either when one bird knocked another from its perch, or when two birds lunged at each other with feet and bills, screeching loudly. When midair contact occurred, the disputing birds interlocked feet and lunged at each other with bills open; the entangled birds fell through the air, breaking apart before reaching the ground.

STATISTICAL ANALYSES

The loss of one adult from a nesting pair in 1988 may have resulted in extreme agonistic interac-

tions during that year; therefore statistical analysis on frequency of interactions and presence of nonbreeding pairs was restricted to data collected in 1989. Kolmogorov-Smirnov normality tests with Lilliefors significance level (Zar 1996) were conducted to determine whether data deviated significantly from the normal distribution. Where necessary, non-normal data were log transformed prior to analysis to meet the requirements for parametric analysis.

Chi-square contingency analysis was conducted to determine whether wing displays by nesting pairs were associated with perch trees in an area around the nest. Linear regression was applied to evaluate whether the number of approach-withdraw interactions initiated by nesting pairs in particular trees was related to the frequency of wing displays by each pair in that tree.

Inter- and intraspecific agonistic interactions of nesting and nonbreeding macaws were examined to evaluate the association between breeding status and conflict outcome. The relationship between frequency of agonistic interactions and day of the nesting cycle was evaluated by linear regression on number of wing displays by day and approach-withdraw interactions by day of the nesting cycle.

The frequency of attendance in the nest area by nonbreeding macaws and time spent in perch trees within the nest area were analyzed to determine whether nesting macaws excluded nonbreeding conspecifics from the nest area (defined as 100 m around the nest). Paired *t*-test analysis was conducted on the time spent by the same nonbreeding pairs in trees at the outer edge of the nest area and perch trees within the nest area. Two-sample *t*-tests, with Bonferroni correction to $P < 0.01$ for multiple analyses, was applied to log-transformed data on time spent by nonbreeding pairs in perch trees and nest cavities when nesting pairs were present and when absent. A paired *t*-test was also conducted on log-transformed data of the mean time spent in the nest area, paired by perch tree, for nonbreeding macaws when nesting pairs were present and when absent. Statistical analysis was conducted with SPSS (Norusis 1994), and values are presented as means \pm SE, with $P < 0.05$.

RESULTS

HIGH-INTENSITY AGONISTIC INTERACTIONS

High-intensity agonistic interactions were observed as early as October during nest pros-

pecting prior to breeding, and in late March at the end of the breeding season. However, actual contact was rare in agonistic situations, and high-intensity interactions were observed only four times out of a total of 453 agonistic interactions by nesting macaws in January–March 1989. All high-intensity interactions occurred within 20 m of a nest cavity, and were not preceded by low-intensity interactions, but were elicited by intruding birds perching at the nest entrance. Bill-lunges were utilized twice to chase intruding birds from the nest entrance: on 24 February 1989 by the female of nest C, and on 17 March 1989 by nest pair B (Fig. 1). An aerial chase was used once on 23 March 1989 by nest pair C to remove an intruding pair, which perched at the nest entrance, out of the area (>200 m). Finally, a bill-and-feet contact fight was initiated once on 22 March 1989 by the male of nest C against an intruding bird in perch tree A30 at the moment when the first chick fledged from the nest.

High-intensity interactions occurred with greater frequency during the breeding season of 1988. During this season, one adult of a nesting pair was lost, probably due to predation as feathers and a small wing bone were found near the nest. Potential predators such as the Black Hawk-Eagle (*Spizaetus tyrannus*), Black-and-white Hawk-Eagle (*Spizastur melanoleucus*), and taylor (*Eira barbara*) were observed in the nest area 11 times from 23 March–13 April 1988, and on six occasions the Black Hawk-Eagle made attack dives on nesting Blue-and-yellow Macaws. The remaining adult of the nesting pair continued to feed the two nestlings, but was unable to maintain possession of the perch tree and nest cavity. From 11 March to 20 April 1988, there were 317 agonistic interactions, 23 of which were high intensity. These included 8 aerial chases; 3 bill-lunges; 7 contacts knocking a bird from its perch; and 5 bill-and-feet contact fights. In this case, aerial chases were initiated by an intruding nonbreeding pair known as pair I, which took over the perch trees A60 and A34 and frequently chased the lone nesting macaw from the area.

All bill-and-feet contact fights in 1988 involved pair I, and were elicited when pair I perched at a nesting pair's nest entrance. The longest attack, of 2 min 38 sec, occurred on 30 March 1988, when the lone nesting macaw failed in its attempt to remove the intruding pair

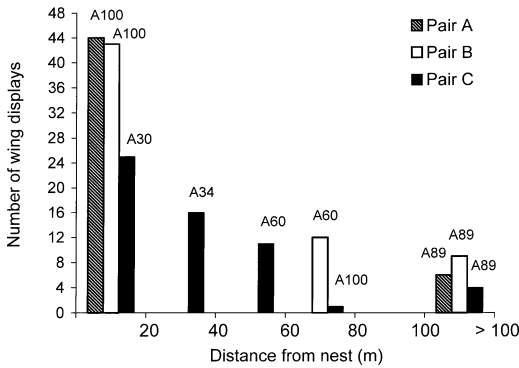


FIGURE 2. Frequency of wing displays in 1989 by nesting pairs of Blue-and-yellow Macaws in perch trees at varying distances from the nest. Labels above the frequency bars refer to trees in Figure 1.

from the nest rim. This resulted in the death of a 2-month-old nestling when it was pulled from the nest by one of the intruding pair. The second nestling was forced to abandon the nest, eventually leaving the area with the parent bird. The intruding pair I may subsequently have nested at the site during the 1989 breeding season, as the facial patterns of nest pair C in 1989 resembled those of nonbreeding pair I in 1988 (Renton 1994).

ASSOCIATION WITH PERCH TREES

Low-intensity agonistic interactions such as the wing display and the approach-withdraw were observed frequently. Nesting pairs did not employ wing displays randomly, but each pair favored particular trees within the nest area ($\chi^2_8 = 143.9, P < 0.001$), and displayed most frequently in perch trees closest to their nest palm (Fig. 2). Nesting pairs displayed and displaced other birds from trees up to 80 m from their nest, though none of the nesting pairs indicated any preference for tree A89, which was located on the outer edge of the nest area 150–200 m from the nest palms (Fig. 1). The number of approach-withdraw interactions initiated by nesting pairs in particular trees was related to the frequency of wing displays given by each pair in that tree ($r^2 = 0.38, F_{1,13} = 7.9, P < 0.02, n = 5$ trees), indicating that wing displays were an expression of territoriality and possession of perch trees.

INTER- AND INTRASPECIFIC INTERACTIONS

Only one interspecific wing display was recorded between nesting Blue-and-yellow Macaws

TABLE 1. Frequency of wing displays given and received by Blue-and-yellow Macaw nesting pairs A, B, and C, and unidentified nonbreeding pairs, in 1989.

Displaying pair	Receiving pair			
	Pair A	Pair B	Pair C	Nonbreeding
Pair A		13	11	41
Pair B	19		3	102
Pair C	6	13		73
Nonbreeding	0	4	6	18
Total received	25	30	20	234

and a pair of Red-and-green Macaws (*Ara chloroptera*) which perched in tree A89. Four interspecific approach-withdraw interactions were recorded for nonbreeding Blue-and-yellow Macaws. On one occasion a pair of Red-and-Green Macaws displaced a pair of Blue-and-yellow Macaws in tree A60, and on three occasions nonbreeding Blue-and-yellow Macaws displaced Red-bellied Macaws in tree A89. No interactions were observed between nesting Blue-and-yellow Macaws and Red-bellied Macaws.

The majority of interactions occurred between nesting and nonbreeding conspecifics. A total of 309 intraspecific wing displays were recorded, of which 281 (91%) were given by nesting pairs, with 77% (216) of wing displays by nesting pairs being directed at nonbreeding conspecifics (Table 1). A total of 198 intraspecific approach-withdraw interactions were recorded, 87% (172) of which were initiated by nesting pairs primarily to displace nonbreeding pairs (81% of approaches by nesting pairs, Table 2).

Only 65 (21%) wing displays and 32 (16%) approach-withdraw interactions occurred between resident nesting pairs of Blue-and-yellow Macaws, most of which involved Pair B (Table 1, 2). Wing displays were given relatively evenly between the three nesting pairs, though slightly more were received by Pair B (Table 1). More approaches were also made to displace Pair B from perch trees, and Pair B almost always withdrew from approaches by the other two nesting pairs (Table 2). Pair B overlapped in use of perch tree A100 with Pair A, and A60 with Pair C (Fig. 2), resulting in a greater frequency of interactions. Pair B tended to use each of the two perch trees when the respective nest pairs were absent, or withdrew from an approach by the other pairs.

TABLE 2. Outcome of intraspecific approach-withdraw interactions between Blue-and-yellow Macaw nesting pairs A, B, and C, and nonbreeding pairs, in 1989.

Approaching pair	Withdrawing pair			Non-breeding
	Pair A	Pair B	Pair C	
Pair A		5	0	26
Pair B	0		1	43
Pair C	7	19		71
Nonbreeding	0	0	1	25
Total withdrawals	7	24	2	165

The frequency of agonistic interactions by nesting pairs of Blue-and-yellow Macaws increased through the nestling period up to fledging of the last nestling (25 March 1989; Fig. 3), and was significantly related to day of the nesting cycle (wing displays: $r^2 = 0.36$, $F_{1,30} = 16.5$, $P < 0.001$; approach-withdraw: $r^2 = 0.20$, $F_{1,30} = 7.3$, $P = 0.01$).

EXCLUSION OF NONBREEDERS

Nonbreeding Blue-and-yellow Macaws gave only 9% of all wing displays and 13% of approach-withdraw interactions, the majority of which were directed at other nonbreeding conspecifics (Tables 1 and 2). In 141 approach-withdraw interactions between nesting and nonbreeding pairs there was only one occasion when a nonbreeding macaw did not withdraw from a nesting macaw, demonstrating that nesting pairs successfully chased nonbreeding conspecifics from the nest area.

Nonbreeding pairs spent significantly more time in trees at the outer edge of the nest area (mean 14.3 ± 2.1 min, range 1.2–34.7 min, $n =$

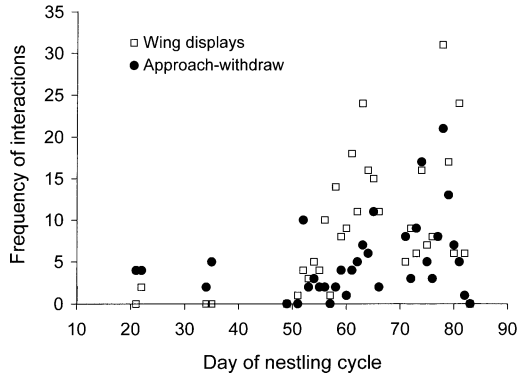


FIGURE 3. Frequency of wing displays and approach-withdraw displacements by nesting pairs of Blue-and-yellow Macaws by day of the nestling phase of the nest cycle (23 January–27 March 1989).

24 pairs) than in trees within the nest area (mean 2.5 ± 0.4 min, range 0.2–7.7 min, $n = 24$, paired $t_{23} = 5.8$, $P < 0.001$). The presence of nesting pairs also limited the time spent by nonbreeding pairs in perch trees within the nest area (Table 3), with nonbreeding pairs spending significantly less time within the nest area when nesting pairs were present than when they were absent (present: mean 2.1 ± 0.2 min, absent: mean 6.7 ± 0.8 min; paired $t_4 = 7.6$, $P = 0.002$).

HISTORY AND OCCUPANCY OF CAVITIES

In 1988 there were 20 dead palms at the study site, 14 of which contained cavities. Between May and December 1988, three of the dead palms with cavities blew down. A further two dead palms with cavities collapsed between May and September 1989, one as a result of the Rio Manu eroding the bank. This represents a loss

TABLE 3. Mean (\pm SE) time spent by nonbreeding pairs of Blue-and-yellow Macaws on nest cavities and perch trees within the nest area (Fig. 1) when resident nesting pairs were present and when absent (n is the number of visits by nonbreeding pairs). Trees A72 and A89 were not used as perch trees by nesting pairs, and were not included in the analysis. Data were transformed by natural log prior to analysis by two-sample t -tests.

Location	Mean \pm SE time (min) in nest area		df	t	P
	Nest pair present (n)	Nest pair absent (n)			
Nest	0.5 ± 0.1 (11)	2.7 ± 1.0 (7)	16	2.9	0.02
A100	2.6 ± 0.5 (29)	4.7 ± 1.6 (9)	33	1.7	0.11
A60	2.2 ± 0.4 (22)	10.3 ± 2.6 (9)	28	4.0	0.002*
A34	2.1 ± 0.3 (24)	6.5 ± 1.7 (10)	30	3.9	0.001*
A30	1.8 ± 0.7 (7)	7.9 ± 1.2 (13)	16	4.6	0.001*

* Significant difference after Bonferroni correction to $P < 0.01$.

of 25% of cavity-bearing dead palms over 2 years.

During the 1988 breeding season, Blue-and-yellow Macaws nested in 5 of the 14 (36%) dead palms, but two nests failed early in the breeding season. In 1989, 4 of the 11 (36%) dead palms with cavities held nests, one of which failed early in the season. Some of the cavities not occupied by Blue-and-yellow Macaws were used by other species of macaw. In 1988, Chestnut-fronted Macaws nested in one cavity, and a Red-bellied Macaw pair roosted in another cavity. In 1989 three cavities were occupied by Red-bellied Macaws: one as a nest, two (in the same dead palm) as roosts. Use of all dead palms as nests or roosts by all macaw species was 43% in 1988, and 55% in 1989.

DISCUSSION

In contrast with insectivorous cavity-nesting birds, macaws do not defend a feeding territory, and parrots are generally nonterritorial in relation to food resources. Territorial behavior of parrots tends to be limited to defense of the nest cavity during the breeding season. The frequency and intensity of agonistic interactions between nesting and nonbreeding macaws suggests that acquisition and control of nest sites and perch trees are important in the reproductive ecology of large macaws. Perch trees may provide valuable lookout points for nesting macaws to maintain vigilance against predators during periods of nest attendance. Frequent nest visitation to feed nestlings may increase the probability of conspicuous foraging adults attracting predators to the nest (Alerstam and Hogstedt 1981). Predators may also learn to recognize areas where nest sites are concentrated at high densities (Larivière and Messier 1998). Hence, limiting the number of conspecifics which nest nearby may reduce the risk of attracting predators to the nest. However, the high frequency of visual and vocal displays exhibited by nesting macaws toward nonbreeding conspecifics may also be more likely to draw attention to the nest site.

Nesting macaws may demonstrate aggression toward nonbreeding pairs in order to reduce the risk of extra-pair copulations or nest parasitism through egg dumping. However, the potential risk of extra-pair copulations or nest parasitism would be greatest during the egg-laying and incubation phases of the nesting cycle, and is un-

likely to explain the intensity of agonistic interactions observed during the nestling phase of the nesting cycle. The frequency of agonistic interactions also increased significantly toward the end of the nesting cycle prior to fledging of the young, when nest parasitism would provide little advantage.

Alternatively, there may be an advantage for nonbreeding pairs in acquiring possession of a cavity which has proven successful in fledging young, or for the resident nesting pair to maintain possession of a successful nest site. The increased frequency of agonistic interactions at the end of the nestling period may be a result of competition to acquire potentially successful nest sites. This may also explain the lack of interspecific agonistic interactions at the nest site, as differing species of macaw are likely to have species-specific requirements for cavity dimensions related to body size (Saunders et al. 1982). Defending an area around the chosen nest site, which encompasses a number of potential cavities, may also help to ensure future nesting opportunities.

In one instance, high intensity interference competition resulted in the death of a final-stage nestling when the lone parent was unable to maintain possession of the nest cavity and perch tree. Potential breeders may gain an advantage where there is intense competition for nest sites by returning to a cavity they acquired in the previous season (Lack 1968). This could be the case for nonbreeding pair I which, having acquired a cavity at the end of the 1988 breeding season, may have reaffirmed possession of cavities and perch trees in the 1989 season. The failure of the lone parent to maintain possession of the cavity and perch trees, even though it was able to continue feeding the young, also indicates the importance of the pair bond in defending the nest site and ensuring breeding success.

Fierce territoriality and competition around cavities has been observed in other parrots (Snyder et al. 1987). Invading pairs of Green-rumped Parrotlets (*Forpus passerinus*) destroy clutches and kill nestlings (Waltman and Beissinger 1992, Beissinger et al. 1998). Wing displays and bill-and-feet contact fights have also been observed for nesting pairs of the Red-and-green Macaw in Manu, and the Scarlet Macaw (*Ara macao*) in Central America (KR, pers. obs.). Such competition is the expected outcome of a dependence on naturally occurring hollows (von

Haartman 1957), and has been noted for other secondary cavity-nesting birds (Krebs 1971, Minot and Perrins 1986, Pribil and Picman 1991).

In both 1988 and 1989, little over a third of the dead palms with cavities were occupied by Blue-and-yellow Macaws. Whether all cavities were of suitable size and condition for nests is not known. However, macaws modified and enlarged cavities in dead palm snags by removing debris, breaking off sections from around the entrance, and chipping at internal cavity walls (KR, pers. obs.). Hence, the resource of cavities at the nest site was not entirely exploited by large macaws. Other factors such as the behavior of nesting pairs may limit the breeding density of macaws at the study site.

Nesting pairs of macaws displayed in and chased conspecifics from trees 80–100 m from their nest cavity. This nest-area requirement of large macaws is greater than that demonstrated by cockatoos, which usually only chased intruding birds from the nest rim, allowing them to remain in the nest tree (Saunders 1982). The territorial requirements of nesting macaws may exclude potential breeders from available cavities both by preventing access to the area, and by limiting the time that nonbreeders can spend investigating cavities. This may limit breeding density of macaws where nest sites are clumped in distribution, and could account for the low occupancy rate of cavities and the high degree of intraspecific competition observed at the nest site.

The high loss rate for cavity-bearing dead palms was substantially greater than the 2.2–4.8% loss per year recorded for tree cavities in eucalyptus forests of Australia (Saunders 1979). Dead palms with cavities may be more unstable and susceptible to windfall than live trees with cavities. Annual recruitment of palm snags through the death of live palms is unknown, but probably occurs sporadically as a result of desiccation during particularly dry years.

A combination of factors may influence the breeding density of large rainforest macaws. Cavities in hardwood trees may be secure and reliable nest sites, but they occur at low densities even in mature forest with many emergent hardwood trees (Saunders et al. 1982, Snyder et al. 1987, Gibbs et al. 1993). Alternatively, cavities in dead palms may be more abundant but localized to specific areas or habitats where the territorial requirements of nesting macaws may

limit breeding density. Hence even in extensive areas of undisturbed rainforest, nest sites may be either limited in number, or patchily distributed and transient in nature.

Provision of nest boxes is an obvious strategy to increase breeding density of psittacines for conservation or management (Snyder et al. 1987, Beissinger and Bucher 1992). However, this approach needs to take into account behavioral and nest-site requirements of the species concerned. It may be unrealistic to provide nest boxes in terms of one nest box per pair of macaws or parrots. The territorial area requirements and agonistic behavior of large macaws suggest that nesting pairs may attempt to maintain an area encompassing a number of potential nest sites. Therefore, a number of nest boxes may need to be placed for each pair, with pairs located at least 100–200 m apart. Furthermore, the high degree of association with perch trees demonstrated by nesting macaws suggests that this may be a key element in nest-site selection, the importance of which may often be overlooked in the positioning of nest boxes.

The factors influencing breeding density of large psittacines are likely to be complex, and may include availability of nest sites, competition, predation, and food supply, as well as maturity, experience, and condition of mated pairs. Intense intraspecific competition over nest sites may be a result of limited breeding opportunities (Beissinger 1996), which may influence many aspects of the reproductive ecology of psittacines.

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