

Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru

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Received 19 June 2008; accepted 18 September 2008

ABSTRACT. Competition for nest sites by sympatric species can lead to resource partitioning among species. We examined the partitioning of cavity resources by Red-and-green Macaws (*Ara chloropterus*), Blue-and-yellow Macaws (*A. ararauna*), and Scarlet Macaws (*A. macao*) in the lowland forest of southeast Peru. Red-and-green Macaws nested primarily in cavities in emergent *Dipteryx* trees, and Blue-and-yellow Macaws nested predominantly in palm snags. Scarlet Macaws had the broadest nesting niche, and their use of cavities overlapped that of the other two species. These differences in cavity use may be related to differences in size, with Red-and-green Macaws the largest of the three species (90 cm long, 1050–1320 g), followed by Scarlet Macaws (85 cm long, 1060–1123 g) and Blue-and-yellow Macaws (70 cm long, 1086 g). We did not observe interspecific conflicts between Blue-and-yellow Macaws and the other two species. However, Scarlet and Red-and-green macaws frequently compete for cavities, perhaps contributing to the use of a wider range of cavity resources by the smaller, less competitive Scarlet Macaws. For the three macaw species combined, 40 of 84 nests (48%) were successful, fledging either one or two young (mean = 1.4 ± 0.43). The overall reproductive output (including failed nests) was 0.60 ± 0.68 fledglings per nesting pair, with no difference between macaw species ($P > 0.18$). A lack of alternative nest substrates for large macaws may drive resource partitioning by sympatric species, with specialization on either emergent trees or palm snags, whereas less competitive species like Scarlet Macaws need to be flexible and use a variety of nest sites.

RESUMEN. Uso de cavidades y éxito reproductivo de las guacamayas en la selva tropical húmeda del sureste de Perú

La competencia por sitios de anidación entre especies simpátricas favorece la repartición de recursos. Evaluamos la repartición del recurso de cavidades entre la guacamaya roja (*Ara chloropterus*), guacamaya azul y amarilla (*A. ararauna*), y guacamaya escarlata (*A. macao*) en la selva tropical húmeda del sureste de Perú. La guacamaya roja anidó principalmente en cavidades en árboles emergentes de *Dipteryx*, y la guacamaya azul y amarilla anidó en palmeras muertas. La guacamaya escarlata presentó el nicho de anidación más amplio, sobrelapando su uso de cavidades con las otras dos especies. Estas diferencias en uso de cavidades podrían estar relacionadas con diferencias en tamaño corporal, la guacamaya roja es la especie más grande (90 cm largo, 1050–1320 g), seguido por la guacamaya escarlata (85 cm largo, 1060–1123 g) y la guacamaya azul y amarillo (70 cm largo, 1086 g). No observamos conflictos interespecíficos de la guacamaya azul y amarilla con las otras dos especies. Sin embargo, las guacamayas roja y escarlata competieron frecuentemente por las cavidades, que contribuiría al rango más amplio de cavidades usadas por la más pequeña, menor competitiva, guacamaya escarlata. Para las tres especies, 40 de 84 nidos (48%) fueron exitosos, con uno o dos volantones (promedio = 1.4 ± 0.43). La productividad reproductiva (incluyendo nidos fracasados) fue de 0.60 ± 0.68 volantones por pareja, que no varió entre las especies ($P > 0.18$). Una falta de sustratos alternos para anidación por las guacamayas podría impulsar la repartición de recursos entre las especies simpátricas, con especialización sobre árboles emergentes o palmeras muertas, mientras la menor competidora guacamaya escarlata necesita ser flexible, utilizando una variedad de sitios de anidación.

Key words: *Ara ararauna*, *Ara chloropterus*, *Ara macao*, Manu, niche breadth, resource partitioning, secondary cavity-nesting, Tambopata, tropical moist forest

Nesting habits may contribute to the vulnerability of bird species, and many cavity-nesting birds are classified as threatened (Monterrubio-Rico and Escalante-Pliego 2006). The family

Psittacidae has the greatest number and proportion of species that are obligate secondary cavity nesters (Saunders et al. 1982, Monterrubio-Rico and Escalante-Pliego 2006) and includes more threatened species than any other bird family (Bennett and Owens 1997).

Cavities in emergent trees and palm snags represent key nest-site resources for several

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species of parrots in the lowland forests of the Amazon basin (Brightsmith 2005a). Competition for nest sites may not be a limiting pressure for smaller parrots (Brightsmith 2005b). However, the greater size-specific cavity requirements of large macaws that nest concurrently (Brightsmith 2005a) may lead to increased competition for nest sites (Renton 2004). Among these, Blue-and-yellow Macaws (*Ara ararauna*), Red-and-green Macaws (*A. chloropterus*), and Scarlet Macaws (*A. macao*) are large-bodied, obligate cavity nesters, sympatric over extensive areas of lowland forest in South America (Forshaw 1989).

Although most psittacine species have low reproductive rates (Masello and Quillfeldt 2002), little is known about the reproductive behavior of large macaws. Studies in Peru and Brazil indicate that Red-and-green Macaws have 40–50% nest success and produce 0.53–0.8 fledglings per pair, Scarlet Macaws have 64–67% nest success with 0.71–0.9 fledglings per pair, and Blue-and-yellow Macaws have 50–72% nest success and 0.5–1.0 fledglings per pair (Munn 1992, Nycander et al. 1995, Bianchi 1998, Brightsmith and Bravo 2006).

Information about the nest-site requirements and reproductive output of wild populations is needed to model population dynamics (Boyce 1992) and develop effective strategies for conservation and management of threatened species (Renton 2000). Our objective was to evaluate, at a regional level, how natural cavities are partitioned among three sympatric species of large macaws, and how this impacts nest success and reproductive output.

METHODS

We located macaw nests in the tropical moist forest of southeastern Peru, in the Manu Biosphere Reserve (71°02'W, 12°14'S to 71°38'W, 11°55'S) during 1988 and 1989, and in the Tambopata National Reserve (69°37'W, 13°08'S) from 2000 to 2007. Average annual rainfall is just over 2000 mm in Manu and 3200 mm in Tambopata, with 87% of the annual rainfall occurring during the rainy season from October to April. Temperatures throughout the year fluctuate by only 4–6°C, with a mean of 25°C (Terborgh 1983, Brightsmith 2004).

Our two study areas were located along the floodplains of the Manu River and the

Tambopata River; both are tributaries of the Madre de Dios River, but are 180 km apart, increasing the likelihood that these represent separate macaw populations in the same region and forest type. The Manu River forms a 6–8 km wide meander belt with ox-bow lakes, some of which develop into palm swamps. Vegetation ranges from inundated areas bordering the river to mature climax forest with a closed canopy at 30–35 m, and emergent trees of *Dypterix micrantha*, *Ceiba pentandra*, and *Poulsenia armata* reaching 55–60 m (Foster 1990). Beyond the floodplain are older terraces of upland *terra firme* forest that we accessed where they occurred close to the river. The Manu study site is free of anthropogenic disturbance of hunting and habitat modification, as evidenced by the large stands of valuable timber species such as *Cedrela odorata* and *Swietenia macrophylla* that are still conspicuous along the river (Foster 1990). The Tambopata study site is located along the faster flowing, braided Tambopata River and included areas of floodplain and *terra firme* forest within 2 km of the river. Palm swamps occurred in low-lying areas at the base of *terra firme* locations. The Tambopata study site experienced some selective logging in the past, but is currently free of anthropogenic disturbance.

We searched for nests in November and December during the nest prospecting and early incubation phases of the nesting cycle. Nest searches were conducted by traveling along the Manu River in a motorized canoe and by walking trails at sites in Cocha Cashu, Cocha Totorra, and Cocha Juarez. In Tambopata, nest searches were conducted along trails and river edges around the Tambopata Research Center.

We located potential cavities based on the behavior and vocalizations of macaw pairs and, for all cavities inspected by macaws, noted the species of tree or palm in which the cavity was located. A cavity was confirmed as an active nest if an adult macaw remained in the cavity while the other member of the pair left to forage, and we observed either behavior associated with mating or regurgitated feeding of one individual by the other. In both Manu and Tambopata, daily observations were conducted at nests from January to May to verify continued nesting activity. At Manu, nest cavities were not accessed, but we were able to determine the number of full-grown nestlings by observations of young at the nest entrance prior to fledging. Close to fledging,

nestlings spend most of the day perched at the nest entrance, frequently flapping their wings in preparation for flight (K. Renton, pers. observ.). Nests were observed continuously during this period to confirm the fledging of young from the nest. Successful nests were defined as those that fledged at least one young.

In Tambopata, the number of nestlings was determined by inspecting nest cavities using single-rope ascending techniques (Perry 1978, Perry and Williams 1981). From 2000 to 2002, we inspected nest cavities every 3–10 d from the period just prior to laying until fledging of the last chick. However, beginning in 2003, we did not inspect nests for 25 d after the first egg was laid to reduce the risk of nest disturbance during incubation.

We considered only natural cavities for the analysis of cavity use, and did not include Blue-and-yellow Macaw nests in managed palms studied by Brightsmith and Bravo (2006) during 1994–2003. Cavities inspected by macaws or used as nests in successive years were considered only once in our analysis of cavity use, but all nesting attempts were included in the analysis of reproductive output. We excluded cavities inspected by macaws, but not used as nests from evaluation of nest-site reuse because these may not be of a suitable condition for nesting. However, we did not verify whether nest cavities used only once were potentially available and in suitable condition in other years.

To determine if macaw populations at Manu and Tambopata differed in cavity use, we used the Wilcoxon paired test for nonparametric data, with cavity use between the two areas paired by species of tree or palm. We used chi-square contingency analysis to evaluate the use of cavities in trees or palm snags by the three species of macaws, the frequency of nest-cavity reuse among macaw species, and whether nest failure or success influenced the reuse of cavities. The degree to which an observed cell frequency differed from expected was evaluated by calculating the adjusted standardized residuals (Quinn and Keough 2002).

We used Levins' standardized niche breadth index to evaluate the use of cavities in tree species or palm snags by the three species of macaws, with a value close to 0 indicating specialization on a few types of cavity resources and a value close to 1 indicating a broad use of cavity resources (Levins 1968, Colwell and Futuyma

1971). We then applied the Morisita index of similarity to evaluate community organization or overlap in the use of different species of tree or palm between the three species of macaw (Krebs 1989).

For repeat nesting attempts in the same nest cavity, we calculated the mean number of young fledged from successful nests and the mean reproductive output over all nesting attempts. The number of young fledged from successful nests and the overall reproductive output (including failed nests) did not present normal distributions. Therefore, we used Mann–Whitney U -tests to compare reproductive output between the two study areas of Manu and Tambopata, and used Kruskal–Wallis ANOVA to compare the productivity of successful nests and overall reproductive output between the three species of macaw (Zar 1999). We applied the $P < 0.05$ significance level for statistical tests and presented descriptive statistics as means ± 1 SD.

RESULTS

Macaws inspected 77 natural cavities as potential nest sites, with all located in either dead palm snags ($N = 39$ cavities) or emergent trees ($N = 38$ cavities). We found no difference in the use of cavities in each tree or palm species by macaws in Manu and Tambopata ($z_8 = 0.5$, $P = 0.63$). However, the three species of macaws differed in their use of cavities in palm snags or trees ($\chi^2_2 = 35.9$, $P < 0.001$). Blue-and-yellow Macaws used more palms than expected (cell $z = +20.6$), with 91% of cavities in palm snags, whereas Red-and-green Macaws showed the reverse pattern of 88% of cavities in trees (cell $z = +7.7$) and fewer in palm snags (Fig. 1).

Blue-and-yellow Macaws inspected 32 cavities, almost exclusively in dead palm snags of *Mauritia flexuosa* (56%) and *Iriartea deltoidea* (34%; Fig. 1). By comparison, of 16 cavities inspected by the Red-and-green Macaw, 11 (69%) were in live emergent trees of *Dipteryx micrantha* (Fig. 1). Scarlet Macaws demonstrated the widest range of cavity resource use, inspecting 29 cavities in various species of emergent trees including *Dipteryx micrantha* (34%), *Calycophyllum* sp. (10%), *Hymenaea oblongifolia* (7%), and *Erythrina* sp. (7%), as well as 28% of cavities in *Iriartea deltoidea* palms (Fig. 1).

Due to their predominant use of cavities in emergent *Dipteryx* trees, Red-and-green Macaws

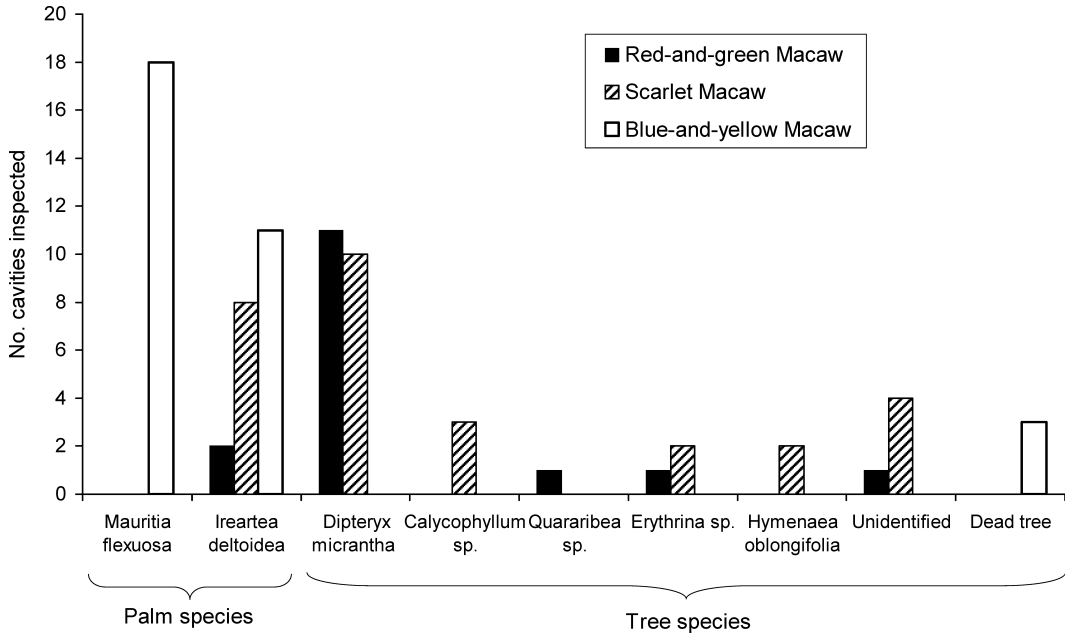


Fig. 1. Number of cavities in palms and tree species inspected or used as nests by three species of large macaw in the lowland tropical moist forest of southeast Peru (Manu: 1988–1989, and Tambopata: 2000–2007).

had a narrow niche breadth of cavity resource use ($B = 0.167$). Blue-and-yellow Macaws also had a narrow niche breadth of $B = 0.209$, using only two species of palm for nesting. By comparison, Scarlet Macaws had a broad niche breadth of cavity resources for nesting ($B = 0.545$). Scarlet Macaws also demonstrated a high degree of similarity or overlap in use of cavities with Red-and-green Macaws (Morisita index = 0.845), and in our study, three cavities in *Dipteryx micrantha* trees were used by both species of macaws in different years. We found less overlap in the use of cavities by Scarlet and Blue-and-yellow macaws (Morisita index = 0.300).

By comparison, Red-and-green and Blue-and-yellow macaws exhibited the least similarity in cavity use (Morisita index = 0.096).

Overall, we observed 112 cavity inspections by macaws, with 84 (75%) inspections resulting in active nests (Table 1). The percentage of inspections that led to a nesting attempt in that cavity was 71% for both Blue-and-yellow Macaws ($N = 24$ nests) and Red-and-green Macaws ($N = 17$ nests) and 80% for Scarlet Macaws ($N = 43$ nests).

Macaws nested in 57 distinct cavities, and nests in tree cavities were reused more frequently than nests in palm snags ($\chi^2_1 = 7.8$, $P < 0.01$).

Table 1. Outcome of cavity inspections and nest attempts by large macaws in lowland, tropical moist forest of southeast Peru (Manu: 1988–1989, and Tambopata: 2000–2007).

| Parameters | Red-and-green Macaw | Scarlet Macaw | Blue-and-yellow Macaw | All species combined |
|---|---------------------|---------------|-----------------------|----------------------|
| Cavity inspections by macaws | 24 | 54 | 34 | 112 |
| Confirmed nests | 17 | 43 | 24 | 84 |
| Successful nests | 7 | 20 | 13 | 40 |
| Total number fledglings | 11 | 29 | 17 | 57 |
| Fledglings/successful nest ^a | 1.6 ± 0.4 | 1.4 ± 0.4 | 1.3 ± 0.5 | 1.4 ± 0.4 |
| Fledglings/confirmed nest ^a | 0.55 ± 0.64 | 0.57 ± 0.70 | 0.65 ± 0.71 | 0.60 ± 0.68 |

^aMean ± 1 SD.

Of 28 tree cavities used as nests, 12 (43%) were used more than once, whereas only 3 of 29 palm snag nest sites (10%) were reused by macaws. The frequency of nest-cavity reuse also differed significantly among the three species of macaws ($\chi^2_2 = 12.2$, $P < 0.005$). Blue-and-yellow Macaws used more cavities than expected just once (cell $z = 8.6$), with only one nest (4%) reused. By comparison, Red-and-green Macaws reused six nest cavities (60%), more than expected (cell $z = 4.2$), and Scarlet Macaws reused eight nest cavities (33%). However, success or failure of nesting attempts did not influence the frequency of cavity reuse ($\chi^2_1 = 1.7$, $P > 0.1$).

Overall nest success for the three species of macaws was 48% (Table 1). Successful nests fledged either one or two young (mean = 1.4 ± 0.43 fledglings), and the overall reproductive output (including failed nests) was 0.60 ± 0.68 fledglings per nesting pair (Table 1). We found no difference among the three species in either the number of young fledged per successful nest ($H_{2,28} = 3.4$, $P = 0.18$) or reproductive output of nesting pairs ($H_{2,56} = 0.3$, $P = 0.87$; Table 1). Similarly, reproductive output of macaws did not differ between the two study areas ($U_{55} = 305$, $P = 0.11$).

We determined the cause of nest failure for 8 of 44 failed nests (18%). Two nest palms fell into the river and another fell over, killing the nestling. Two Scarlet Macaw nests failed due to agonistic interactions between competing pairs. One Scarlet Macaw nest failed when an invading pair of Scarlet Macaws killed the > 40-d-old chicks and took over the cavity. At another nest, one egg was crushed and a small nestling died as a pair of Scarlet Macaws attempted to defend their cavity from a pair of invading Red-and-green Macaws. Tayras (*Eira barbara*; Mustelidae) were observed climbing the tree or entering three macaw nest cavities. Toucans were also occasionally seen in nest areas and may be potential predators on eggs. Large hawk eagles were observed making attack dives on adult nesting macaws, and may have been the cause of the loss of one adult from each of two Blue-and-yellow Macaw nests in a *Mauritia* swamp nesting area (Renton 2004).

DISCUSSION

The three species of macaws exhibited variation in the use of nest cavities. Red-and-green

Macaws exhibited a preference for cavities in mature, emergent trees and Blue-and-yellow Macaws nested predominantly in palm snags, resulting in a high degree of cavity resource partitioning. However, the use of cavities by Scarlet Macaws overlapped that of both Red-and-green and Blue-and-yellow macaws.

Differences between species in the use of nest sites may be related to size, with Red-and-green Macaws the largest of the three species (90 cm long and 1050–1320 g body mass; Forshaw 1989), followed by Scarlet Macaws (85 cm long and 1060–1123 g; Forshaw 1989), and Blue-and-yellow Macaws (70 cm long and an average mass of 1086 g [range = 907–1240 g]; D. Brightsmith, unpubl. data). Larger Red-and-green Macaws may require larger cavities in emergent trees. Australian cockatoos also demonstrate species specific nest-cavity requirements related to body size (Saunders et al. 1982).

The three macaw species exhibit intraspecific competition for nest sites (Renton 2004). However, we did not observe interspecific conflicts between Blue-and-yellow Macaws and the other two species. Blue-and-yellow Macaws nest primarily in palm snags and most commonly nest in *Mauritia* swamps (Forshaw 1989, Nycander et al. 1995, Gonzalez 2003, Brightsmith and Bravo 2006). *Mauritia* palm snags are not used by Red-and-green Macaws and are rarely used by Scarlet Macaws, reducing the likelihood of aggressive interactions with Blue-and-yellow Macaws.

By comparison, Scarlet Macaws and Red-and-green Macaws frequently compete for cavities in emergent trees. Agonistic interactions between Scarlet and Red-and-green macaws at active nests have been recorded annually in Tambopata and may result in cavity takeover (Nycander et al. 1995, DJB, pers. observ.). The smaller Scarlet Macaws are at a disadvantage in disputes with larger Red-and-green Macaws for ownership of tree cavities, perhaps contributing to their use of a wider range of cavity resources.

The narrow nest-site niches of both Red-and-green and Blue-and-yellow macaws suggest that these species have particular criteria for selecting suitable nest cavities, making them less likely to use alternative nest sites. By contrast, Scarlet Macaws use a wide range of nest sites, suggesting more flexibility in adopting alternative cavity nest sites. For example, Scarlet Macaws readily use artificial nests constructed

of different materials, whereas neither Red-and-green nor Blue-and-yellow macaws have used artificial nest boxes in the region (Nycander et al. 1995, Bianchi 1998, Brightsmith and Bravo 2006). Using artificial nest boxes to improve the reproductive output of wild parrot populations can be a useful conservation strategy, but is not always successful (Snyder et al. 1987). The degree of nest-site specialization may influence the likelihood that a particular species will use nest boxes.

Overall, 25% of macaw pairs inspecting cavities did not eventually nest in that cavity. These pairs may be selecting cavities and establishing ownership for future breeding attempts (Renton 2004). Alternatively, inspected cavities may have been too small for use as a nest site. Scarlet Macaws have been observed inspecting cavities that were too small or shallow for nesting (KR and DJB, pers. observ.). Cavities may also be unsuitable for nesting if, for example, they are waterlogged or infested with pests. We did not evaluate cavity availability in our study and, therefore, could not determine whether unused nest cavities were still available and of adequate condition for nesting in all years. However, by frequently inspecting cavities, macaws may acquire information about cavity resource availability and the location and condition of potential nest cavities.

Nest cavities in live trees were reused more often than those in palm snags, and Red-and-green Macaws reused 60% of their nest cavities, mainly in emergent trees. Cavities in emergent, hardwood trees may be secure, durable and reliably available between years, making them a highly valued resource and promoting competition and increased tendency for reuse of these cavities. Larger Red-and-green Macaws may be better able to maintain long-term defense of such a resource, facilitating their specialization on emergent tree cavities for nesting.

By comparison, the limited reuse of nest cavities in palm snags (10%) may reflect their limited lifespan, with dead palm snags lasting only 4–7 years before collapsing (Brightsmith and Bravo 2006). Palm cavities may also be more susceptible to water logging because the entrance is often at the top opening of the snag (Brightsmith and Bravo 2006). Therefore, macaws that nest in palm snags must acquire new cavities more frequently, possibly requiring frequent inspection of palm snags to locate

adequate nest site and leading to disputes with other pairs of macaws.

Brightsmith (2005b,c) suggested that predation pressure may have been the main factor driving smaller parrot species to adopt novel nesting substrates such as termitaria or burrows. However, competition may be greater for larger species of macaws that require canopy-level cavities of greater size that are limited in availability. Primary lowland forest in New Britain, Papua New Guinea, had a density of 0.8 potential nest cavities per ha (Marsden and Pilgrim 2003), whereas primary subtropical semi-deciduous forest in Argentina had 1.3 canopy-level cavities per ha (Cockle et al. 2008). Cavities in dead palms may occur at high densities, but are restricted to floodplain and swamp habitats (Gonzalez 2003, Renton 2004). Healthy *Mauritia* palm swamps may have 171–545 live palms and 7–22 dead palm snags per ha, whereas swamps that are dying out may have 263 dead palms per ha (Brightsmith and Bravo 2006). This compares with estimates of 3.5 standing dead snags per ha in gallery forest of central Venezuela and 11–20 snags per ha in lowland wet and moist forests of Costa Rica and Belize (Gibbs et al. 1993). However, these studies gave no indication of whether standing dead snags provide cavities suitable for use by secondary cavity nesters.

Large macaws in the lowland forest of Amazonia may have few options as far as adopting novel nest substrates because they are too large to use termitaria, and cliff-nesting may not be feasible in the relatively flat terrain over much of their range. However, Red-and-green Macaws reportedly sometimes nest in cliffs along canyons in the upper reaches of river tributaries (Forshaw 1989). The lack of alternative nest substrates for large macaws may drive resource partitioning by sympatric species, with specialization on either emergent trees or palm snags and species like Scarlet Macaws that are less able to successfully compete for high-quality sites needing to be flexible and use a variety of nest sites.

Due to their apparent preference for nest sites in emergent *Dipteryx* trees, Red-and-green Macaws may be more vulnerable to loss of nest sites through modification or loss of mature primary forests. *Dipteryx* are slow-growing hardwood trees that may live for over 1000 yr (Chambers et al. 1998). Hence, the large, high cavities in these trees represent a permanent,

reliable nest resource for large macaws that, if lost, would take hundreds of years to replace. By comparison, palms may grow and die within 50 yr (Brightsmith and Bravo 2006), permitting the formation of new palm snags during the lifespan of adult macaws. Blue-and-yellow Macaws frequently use disturbed areas where palm snags and dead trees are common (Renton 2002, 2004, Brightsmith 2005a, Brightsmith and Bravo 2006). Scarlet Macaws may also use these habitats (Gonzalez 2003, Renton 2006). However, Red-and-green Macaws are less likely to use disturbed areas, preferring cavities in emergent trees of primary forest for nesting. Hence, the nest-site requirements and breeding habitat of large macaws should be considered when evaluating the potential vulnerability of species to human pressures and habitat modification.

ACKNOWLEDGMENTS

The research was supported by the Wildlife Conservation Society (Manu), Earthwatch Institute, Schubot Exotic Bird Health Center, and Rainforest Expeditions (Tambopata). Field assistance for the location and follow-up of macaw nests was provided by A. Huaman (Manu), and R. Wilkerson, M. Dragiewicz, O. Gonzales, A. Figari, D. Matsufuji, K. Quinteros, G. Vigo, A. Sanchez, and many volunteers (Tambopata). DJB thanks K. Holle, E. Nycander, and the staff of Rainforest Expeditions for facilitating work in Tambopata. KR is grateful to C.A. Munn for the opportunity to participate as a research volunteer in Manu. The Instituto Nacional de Recursos Naturales (INRENA) in Peru granted research permits for the studies. The Instituto de Biología, Universidad Nacional Autónoma de México and the Schubot Exotic Bird Health Center at Texas A&M University, provided facilities for the preparation of this manuscript. We are grateful to J. W. Wiley and three anonymous reviewers for constructive comments on the manuscript.

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