

PARROT NESTING IN SOUTHEASTERN PERU: SEASONAL PATTERNS AND KEYSTONE TREES

Author(s): DONALD J. BRIGHTSMITH

Source: The Wilson Bulletin, 117(3):296-305. 2005.

Published By: The Wilson Ornithological Society

DOI: <http://dx.doi.org/10.1676/03-087A.1>

URL: <http://www.bioone.org/doi/full/10.1676/03-087A.1>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

PARROT NESTING IN SOUTHEASTERN PERU: SEASONAL PATTERNS AND KEYSTONE TREES

DONALD J. BRIGHTSMITH¹

ABSTRACT.—Parrots that inhabit tropical lowland forests are difficult to study, are poorly known, and little information is available on their nesting habits, making analysis of community-wide nesting patterns difficult. I present nesting records for 15 species of psittacids that co-occur in southeastern Peru. The psittacid breeding season in this area lasted from June to April, with smaller species nesting earlier than larger species. Why smaller species bred earlier is uncertain, though it may be related to interspecific competition for nest sites or variations in food availability. This study identified two keystone plant resources used by nesting parrots: *Dip-teryx micrantha* (Fabaceae) and *Mauritia flexuosa* (Arecaceae). Local threats to these plant species are discussed. Received 25 August 2003, accepted 14 April 2005.

Nesting is a critically important stage in the natural history of all bird species. Reproductive failure has caused numerous conservation crises, so knowledge of nesting habits is critical (Ratcliffe 1967, Herkert et al. 2003). The nesting ecology of many tropical species remains poorly documented, especially for canopy nesters in dense, lowland tropical forests. The family Psittacidae is the most endangered large avian family in the world, making its study a conservation priority (Bennett and Owens 1997, Collar 1997). Most of our knowledge of parrot nesting comes from anecdotal accounts by early collectors (Huber 1933), regional avifaunal compendia (Cherrie 1916, Havershmidt 1968), detailed studies of individual taxa (reviewed in Masello and Quillfeldt 2002), and the monumental compendium of Forshaw (1989).

New World parrot diversity is highest in the western Amazon Basin, where communities commonly include more than 15 species (Roth 1984, Montambault 2002). This diversity peaks in southeastern Peru, where 18 to 20 species have been reported at various sites (Terborgh et al. 1984, Foster et al. 1994). However, the nesting season for all but five species in the region remains undocumented, making community-level analyses impossible. Here, I report on the nesting season for 15 species of sympatric parrots inhabiting lowlands of the western Amazon Basin in southeastern Peru.

Land clearing and pressures on global forest resources are constantly increasing. As for-

est areas shrink, conservationists must prioritize their conservation efforts. Large, old trees and the cavities they contain are vital for the persistence of many cavity-nesting birds (Mawson and Long 1994, Poulsen 2002). However, cavity nesters usually do not use trees in proportion to their abundance, suggesting that some tree species are more important than others to these birds (Martin and Eadie 1999, Monterrubio and Enkerlin 2004). In this study, I compiled nesting records for 15 species to determine which trees were most important to the nesting parrot community in southeastern Peru.

METHODS

Study area.—I studied parrot nesting in the Departamento de Madre de Dios in southeastern Peru. The primary site was the Tambopata Research Center (13° 07' S, 69° 36' W; 250 m in elevation) on the border between the Tambopata National Reserve (275,000 ha) and Bahuaja-Sonene National Park (537,000 ha). The center is located in a small (<1 ha) clearing surrounded by a mix of mature floodplain forest, riparian successional forest, *Mauritia flexuosa* (Arecaceae) palm swamps, upland forest, and bamboo (Foster et al. 1994, Griscom and Ashton 2003; DJB pers. obs.). The forest is classified as tropical moist forest (Holdridge 1967). The site is adjacent to a 500-m-long, 30-m-high riverbank clay lick, where up to 1,000 macaws and parrots gather daily, resulting in high parrot densities in the area (Brightsmith 2004a). Annual rainfall is 3,200 mm. The dry season extends from April to October, during which monthly rainfall averages 90–250 mm (Brightsmith 2004a). Ad-

¹ Duke Univ., Dept. of Biology, Durham, NC 27708, USA; e-mail: djb4@duke.edu

ditional nesting records come from Posada Amazonas Lodge in the Native Community of Infierno (12° 48' S, 69° 18' W; 195 m in elevation; 2,800 mm annual rainfall; Pearson and Derr 1986, Brightsmith and Aramburú 2004) and Cocha Cashu Biological Station in Manu National Park (11° 54' S, 71° 18' W; 400 m in elevation; 2,000 mm annual rainfall; Terborgh 1983, Terborgh et al. 1984). These two sites are characterized by similar vegetation and dry seasons, and they are located 50 km north-northeast and 250 km northwest of Tambopata Research Center, respectively.

Nesting records.—Nesting records consisted of two types: confirmed nests and birds at cavities. Confirmed nests were locations where I observed eggs or chicks. Observations of birds at cavities, where contents were not checked, were included only when birds were observed repeatedly at the cavity and where behavioral cues suggested incubation or feeding of young. Single observations of birds at cavities were not included, as parrots may visit cavities when not breeding.

Most of the nesting records were from July to August (1998) and November to April (1999 to 2003) in Tambopata and September to November (1993, 1995, 1996, and 1997) in Manu. I collected additional unpublished nesting records from researchers and guides with experience working in southeastern Peru. These other observers were stationed at Tambopata year-round.

Data analysis.—I tested the relationship between body size and the onset of breeding using a rank correlation of body mass versus month of first breeding and a *t*-test ($\alpha = 0.05$) of month of first breeding for large (>250 g) versus small (<250 g) psittacids (Gibbons 1985). Body-mass data are from Dunning (1993).

RESULTS

Red-and-green Macaw (Ara chloroptera).—Twelve nests of this species were monitored in Tambopata between 1993 and 2003. I determined laying date for nine nests: September ($n = 1$), November ($n = 7$), and December ($n = 1$). Fledging was confirmed in January ($n = 1$) and March ($n = 5$; Table 1). Most nests were in cavities of live, emergent *Dipteryx* (Fabaceae) trees ($n = 7$), although one nest was in a cavity of an unidentified

tree. One pair, consisting of a wild bird and a hand-raised bird released to the wild, nested in wooden nest boxes in 2 years (see Nycander et al. 1995 for a description of the nest boxes). Three nests were in floodplain forest (one <10 m from the river edge) and nine were in *terra firme* forest.

Blue-and-yellow Macaw (Ara ararauna).—Seventy-two nests in at least 50 different cavities were recorded. Most cavities (47 of 50) were in dead *Mauritia flexuosa* palms. Because it is difficult to climb dead palms, only 21 nest trees were climbed, and nest contents were checked infrequently. I estimated that egg laying occurred in November ($n = 9$), December ($n = 2$), and January ($n = 2$). I confirmed fledging in late February ($n = 1$), March ($n = 4$), and May ($n = 1$). Fifty of these nests were in a 3-ha section of naturally dying *Mauritia flexuosa* palm swamp, where dead palms occurred at a density of >200 per ha (A. Bravo and DJB unpubl. data). Sixteen nests were in a small (<0.25 ha) section of a swamp being managed to encourage nesting of Blue-and-yellow Macaws (Nycander et al. 1995). Three other nests were in tall, dead palms that rose above the surrounding vegetation in an otherwise healthy palm swamp. Two nests were in floodplain forest in dead *Iriartea* palms <10 m from the river edge. One additional nest was in an unidentified dead, hollow tree in *terra firme* forest, 10 m from the edge of a cliff that overlooked the Tambopata River. The cavity was a deep, open-topped tube, similar in structure to a hollow palm.

Scarlet Macaw (Ara macao).—I studied 55 clutches at 26 different nest sites. I was certain of first-clutch initiation for 40 nests: late October ($n = 1$), November ($n = 32$), and December ($n = 7$). When the first clutch was lost or did not hatch, 35% (7 of 20) of the birds re-laid in the same nest. Second clutches were initiated in late December ($n = 4$) or early January ($n = 3$). Fledging took place in February ($n = 4$), March ($n = 14$), and April ($n = 2$). No eggs from second clutches hatched. Nests were found in natural cavities of live *Dipteryx micrantha* ($n = 6$), live *Hymenaea oblongifolia* (Fabaceae; $n = 1$), dead *Iriartea* palm ($n = 1$), and in artificial nest boxes made of wood or PVC pipe ($n = 18$). No nests were found in dead *Mauritia* palms. Nests were in

floodplain forest ($n = 15$), *terra firme* forest ($n = 9$), and *Mauritia* palm swamp ($n = 1$); the habitat for one nest was not recorded.

Chestnut-fronted Macaw (Ara severa).—Birds were observed attending seven cavities from November to February (Table 1). Observers saw the nest contents in only one cavity; the nest was in a dead *Mauritia flexuosa* palm in the dying section of swamp discussed under Blue-and-yellow Macaw. It contained chicks in February. The other nests were in canopy branches of emergent *Dipteryx micrantha* trees ($n = 6$). All of the nest cavities were in trees that were relatively isolated from the surrounding vegetation in *terra firme* forest ($n = 4$), floodplain forest ($n = 2$), or *Mauritia* palm swamp ($n = 1$).

Red-bellied Macaw (Orthopsittaca manilata).—I observed birds attending 26 cavities in Tambopata from October to February. Four nests contained eggs or chicks, and I estimated that eggs were laid in October ($n = 2$) and November ($n = 2$). All nests were in dead *Mauritia flexuosa* palms; three nests were in the small (<0.25 ha) section of managed palm swamp, and 22 nests were in the 3-ha section of naturally dying *Mauritia flexuosa* swamp. Both habitats are described above in the section on Blue-and-yellow Macaw.

White-eyed Parakeet (Aratinga leucophthalmus).—In January, my assistants observed birds repeatedly attending a cavity in a dead palm in the center of a farm field. The pair was likely incubating or brooding because one bird entered the palm and refused to leave, even when observers knocked on the trunk of the palm.

Dusky-headed Parakeet (Aratinga weddellii).—No chicks of this species were seen; all three records reported here are of birds attending cavities in dead trees or dead branches in live trees. The reports from Tambopata come from July, December, and January. These observations are congruent with a report from local residents who say that the species nests “year-round” (Sixto Duri pers. comm.). Nest cavities were in a dead tree of an unknown species ($n = 1$), a dead palm ($n = 1$), and a dead branch in a live *Cecropia* (Cecropiaceae) tree ($n = 1$). The nesting habitats included river edge ($n = 1$), small farm ($n = 1$), and a large natural gap in *terra firme* forest ($n = 1$).

Scarlet-shouldered Parrotlet (Touit hueitii).—This species is rare at the study sites. From August to September 1998, guides and guests at Tambopata Research Center repeatedly saw two birds at a hole in an arboreal termite mound 3.5- to 4-m above the ground. The site was in *terra firme* forest with a mix of trees and bamboo (*Guadua sarcocarpa*). The birds were seen regularly attending the cavity over a period of a few weeks.

Red-crowned Parakeet (Pyrrhura roseifrons).—I located one nest of this species during October 1997 in Manu National Park. The nest was approximately 9 m high in a live tree in late-successional floodplain forest. One newly hatched chick and three eggs were seen on 4 October. A total of four birds attended this nest. They appeared to be adults, although two of the birds had less red on the head and may have been young from the previous year. During my last visit to the nest (4 November), I heard young birds begging inside the cavity.

White-bellied Parrot (Pionites leucogaster).—Two live featherless chicks were found at the base of a suspected nesting tree in October, indicating that eggs were laid in August; fledging would have occurred in November or early December. Birds were seen attending three additional cavities in Tambopata and Manu from September to February. The nest cavities were in canopy branches of live trees (two *Dipteryx micrantha* and one unknown species).

Blue-headed Parrot (Pionus menstruus).—Five nests of this species were found, all from June to November (Table 1). Laying dates were calculated for two nests: late May or early June ($n = 1$) and September ($n = 1$). Chicks were seen in three nests. Fledging in November was confirmed at one nest. Nest sites were dead palms ($n = 2$) and PVC nest boxes ($n = 2$). All nests were near some sort of forest edge: river edge ($n = 2$), clearing edge ($n = 1$), and a steep drop-off in *terra firme* forest ($n = 1$). Habitat was not recorded for one nest.

Yellow-crowned Parrot (Amazona ochrocephala).—A member of this species was seen attending a dead palm from at least December to March in mature floodplain forest (A. del Campo pers. comm.). However, local people report that the chicks of this species fledge in October. Birds were also seen briefly at three

TABLE 1. Parrot nesting phenology, by month and by season (dry or wet), in southeastern Peru (Departamento de Madre de Dios), 1993–1999. An “X” indicates peak breeding season (and chicks or eggs seen in the nest), “o” indicates periods when few birds breed, and “C” indicates that birds were observed regularly attending cavities (but no eggs or nestlings observed).

Species	Mass ^a	Dry season						Wet season						
		Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	
Red-and-green Macaw (<i>Ara chloroptera</i>)	1,250				o	o	X	X	X	X	X	X		
Blue-and-yellow Macaw (<i>Ara ararauna</i>)	1,125						X	X	X	X	X	X	o	o
Scarlet Macaw (<i>Ara macao</i>)	1,015					o					X	X	o	
Mealy Parrot (<i>Amazona farinosa</i>)	610										X	X	X	X
Yellow-crowned Parrot (<i>Amazona ochrocephala</i>)	510										C	C	C	C
Chestnut-fronted Macaw (<i>Ara severa</i>)	430										X	X	X	X
Red-bellied Macaw (<i>Orthopsittaca manilata</i>)	370								X	X	X	X	X	X
Blue-headed Parrot (<i>Pionus menstruus</i>)	247	X	X	X	X	X	X	X	X	X	X	X	X	X
White-eyed Parakeet (<i>Aratinga leucophthalmus</i>)	157											C		
White-bellied Parrot (<i>Pionites leucogaster</i>)	155						X	X	X	X	C	C	C	
Dusky-headed Parakeet (<i>Aratinga weddellii</i>)	108		C											
Cobalt-winged Parakeet ^b (<i>Brotogeris cyanoptera</i>)	67			X	X	X	X	X	X	X				
Red-crowned Parakeet (<i>Pyrrhura roseifrons</i>)	65				X	X	X	X	X	X				
Scarlet-shouldered Parrotlet (<i>Touit huetii</i>)	60			C	C	C	C	C	C	C				
Tui Parakeet ^b (<i>Brotogeris sanctithomae</i>)	59			X	X	X	X	X	X	X				

^a Mass data from Dunning (1993).

^b Nest data from Brightsmith (2004b).

other cavities in floodplain forest (*Dipteryx micrantha*, *Erythrina* sp. and an unknown species; A. del Campo and J. I. Rojas pers. comm.).

Mealy Parrot (Amazona farinosa).—I observed two nests of this species. Eggs were laid in December ($n = 1$) and January ($n = 1$). Both nests were in floodplain forest; one had two eggs, the other one egg and one chick. One was in a dead *Iriartea* palm, the other in a natural cavity in a live emergent *Dipteryx micrantha* tree.

Relationship between body size and breeding season.—Most parrots and parakeets bred from June to November, whereas the macaws, Mealy Parrot, and White-eyed Parakeet nested from November to March (Table 1). Smaller parrot species initiated nesting significantly earlier in the season than larger parrots. This trend held for all 15 species (rank correlation: $r = 0.70$; t -test: $t = 3.08$, $df = 13$, $P = 0.009$; species listed in Table 1) and for the 11 species of which I observed chicks or eggs (rank correlation: $r = 0.81$; t -test: $t = 5.25$, $df = 9$, $P < 0.001$). I was unable to analyze body size versus nesting season using only phylogenetically independent contrasts because there is no complete phylogeny of New World parrots (Wolf et al. 1998, Tavares et al. 2004). However, the available partial phylogenies show that there are at least two independent comparisons in the data set: Red-bellied Macaw versus Blue-and-yellow Macaw and Blue-headed Parrot versus Mealy Parrot (Russello and Amato 2003, Ribas and Miyaki 2004). In both cases, the smaller species nests first.

DISCUSSION

During this study, nests or suspected nest sites were found for 13 of the 20 species of psittacids. This includes the first nest-site description for Scarlet-shouldered Parrotlet and the second for White-bellied Parrot. For White-bellied Parrot, the only previous nesting record is of an incubating female in a tree cavity in eastern Brazil (Forshaw 1989). Of the seven psittacid species for which nests were not discovered, previous nest data are available for three. In Manu National Park, Cobalt-winged Parakeet (*Brotogeris cyanoptera*) and Tui Parakeet (*B. sanctithomae*) both nest in termite mounds, lay eggs in August and September, and have chicks from mid-

September to mid-November (Brightsmith 2000, 2004b). Amazonian Parrotlets (*Nannopsittaca dachilleae*) in Tambopata attended a tree cavity in July and September (O'Neill et al. 1991). Of the remaining four species, none has been found nesting in the region: Dusky-billed Parrotlets (*Forpus sclateri*) were seen going in and out of a tree cavity in July in northern Peru (Forshaw 1989). No nests have been reported for Orange-cheeked Parrots (*Pionopsitta barrabandi*), but sightings of recently fledged young of this species at the Tambopata clay lick in December and February suggest that the birds may lay eggs in October or earlier (DJB pers. obs.). In Brazil, recently fledged Orange-cheeked Parrots also were seen during February and early March (Roth 1984, Forshaw 1989). No nesting information is available for Black-capped Parakeet (*Pyrrhura rupicola*) or Blue-headed Macaw (*Propyrrhura couloni*; Forshaw 1989, Collar 1997, Juniper and Parr 1998).

The finding that smaller species bred earlier was unexpected, but it could be related to interspecific competition for nest sites or variations in the availability of food resources (Roth 1984). Competition between species is potentially important because Chestnut-fronted Macaws, Mealy Parrots, Yellow-crowned Parrots, toucans (*Ramphastos* spp.), Scarlet Macaws, and Red-and-green Macaws all overlapped in their nest-site preferences (DJB unpubl. data). However, most of the smaller species that nested early in the season used substrates and cavities ignored by larger birds (e.g., termite mounds, thin dead palms, and small cavities; DJB pers. obs.) suggesting that something other than just competition drives the nesting phenology patterns I observed.

Seasonal differences in nesting may be due to differences in diet and food availability. The smaller parrots that nest in the dry season usually eat more nectar, flowers, and small seeds than larger species (Roth 1984, Desenne 1994; see also Terborgh 1983 for similar patterns exhibited by primates). Flowering in many tropical communities peaks in the dry season (van Schaik et al. 1993, Fenner 1998) and many wind-dispersed plants fruit in the dry season, when deciduous canopy trees lose their leaves and higher wind velocities produce ideal dispersal conditions (Fenner 1998). Because flowers and small wind-dispersed

seeds are relatively low-quality foods that require a large energy investment to harvest, smaller-bodied parrots should have an advantage when exploiting these resources (Terborgh 1983). As a result, larger species should incur comparatively greater food shortages in the dry season than smaller species, explaining the wet season breeding of larger parrots found in Tambopata. Notably, the earliest-breeding species was the mid-sized Blue-headed Parrot; members of its genus (*Pionus*) are known to eat many flowers (Galetti 1993).

Nest searching was not conducted with equal intensity in all months. Although sampling efforts were more intense later in the season, most of my nesting records for small species come from the early part of the season. I have had crews observing macaws continuously from November 2000 to May 2004, and they did not witness large macaws nesting earlier in the season. Conducting more nest searches from May through August would likely reveal additional small species breeding, corroborating the trend we found.

Few studies have addressed parrot nesting seasonality at the community level. Roth (1984) hypothesized that congeners staggered breeding to avoid competition for food. His data support the pattern for *Aratinga* and *Amazona*, where smaller species did nest earlier, but *Pyrrhura* and *Ara* overlapped extensively. My data, however, do not support temporal spacing by congeners, and my analysis of Roth's (1984) data shows that smaller species tended to nest earlier, but not significantly so (rank correlation: $r = 0.34$; t -test: $t = 0.94$, $df = 12$, $P = 0.37$). Future studies should investigate the interplay of competition for nest sites, diet, and phenological cycles in determining the seasonality of parrot breeding.

My study highlighted two types of sites that are very important to nesting parrots: emergent *Dipteryx micrantha* trees and dead palms. Six species were recorded using large, emergent *Dipteryx micrantha* trees, and 75 and 88% of the natural nests used by Scarlet and Red-and-green macaws, respectively, were in these trees (see also Nycander et al. 1995). Large emergents of this species often contained dozens of cavities, and individual trees often had multiple pairs of macaws nesting in them simultaneously (A. Hepworth and DJB unpubl. data). Because *Dipteryx micrantha*

can live for over 1,000 years, cavities in these trees may remain useable by macaws for decades or centuries (Chambers et al. 1998; but see Fichtler et al. 2003). As a result, hundreds of macaw chicks may be produced from a single tree during its lifetime. The fruits of *Dipteryx* species are also a keystone resource for a variety of tropical frugivores and granivores, including Great Green Macaws (*Ara ambigua*; G. Powell unpubl. data), bats (*Artibeus* spp.; Romo 1997), squirrels (*Sciurus* spp.), and agoutis (*Dasyprocta* spp.; Emmons 1984, Forget 1993)

Unfortunately, *Dipteryx* trees are increasingly logged throughout their range. *Dipteryx* wood is in high demand for hardwood flooring (Toledo and Rincón 1999, Wood Flooring International 2003) and, in Peru, people use the wood to make charcoal. Landowners sell trees >1 m in diameter for as little as US \$30 (A. Hepworth unpubl. data). The recent increased harvest of *Dipteryx panamensis* in Costa Rica is the most probable cause for the precipitous decline of Great Green Macaws in that country (Bjork and Powell 1995, Chassot and Monge 2002). Management schemes involving planting of *Dipteryx* trees are underway in Costa Rica. This can produce fruiting trees, but large, gnarled adult trees riddled with useable cavities are practically irreplaceable, as they take hundreds of years to grow.

Palms have long been recognized as vital to the survival of tropical frugivores and granivores (Emmons 1984, Henderson 1995). In fact, several New World parrots are thought to be almost completely dependent on palms for food, nesting sites, or both (Yamashita 1987, Forshaw 1989, Yamashita and Valle 1993, Yamashita and Barros 1997, Salaman et al. 2001). Eight parrot species were observed nesting in palms during this study, and reports from the literature show that two additional species also use palms (Red-and-green Macaw and Dusky-headed Parakeet; Forshaw 1989, Nycander et al. 1995). In sum, half of the parrot species in this community nest in palms and palms are important not only for specialists, but for many generalists as well.

Mauritia flexuosa palms are particularly valuable resources for parrots (Forshaw 1989, Bonadie and Bacon 2000). In Peru, at least seven species of psittacids nest in *Mauritia* palms (González 2003; this study), and studies

on Trinidad show that palm swamps are key to the maintenance of parrot populations (Bonadie and Bacon 2000). Dying palm swamps are particularly valuable because parrots nest at high densities in these sites. González (2003) reported aggregations of macaws in dying sections of *Mauritia* palm swamps in northern Peru, similar to what I report for Tambopata. Nesting densities there (0.075 nests/ha; range = 0.038–0.128/ha) were 100× smaller than those in Tambopata (>29 nests in 3 ha or >9.7/ha). In northern Peru, the parrots spread out over larger areas of dying swamp, and parrot collectors regularly reduced the nest densities (González 2003). In Tambopata, the birds were concentrated in a small, protected area near a large clay lick (Brightsmith 2004a). Breeding near the clay lick may be particularly important because adult parrots feed their nestlings clay and concentrate their use of the lick during the breeding season (DJB unpubl. data).

Areas of palm swamp can die synchronously in response to flooding and other events that result in depositions of large sediment loads (Kahn 1988, González 2003; DJB pers. obs.). How long the dead palms remain useable for nesting parrots under natural conditions is unknown. However, *Mauritia* palms that died when their tops were cut off remained upright an average of 4 to 5 years before they fell (Nycander et al. 1995; DJB unpubl. data). The short, useful lifetime of individual dead palms suggests that dying palm swamps slowly shift in the landscape as new areas die and old areas become unusable. Like most parrots, those that nest in these dead swamps probably “wander,” tracking shifts in food resources and nest-site availability (Collar 1997, Renton 2002). As a result, dying palm swamps probably serve as breeding “source” areas in landscape-level source-sink dynamics and play a disproportionately large role in maintaining regional populations of these long-lived and highly mobile psittacids.

Palms are valuable to local people, and dozens of species are used for food, fiber, construction materials, fuel, and medicines (Vásquez and Gentry 1989, Henderson 1995). Overexploitation is common and its potential impact on the ecosystem is great (Johnson 1986, Bonadie and Bacon 2000). *Mauritia flexuosa* swamps cover at least 2 million ha in

the Iquitos region alone, but they are threatened because local people commonly cut entire trees to harvest weevil larvae (Dryophthoridae: *Rhynchophorus palmarum*) and fruit (Peters et al. 1989, Vasquez and Gentry 1989). However, many psittacids, game species, and large-bodied seed dispersers that move between the swamps and the surrounding landscape also depend on these fruits (Bodmer 1990, Bonadie and Bacon 2000). As a result, the loss of these swamps would have great impacts on the ecosystem.

The two primary nesting resources exploited by parrots in southeastern Peru are structurally different. In fact, they represent opposite ends of the tree-cavity spectrum. The dead palms are hollow tubes with open tops that allow rain to enter. They are thin-walled, poorly insulated, and flimsy; also, they last for only a few years before collapsing. In comparison, *Dipteryx* cavities have thick walls of hard wood, full roofs that provide protection from the rain, and are usually in live sections of solid trees that live for centuries (Chambers et al. 1998; DJB pers. obs.). It is surprising that two such different substrates attracted the majority of nesting parrots. The only characteristic they shared was their isolation from the surrounding vegetation. Dead-palm nest sites were almost always in the open: along river edges, in dead swamps, above the surrounding canopy, or in forest openings. The *Dipteryx* cavities were far from heavy epiphyte and vine cover, distant from adjacent trees, and high above the ground. This suggests that protection from non-volant predators has a great influence on parrot nest-site selection (Massello and Quillfeldt 2002, Brightsmith 2005a, 2005b).

The availability of suitable nest sites limits the reproductive output of many cavity-nesting species, especially in anthropogenically modified landscapes (Newton 1994). This study suggests that *Dipteryx micrantha* and *Mauritia flexuosa* are keystone tree species for parrots nesting in southeastern Peru. Clearing for agriculture, targeted destruction of parrot nests by collectors, and selective felling of key tree species will reduce the density of suitable nest cavities. Future studies should continue to identify key nesting resources for parrots and other cavity-nesting species so

that these important habitat features can be conserved in tropical landscapes.

ACKNOWLEDGMENTS

I thank the following people for contributing nest records, library work, and support in the field: G. Arrospe, D. Brooks, A. del Campo, C. Carrasco, D. Combs, Sixto Duri, Silverio Duri, J. González, A. Hepworth, H. Lavado, R. Masias, R. von May, A. Mishaja, J. Moscoso, E. Nycander, R. Olivera, J. Pesho, R. Piñana, J. I. Rojas, A. Valdez, and L. Zapater. Thanks also to my assistants in Manu and Tambopata, the staffs of Cocha Cashu Biological Station and Tambopata Research Center, and the Native Community of Infierno for permission to work on their lands. Thanks also to the offices of the Instituto Nacional de Recursos Naturales (INRENA) in Lima, Cuzco, and Puerto Maldonado. Earlier drafts of this work were improved by the comments of E. Villalobos, J. Wiley, L. Pautrat, and two anonymous reviewers. This work was funded by the National Science Foundation (grant number DEB-95-20800), Conservation Food and Health Foundation, EarthWatch Institute, Rainforest Expeditions (www.perunature.com.pe), Raleigh-Durham Cage Bird Society, Amigos de las Aves USA, and W. and L. Smith.

LITERATURE CITED

- BENNETT, P. M. AND I. P. F. OWENS. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society of London, Series B* 264:401-408.
- BJORK, R. AND G. V. N. POWELL. 1995. Buffon's Macaw: some observations on the Costa Rican population, its lowland forest habitat and conservation. Pages 387-392 *in* The large macaws: their care, breeding and conservation (J. Abramson, B. L. Spear, and J. B. Thomsen, Eds.). Raintree Publications, Ft. Bragg, California.
- BODMER, R. E. 1990. Responses of ungulates to seasonal inundations in the Amazon floodplain. *Journal of Tropical Ecology* 6:191-201.
- BONADIE, W. A. AND P. R. BACON. 2000. Year-round utilization of fragmented palm swamp forest by Red-bellied Macaws (*Ara manilata*) and Orange-winged Parrots (*Amazona amazonica*) in the Nariva Swamp (Trinidad). *Biological Conservation* 95:1-5.
- BRIGHTSMITH, D. J. 2000. Use of arboreal termitaria by nesting birds in the Peruvian Amazon. *Condor* 102:529-538.
- BRIGHTSMITH, D. J. 2004a. Effects of weather on avian geophagy in Tambopata, Peru. *Wilson Bulletin* 116:134-145.
- BRIGHTSMITH, D. J. 2004b. Nest sites of termitarium nesting birds in SE Peru. *Neotropical Ornithology* 15:319-330.
- BRIGHTSMITH, D. J. 2005a. Competition, predation and nest niche shifts among tropical cavity nesters: phylogeny and natural history evolution of parrots (Psittaciformes) and trogons (Trogoniformes). *Journal of Avian Biology* 36:64-73.
- BRIGHTSMITH, D. J. 2005b. Competition, predation and nest niche shifts among tropical cavity nesters: ecological evidence. *Journal of Avian Biology* 36:74-83.
- BRIGHTSMITH, D. J. AND R. ARAMBURÚ. 2004. Avian geophagy and soil characteristics in southeastern Peru. *Biotropica* 36:534-543.
- CHAMBERS, J. Q., N. HIGUCHI, AND J. P. SCHIMMEL. 1998. Ancient trees in Amazonia. *Nature* 391:135-136.
- CHASSOT, O. AND G. MONGE. 2002. Great Green Macaw: flagship species of Costa Rica. *PsittaScene* 53:6-7.
- CHERRIE, G. K. 1916. A contribution to the ornithology of the Orinoco region. *Museum of Brooklyn Institute of Arts and Sciences Bulletin* 2:133-374.
- COLLAR, N. J. 1997. Family Psittacidae. Pages 280-479 *in* Handbook of the birds of the world, vol. 4: sandgrouse to cuckoos (J. del Hoyo, A. Elliott, and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.
- DESENNE, P. 1994. Estudio preliminar de la dieta de 15 especies de psitácidos en un bosque siempreverde, Cuenca del Río Tawadu, Reserva Forestal El Caura, Edo. Bolívar. Pages 25-42 *in* Biología y conservación de los psitácidos de Venezuela (G. Morales, I. Novo, D. Bigio, A. Luy, and F. Rojas-Suarez, Eds.). Gráficas Giavimar, Caracas, Venezuela.
- DUNNING, J. B. 1993. CRC handbook of avian body masses. CRC Press, London, United Kingdom.
- EMMONS, L. H. 1984. Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica* 16:210-222.
- FENNER, M. 1998. The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics* 1:78-91.
- FICHTLER, E., D. A. CLARK, AND M. WORBES. 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ¹⁴C. *Biotropica* 35:306-317.
- FORGET, P. M. 1993. Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* 94:255-261.
- FORSYTH, J. M. 1989. Parrots of the world, 3rd ed. Lansdowne Editions, Melbourne, Australia.
- FOSTER, R. B., T. A. PARKER, A. H. GENTRY, L. H. EMMONS, A. CHICCHÓN, T. SCHULENBERG, L. RODRÍGUEZ ET AL. 1994. The Tambopata-Candamo Reserved Zone of southeastern Peru: a biological assessment. RAP Bulletin, no. 6. Conservation International, Washington, D.C. www.conservation.org/xp/CABS/publications/cabs.publresearch/rap-bulletins/terrestrial.rap-bulletins/terrappbulletins.xml (accessed May 2004).
- GALETTI, M. 1993. Diet of the Scaly-headed Parrot (*Pionus maximiliani*) in a semideciduous forest in southeastern Brazil. *Biotropica* 25:419-425.
- GIBBONS, J. D. 1985. Nonparametric methods for quan-

- titative analysis. American Sciences, Columbus, Ohio.
- GONZÁLEZ, J. A. 2003. Harvesting, local trade, and conservation of parrots in the northeastern Peruvian Amazon. *Biological Conservation* 114:437–446.
- GRISCOM, B. W. AND P. M. S. ASHTON. 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in southeastern Peru. *Forest Ecology and Management* 175:445–454.
- HAVERSHMIDT, H. 1968. *Birds of Surinam*. Oliver and Boyd, London, United Kingdom.
- HENDERSON, A. 1995. *The palms of the Amazon*. Oxford University Press, New York.
- HERKERT, J. R., D. L. REINKING, D. A. WIEDENFELD, M. WINTER, J. L. ZIMMERMAN, W. E. JENSEN, E. J. FINCK ET AL. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. *Conservation Biology* 17:587–594.
- HOLDRIDGE, L. R. 1967. *Life zone ecology*, revised ed. Tropical Science Center, San Jose, Costa Rica.
- HUBER, W. 1933. Birds collected in northeastern Nicaragua in 1922. *Proceedings of the Academy of Natural Sciences Philadelphia* 84:205–249.
- JOHNSON, D. V. 1988. Worldwide endangerment of useful palms. Pages 268–273 in *The palm—tree of life: biology, utilization, and conservation* (M. J. Balick, Ed.). New York Botanical Garden, Bronx, New York.
- JUNIPER, T. AND M. PARR. 1998. *Parrots: a guide to parrots of the world*. Yale University Press, New Haven, Connecticut.
- KAHN, F. 1988. Ecology of economically important palms in the Peruvian Amazon. Pages 42–49 in *The palm—tree of life: biology, utilization, and conservation* (M. J. Balick, Ed.). New York Botanical Garden, Bronx, New York.
- MARTIN, K. AND J. M. EADIE. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecology and Management* 115:243–257.
- MASELLO, J. F. AND P. QUILLFELDT. 2002. Chick growth and breeding success of the Burrowing Parrot. *Condor* 104:574–586.
- MAWSON, P. R. AND J. L. LONG. 1994. Size and age parameter of nest trees used by four species of parrot and one species of cockatoo in southwest Australia. *Emu* 94:149–155.
- MONTAMBAULT, J. R. 2002. Informes de las evaluaciones biológicas Pampas del Heath, Perú; Alto Madidi, Bolivia; y Pando, Bolivia. RAP Bulletin 24. Conservation International, Washington, D.C. www.biodiversityscience.org/xp/CABS/publications/cabs_publ_research/rap_bulletins/terrestrial_rap_bulletins/terrappbulletins.xml (accessed May 2004).
- MONTEERRUBIO, T. AND E. C. ENKERLIN. 2004. Present use and characteristics of Thick-billed Parrot nest sites in northwestern Mexico. *Journal of Field Ornithology* 75:96–103.
- NEWTON, I. 1994. Experiments on the limitation of bird breeding densities: a review. *Ibis* 136:397–411.
- NYCANDER, E., D. H. BLANCO, K. M. HOLLE, A. DEL CAMPO, C. A. MUNN, J. I. MOSCOSO, AND D. G. RICALDE. 1995. *Manu and Tambopata: nesting success and techniques for increasing reproduction in wild macaws in southeastern Peru*. Pages 423–443 in *The large macaws: their care, breeding and conservation* (J. Abramson, B. L. Spear, and J. B. Thomsen, Eds.). Raintree Publications, Ft. Bragg, California.
- O'NEILL, J. P., C. A. MUNN, AND I. FRANKE. 1991. *Nannopsittaca dachilleae*, a new species of parrotlet from eastern Peru. *Auk* 108:225–229.
- PEARSON, D. L. AND J. A. DERR. 1986. Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. *Biotropica* 18:244–256.
- PETERS, C. M., M. J. BALICK, F. KAHN, AND A. B. ANDERSON. 1989. Oligarchic forests of economic plants in Amazonia: utilization and conservation of an important tropical resource. *Conservation Biology* 3:341–349.
- POULSEN, B. O. 2002. Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. *Biodiversity and Conservation* 11:1551–1566.
- RATCLIFFE, D. A. 1967. Decrease in eggshell weight in certain birds of prey. *Nature* 215:208–210.
- RENTON, K. 2002. Seasonal variation in occurrence of macaws along a rainforest river. *Journal of Field Ornithology* 73:15–19.
- RIBAS, C. C. AND C. Y. MIYAKI. 2004. Molecular systematics in *Aratinga* parakeets: species limits and historical biogeography in the '*solstitialis*' group, and the systematic position of *Nandayus nenday*. *Molecular Phylogenetics and Evolution* 30:663–675.
- ROMO, M. 1997. Seasonal variation in fruit consumption and seed dispersal by canopy bats (*Artibeus* spp.) in a lowland forest in Perú. *Vida Silvestre Neotropical* 5:110–119.
- ROTH, P. 1984. Repartição do habitat entre psitacídeos simpátricos no sul da Amazônia. *Acta Amazonica* 14:175–221.
- RUSSELLO, M. A. AND G. AMATO. 2003. A molecular phylogeny of *Amazona*: implication for Neotropical parrot biogeography, taxonomy and conservation. *Molecular Phylogenetics and Evolution* 30:421–437.
- SALAMAN, P., A. CORTÉS, P. FLOREZ, J. C. LUNA, O. NIETO, J. F. CASTAÑO, AND G. SUAREZ. 2001. Proyecto *Ognorhynchus* progress report IV. www.ognorhynchus.com/report4.htm (accessed August 2003).
- TAVARES, E. S., C. YAMASHITA, AND C. Y. MIYAKI. 2004. Phylogenetic relationships among some Neotropical parrot genera (Psittacidae) based on mitochondrial sequences. *Auk* 121:230–242.
- TERBORGH, J. 1983. *Five New World primates: a study in comparative ecology*. Princeton University Press, Princeton, New Jersey.

- TERBORGH, J., J. W. FITZPATRICK, AND L. H. EMMONS. 1984. Annotated checklist of birds and mammals species of Cocha Cashu Biological Station, Manu National Park, Peru. *Fieldiana Zoology* 21:1–29.
- TOLEDO, E. AND C. RINCÓN. 1999. Utilización industrial de nuevas especies forestales en el Perú. *Camara Nacional Forestal*, Lima, Peru.
- VAN SCHAIK, C. P., J. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.
- VÁSQUEZ, R. AND A. H. GENTRY. 1989. Use and misuse of forest-harvested fruits in the Iquitos area. *Conservation Biology* 3:350–361.
- WOLF, C. M., T. GARLAND, AND B. GRIFFITH. 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. *Biological Conservation* 86:243–255.
- WOOD FLOORING INTERNATIONAL. 2003. Species hardness. www.wflooring.com/TechnicalInfo/Species_Tech_Info/species_hardness.htm (accessed May 2004).
- YAMASHITA, C. 1987. Field observations and comments on the Indigo Macaw (*Anodorhynchus leari*), a highly endangered species from north-eastern Brazil. *Wilson Bulletin* 99:280–282.
- YAMASHITA, C. AND Y. M. DE BARROS. 1997. The Blue-throated Macaw *Ara glaucogularis*: characterization of its distinctive habitats in savannahs of the Beni, Bolivia. *Ararajuba* 5:141–150.
- YAMASHITA, C. AND M. DE P. VALLE. 1993. On the linkage between *Anodorhynchus* macaws and palm nuts, and the extinction of the Glaucous Macaw. *Bulletin of the British Ornithological Club* 113:53–59.