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Ecology and management of nesting blue-and-yellow macaws (*Ara ararauna*) in *Mauritia* palm swamps

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Abstract. This paper reports on the nesting ecology of blue-and-yellow macaws (*Ara ararauna*) and the structure, conservation, and management of the *Mauritia flexuosa* palm swamps where they nest: clutch size averaged 2.6 and the number of chicks fledged per nesting attempt was 0.5. Macaws nested in tall dead palms in healthy palm swamps and in palms of all heights in open dieing palm stands. All nesting palms rose well above the surrounding vegetation presumably to discourage terrestrial predators. PVC nest boxes failed to attract nesting blue-and-yellow macaws. A small section of palm swamp was managed to encourage macaw nesting by cutting the tops off of *M. flexuosa* palms and clearing the understory vegetation. The palms remained standing from 4 to 7 years and were occupied by nesting macaws at a rate of 24%. The data presented here suggest that cutting five palms a year in perpetuity would produce a stand of approximately 20 standing dead palms used by 6 or more pairs of macaws annually. However, macaw occupancy rates would depend on the density of macaws and density of naturally occurring nest sites. This management scheme could be conducted on a 100-year rotation in an area of 1–4 ha or more depending on the palm density. Such a colony could be used to increase reproductive success of blue-and-yellow macaw populations, create a valuable ecotourism resource, and concentrate macaw nesting in protected areas.

Abbreviations: TRC – Tambopata Research Center, one of the primary field sites; BSNP – Bahuaja-Sonene National Park, Peru one of the primary field sites

Introduction

The family Psittacidae is the most endangered large bird family in the world due to a combination of habitat loss, hunting and capture for the pet trade (Bennett and Owens 1997; Collar 1997). Many management techniques have been developed to help the recovery of cavity nesting birds including parrots, but more information is needed to conserve endangered populations and manage valuable species for consumptive or non-consumptive uses (Beissinger and Bucher 1992a, b; Munn 1992; Jackson 1994; Newton 1994; Nycander et al. 1995; Christian et al. 1996). While research on parrots has increased in the past decade, detailed studies have been conducted on only approximately 10% of the species (Masello and Quillfeldt 2002). For the remaining species our natural history knowledge comes from accounts of early naturalists, regional avifaunas and species accounts in family-level compendiums (Cherrie 1916; Huber 1933; Hilty and Brown 1986; Havershmidt and Mees 1994; Collar 1997; Juniper and Parr 1998).

Blue-and-yellow macaws (*Ara ararauna*) are found in lowland forests, savannahs and gallery woodlands from eastern Panama to Bolivia and southeastern Brazil (Forshaw 1989). Like most large macaws, the species has a low reproductive rate and reproduction may be limited by a lack of suitable nest sites (Munn 1992; Nycander et al. 1995; Vaughan et al. 2003). Blue-and-yellow macaws are still common in remote sites and protected areas, but are declining in areas near human population centers due to habitat alteration and persecution for the pet trade (Forshaw 1989; Mulliken and Thomsen 1995; Juniper and Parr 1998).

Mauritia flexuosa (L. f.) palms are an important nesting resource for blue-and-yellow macaws and many other psittacids (Nycander et al. 1995; Bonadie and Bacon 2000; González 2003; Brightsmith 2005). This large, single-stalked palm grows up to 30 m tall and 30–60 cm in diameter, and occurs throughout northern South America east of the Andes from Trinidad and Venezuela to Bolivia and eastern Brazil (Henderson 1995, Penn 1999). The species can grow in a variety of habitats, but is usually found in permanently swampy areas where it forms dense, nearly monospecific stands (Kahn and de Granville 1992; Penn 1999). The palm is dioecious and the fruits are an important food source for many vertebrates including macaws, parrots, tapirs, peccaries, fish, turtles, and monkeys (Goulding 1989; Bodmer 1990; Bonadie and Bacon 2000). Humans also consume the fruit in great quantities – as many as 15 metric tons daily in Iquitos, Peru – and most of this fruit is harvested by cutting the female trees (Padoch 1988; Vásquez and Gentry 1989). In many areas this palm is abundant, covering over four million ha in Peru alone (Penn 1999). However, female *M. flexuosa* have been basically eliminated near many population centers in Peru by fruit harvesting. These palm swamps are also under great threats from farming and fire on the island of Trinidad (Kahn 1988; Peters et al. 1989; Vásquez and Gentry 1989; Penn 1999; Bonadie and Bacon 2000; Oehler et al. 2001).

Nycander et al. (1995) showed that artificially decapitated *M. flexuosa* attract groups of nesting blue-and-yellow macaws useable for ecotourism. However, they were unable to evaluate the long-term sustainability of this technique. They also suggest that artificial nest boxes hung in swamps might attract nesting colonies of blue-and-yellow macaws without the need to cut palms. In this paper, we present data on blue-and-yellow macaw nesting, show that these birds did not use artificial nest boxes, evaluate *M. flexuosa* management techniques and discuss the potential for such management to conserve both macaws and palm swamps.

Methods

Study site

Macaw nesting and palm swamp characteristics were studied in the Department of Madre de Dios, southeastern Peru between November 1999 and March 2004. The area receives 3200 mm of rain annually, has a weak dry season from April to September and is classified as tropical moist forest (Tosi 1960; Brightsmith 2004). The study was conducted in four different sections of *M. flexuosa* swamp. The first two swamp areas were located the 537,000 ha Bahuaja Sonene National Park (BSNP) at 250 m elevation (13°17′ S, 69°36′ W). Here, the swamp has a dense closed canopy composed almost exclusively of *M. flexuosa* palms and the canopy contains almost no dicotyledons. In this swamp two sections were studied: (1) healthy sections of the swamp, heretofore referred to as 'healthy BSNP swamp' and (2) a dieing 3 ha section of the same swamp where a small stream was filling the area with sand and gravel from a nearby hillside and slowly killing the palms ('dieing BSNP swamp'). Only low shrubs, grass and a few juvenile palms were growing on the newly deposited gravel and sand among the dead and dieing palms (Figure 1). The third study area was a 13 ha swamp adjacent to Tambopata Research Center (TRC) in the 275,000 ha Tambopata National Reserve (13°08′ S, 69°37′ W; 250 m. elevation). The canopy of this swamp is also dominated by *M. flexuoa*, but the canopy also contained small numbers of *Euterpes precatoria* (Araceae), *Hura crepitans* (Euphorbiaceae), and other species. This site will be referred to as 'healthy TRC swamp,' The fourth site was a <1 ha section of the preceding TRC swamp where the understory vegetation was cleared and the tops of 42 palms removed between 1992 and 1999. This site will be referred to as 'managed TRC swamp.' See the 'Habitat management' section below for more information on this area. All four study sites were within 16 km of each other and near a large clay lick where dozens of *A. ararauna* and up to 28 bird species consumed soil daily (Brightsmith 2004). The study site was set in a matrix of thousands of hectares of natural habitat free from hunting and anthropogenic habitat disturbance.

Palm swamp structure

We measured densities of trunked palms, acaulescent juveniles and seedlings of *M. flexuosa* in 11 plots in February 2001 and March 2002. Trunked palms included a mix of adults and trunked juveniles. Acualescent juveniles were plants >1.5 m in height that had no visible aboveground trunk. Seedlings were all palms <1.5 m in height. In each plot, we measured the DBH and height of all dead palms and five randomly chosen large, trunked palms. Four plots were in healthy BSNP swamp, four in dieing BSNP swamp, six in healthy TRC swamp, and one in managed TRC swamp. In the managed TRC swamp, the

Figure 1. Naturally dieing *Mauritia flexuosa* palm swamp in Bajuaja Sonene National Park, Madre de Dios, Peru, February 2001. Sand and gravel from a nearby hillside, transported by the small stream in the photograph is slowly filling the swamp and killing the palms. In the background the edge of the healthy palm swamp is visible.

plot was placed where the palms were cut in 1992 and 1993 to measure the palm regeneration. In each plot, water depth was measured at 4–16 regularly spaced points.

Nest monitoring

Nests in the dieing BSNP swamp (Figure 1) were found, observed and measured during a 4 day trip during February 2002. Here we systematically observed stands of dead trees in the early mornings (dawn to 7:30 EST), evenings (15:30 – dusk), and irregularly throughout the rest of the day. Trees were considered nests if chicks called from inside, adults remained inside throughout the day or adults entered in the early morning. Often the alarm calls of adults drew our attention to active nests. Our observations at the nearby swamp at TRC showed that at this time of the year most blue-and-yellow macaws had chicks or had abandoned the nest sites for the season, indicating that trees occupied at this time were almost certainly nests. No nests were found in the healthy BSNP swamp. Nests in the healthy TRC swamp were discovered opportunistically and observed for activity approximately once every 7–10 days throughout the nesting season. We observed nests in the managed TRC swamp throughout the breeding seasons from 1999 to 2004. As it was unsafe to climb dead palms directly, we used tensed diagonal or horizontal rope bridges strung between tall live palms near the dead palms to access the nests and record the number of eggs or chicks (Nycander et al. 1995). Due to the great difficulty of this technique, we climbed once every 10–20 days in Dec 1999–March 2000, Nov 2000–March 2001 and Nov 2001–January 2002. After January 2002, the central support tree was deemed unsafe and climbing ceased. Since that time all nest monitoring has been by observation.

Nest measurement

We measured nesting palms' DBH and estimated total height using a clinometer. In March 2000, we measured the depths of the central cavities of the cut palms in the managed TRC swamp by climbing the palms and lowering a weighted tape measure in to the cavity. We also recorded if the cavity was filled with water. In March 2001, we remeasured the depth of the cavities in the six trees cut in 1999.

Artificial nest boxes

Three open-topped PVC nest boxes were hung from live *M. flexuosa* palms in the Managed TRC swamp in July of 2000. The nests were similar in design to artificial nest boxes used successfully by scarlet macaws (*Ara macao*), but were open-topped to mimic the naturally open palm cavities used by the birds (Nycander et al. 1995). We checked these nests once every 10–15 days in the subsequent nesting season (November 2000–March 2001). In March 2001, these artificial nests were removed and two were hung in live, tall, isolated *M. flexuosa* palms in the healthy TRC swamp. These were climbed or observed once every 10–20 days from November 2001–February 2002. The nests were 150, 225 and 262 cm deep and had inside diameters of 36, 30 and 30 cm, respectively. They were lined with 5 cm × 5 cm wire mesh to allow the birds to climb up and down. The bottom was filled to a depth of approximately 30 cm with a mix of sand, gravel and coarse-grained sawdust.

Palm swamp management

The goal of the habitat management was to create nesting colony of blue-and-yellow macaws in a stand of tall, isolated, dead palms surrounded by low vegetation, similar to that of the dieing BSNP swamp. To accomplish this, the understory vegetation was cleared and the tops cut from 41 *M. flexuosa* palms in a small section of the TRC swamp. Palms were cut during the dry season (April through September) in 1992 ($n = 10$), 1993 ($n = 13$), 1995 ($n = 11$), and 1999 ($n = 6$), In 1992 and 1993, the managed area was about 30 m in diameter. In 1995 and 1999, the original area was abandoned and allowed to regenerate and cutting was done in a 40 m diameter area about 10 m away from the first site. After 1999 no palms or regenerating plants were cut, From 2000 to 2004 each visitor to TRC, over 1200 per year, was given a trip evaluation form in which they were asked to list the highpoint of their trip. Data from these replies were used to compare the popularity of the palm swamp with the number of nesting macaws.

Statistical analyses

Differences in palm DBH and height among plots in each habitat type were tested using fixed effects ANOVA (Sokal and Rohlf 1995). Differences in DBH and height for active nests in different habitats and differences in DBH and height among used and unused dead palms and live palms within habitats were tested using Kruskal–Wallis rank sum tests (Gibbons 1985). Differences in palm densities among habitats were also tested using Kruskal–Wallis rank sum tests. When three groups were compared, differences among individual pairs of means were tested using a Tukey multiple comparisons test on the rank sums of the data (Sokal and Rohlf 1995). The strength of the correlation between the percent of tourists listing the visit to the palm swamp as the highlight of their trip to TRC and the number of macaws nesting in the swamp was tested using a rank correlation (Gibbons 1985). Data are presented as means ± standard deviation. For all tests, $\alpha = 0.05$ unless stated otherwise.

Results

Palm swamp structure

The vegetation in the three natural palm swamp areas studied differed significantly. Live *M. flexuosa* palms were significantly taller in the healthy BSNP swamp than in the dieing BSNP swamp or the healthy TRC swamp (ANOVA: $F_{2.44} = 15.3, p < 0.0001$, Table 1). The DBH of live palms was significantly less in the dieing swamp than in either of the live swamps (ANOVA: $F_{2.44} = 15.3$, $p = 0.05$, Table 1). The density of live trunked palms in the healthy BSNP swamp (545 ± 85 per ha) was significantly greater than in either the healthy TRC swamp or dieing BSNP swamp (Kruskal–Wallis $\chi^2 = 7.4$, df = 2, $p = 0.02$, Table 1). In the dieing BSNP, the live trees had very small crowns resulting in a canopy that was almost completely open (Figure 1). Dead palms were rare in both healthy swamps (<25 per ha), but very dense in the dieing BSNP swamp (263 ± 70 per ha, $\chi^2 = 8.9$, df = 2, $p = 0.01$. Table 1). The densities of juvenile

Table 1. Characteristics of three *Mauritia flexuosa* palm swamps in Madre de Dios, Peru.

Swamp type and location	Height (m)	DBH (cm)	Dead Palms (per ha)	Trunked (per ha)	Juveniles (per ha)	Seedlings (per ha)	Plots
Dieing BSNP	12.3 ± 7.3[a]	28.8 ± 4.6[c]	263 ± 70[e]	157 ± 73[g]	80 ± 66[j]	828 ± 1021[k]	4
HealthyBSNP	19.0 ± 6.3[b]	33.0 ± 5.9[d]	22 ± 25[f]	545 ± 85[h]	279 ± 186[j]	3470 ± 4538[k]	4
Healthy TRC	11.0 ± 30[a]	31.9 ± 4.5[d]	7 ± 9[f]	171 ± 154[g]	488 ± 590[j]	5326 ± 2787[k]	6

Within columns, means followed by different letters differed significantly ($\alpha = 0.05$). See text for discussion of statistical tests used. Differences in seedling densities bordered on significant (Kruskal–Wallis $\chi^2 = 5.2$, df $= 2$, $p = 0.07$).

palms did differ among the three sites Kruskal–Wallis $\chi^2 = 2.0$, df $= 2$, $p = 0.36$, Table 1). The densities of seedlings were lower in the dieing BSNP swamp but the difference was only marginally significant (Kruskal–Wallis $\chi^2 = 5.2$, df $= 2$, $p = 0{,}07$, Table 1). The two healthy swamps did not differ in their water depth, but the healthy BSNP swamp had significantly deeper water than the dieing BSNP swamp (healthy TRC 4.15 ± 4.56 cm, $n = 5$ plots, healthy BSNP 6.13 ± 8.49 cm, $n = 4$ plots, dieing BSNP 3.36 ± 1.46 cm, $n = 4$ plots, ANOVA: $F_{2.185} = 6.9$, $p = 0.001$).

Natural macaw nests

We found 33 blue-and-yellow macaw nests in swamps and all were in dead *M. flexuosa* palms. The nesting palms were all isolated from tall surrounding and overhanging vegetation. Nest cavities were straight, vertical, open-topped tubes and the nest floors were beds of rotting palm fibers. Three nests were in tall, dead palms in the healthy TRC swamp. All three were too rotten and isolated from surrounding vegetation to climb so contents were not checked. The nests were occupied throughout the breeding season, but it is uncertain if any young fledged. All the palms were taller than the surrounding canopy and had significantly greater DBH and height than unused dead palms and live *M. flexuosa* in the area (Kruskal–Wallis $\chi^2_{\text{height}} = 14.3$, $\text{df}_{\text{height}} = 2$, $p_{\text{height}} = 0.0008$, Kruskal–Wallis $\chi^2_{\text{DBH}} = 6.6$, $\text{df}_{\text{DBH}} = 2$, $p_{\text{DBH}} = 0.04$ Table 2). Twenty-five nests were in dead *M. flexuosa* in the dieing BSNP swamp. The height and DBH of used and unused dead palms and live palms in the adjacent healthy BSNP swamp did not differ significantly (Kruskal–Wallis $\chi^2_{\text{height}} = 3.0424$, df $= 2$, $p_{\text{height}} = 0.2184$, Kruskal–Wallis $\chi^2_{\text{DBH}} = 2.2068$, df $= 2$, $p_{\text{DBH}} = 0.3317$). Large numbers of Red-bellied macaws (*Orthopsittaca manilata*) were also present in the dieing BSNP swamp and were presumably nesting (Brightsmith In press). Three additional blue-and-yellow macaws nests were found in distinct habitats along the upper Tambopata River but they have been discussed elsewhere (Brightsmith In press).

Table 2. Characteristics of *M. flexuosa* palms in a healthy palm swamp near Tambopata Research Center. Used dead palms had nests of blue-and-yellow macaws.

	Total height	DBH	*N*
Used dead	28.0 ± 3.6 m[a]	40.0 ± 1.3 cm[d]	3
Unused dead	18.9 ± 9.08 m[b]	31.9 ± 4.73 cm[d]	17
Live	11.0 ± 2.96 m[c]	31.3 ± 5.96 cm[d]	21

Data are presented as mean ± standard deviation. Within columns, means followed by different letters differed significantly (ANOVA and Tukey multiple comparisons test Sokal Rohlf 1995).

Artificial nests

Blue-and-yellow macaws did not use any of the five PVC nest boxes hung in the TRC swamp. In the managed swamp area, the birds were never seen entering the PVC nest boxes despite the fact that they nested in dead palms < 10 m away. A pair of Scarlet Macaws (*Ara tnacao*) did use one of the PVC nest boxes in the managed swamp area. No birds were ever seen in the two nest boxes in the healthy swamp area.

Palm dynamics in managed areas

Cutting the tops off the *M. flexuosa* palms in the managed TRC swamp exposed the soft cortex which slowly rotted away leaving a vertical tube of hardened bark-like epidermis. Nine months after cutting, the average depth of the tube-shaped central cavities was 19.1 ± 34.7 cm (range 0–89 cm, $n = 6$). By 21 months after cutting the cavities in these same palms averaged 76 ± 82 cm deep (range 5–210 cm, $n = 6$). Four years after cutting a different group of palms had cavities averaging 552 ± 223 cm deep (range 258–752 cm, $n = 4$). The palms began to fall 4 years after cutting as the hollow tops of some collapsed and others fell over as the roots rotted (Table 3). Seven years after cutting all the palms had fallen ($n = 34$, Table 3). In areas cut in 1992 and 1993, seedling and juvenile densities 8 years later were 3060 per ha and 1940 per ha, respectively.

Macaw nests in managed areas

From 1990 to 2003, we monitored 12 blue-and-yellow macaw nesting attempts in cut *M. flexuosa* palms in the managed TRC swamp. In one nest, the eggs were destroyed when the bottom of the nest collapsed, in one the chick was depredated, and in six, one chick fledged. Four additional palms were defended by macaw pairs but did not fledge chicks (we do not know if they laid eggs in these nests, Table 3). The number of available dead palms and the number of chicks fledged per palm declined steadily throughout the course of the study: from 12 palms and 0.25 chicks fledged per palm in 2000 to 5 palms and 0

Table 3. Age specific persistence and use by macaws of artificially topped *Mauritia flexuosa* palms from 1999 to 2004 in Tambopata Research Center, Peru.

Years since cut	*n* (palms)	Standing	Macaws defended	Successful nest
1	6	100%	17%	0%
2	6	100%	33%	33%
3	6	100%	33%	17%
4	17	47%	63%	38%
5	11	36%	25%	0%
6	24	8%	0%	0%
7	34	0%		

The column '*n*' is the number of palms monitored. All nests were of blue-and-yellow macaws. Most of the palms were cut 4–7 years before the beginning of this study resulting in larger sample sizes for older cohorts. The six successful nests fledged one chick each.

fledged in 2004. Clutch size averaged 2.6 ± 0.53 eggs (range 2–3, $n=7$ clutches). The cut palms used by nesting macaws were significantly deeper and had slightly greater diameters than those that were not used by the birds (Table 4). The nesting palms in the healthy TRC swamp were significantly taller than the nesting palms in the managed TRC swamp and the dieing BSNP swamp (Kruskal–Wallace rank sum test, $\chi^2=9.1$, df $=2$, $p=0.01$, Table 5). There was no difference in DBH among the nesting palms in the three habitats (Kruskal–Wallace rank sum test, $\chi^2=1.74$ df $=2$, $p=0.42$). In 1995, three pairs of red-bellied macaws and two pairs of blue-and-yellow macaws nested in the cut palms in the managed palm swamp. Each nest was climbed once in mid-December: the red-bellied macaw nests contained two chicks, two chicks and two eggs, the blue-and yellow macaw nests contained one chick each (Valdez and del Campo unpubl. data, Brightsmith 2005). No other species of psittacids nested in the managed TRC swamp. On average 6% of tourists visiting Tambopata Research Center listed the palm swamp as the high point of their trip. This percentage dropped from a high of 11% in 2000 to a low of 0.9% in 2003 and was significantly correlated to the total number of macaws nesting in the palm swamp (rank correlation: $R=1$, $n=4$, $p=0.04$, Figure 2).

Table 4. Characteristics of used and unused palms in the managed *Mauritia flexuosa* palm swamp at Tambopata Research Center during the November 1999–April 2000 nesting season.

	Cavity depth (cm)	DBH (cm)	Height (m)	Water in top	*N*
Used	463 ± 277^{a}	37 ± 4.7^{c}	15.7 ± 3.6^{e}	0	5
Not used	4.3 ± 6.8^{b}	31 ± 3.5^{d}	18.4 ± 2.5^{e}	4	6

Water in top indicates the number of palms in which water accumulated in the cavity at the top of the palm. Within columns, means followed by different letters differed significantly (Wilcoxon rank-sum tests, $\alpha=0.05$, Gibbons 1985).

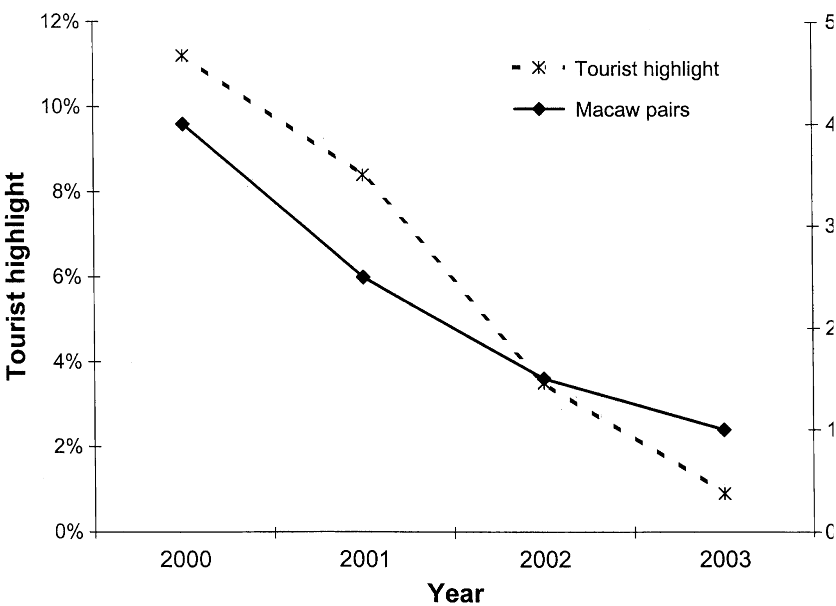
Table 5. Characteristics of blue-and-yellow macaw nesting palms in Tambopata, Peru.

	Height	DBH	*N*
Healthy TRC swamp	28.0 ± 3.6 m[a]	40.0 ± 1.3 cm[c]	3
Dieing BSNP swamp	19.8 ± 4.37 m[b]	35.9 ± 6.06 cm[c]	25
Managed TRC swamp	15.7 ± 3.6 m[b]	37 ± 4.7 cm[c]	5

Within columns, means followed by different letters differed significantly (Kruskal–Wallace rank sum test and Tukey multiple comparison test Sokal and Rohlf 1995).

Discussion

The natural palm swamps under study differed significantly in their structural characteristics. The three swamps represented a continuum of canopy conditions: tall and dense in healthy BSNP swamp, lower and more broken in healthy TRC swamp, and almost completely open in the dieing BSNP swamp. The trend towards higher seedling and juvenile densities in healthy TRC swamp may be due to the more broken canopy allowing more light penetration



Figrue 2. Relationship between the number of nesting macaws and the percentage of tourists listing the macaw nesting colony as the highlight of their visit. Tourism data from Rainforest Expeditions is based on surveys from >1200 tourists per year. The two variables are significantly.correlated (rank correlation: $R = 1$, $n = 4$, $p = 0.04$).

facilitating germination and seedling establishment (Penn 1999). In the dieing BSNP swamp, the influx of sand and gravel from the stream buried the elevated pneumatic roots, decreased overall water depth and suppressed palm regeneration. The resulting palm death produced a habitat with high densities of tall isolated dead palms surrounded by low vegetation. Such palm death due to riverine deposition is apparently common and can produce thousands of hectares of swamp with many dead palms (Kahn 1988; González 2003). These dieing swamps attract high densities of nesting parrots of up to seven species in some areas (Kahn 1988; González 2003).

Blue-and-yellow macaws nest almost exclusively in dead palms and most nests are in *M. flexuosa* palms (Havershmidt 1968; Forshaw 1989; Oehler et al. 2001; Brightsmith In press). The macaw nests we found in the healthy TRC swamp were in outstandingly tall dead palms that rose well above this lower more broken canopy. Macaw nests were never found in shorter dead palms below the swamp canopy. In the dieing BSNP swamp, all the nests were also in trees isolated from surrounding vegetation. Here birds did not have to choose the tallest palms, as nearly all rose well above the <2 m tall herbaceous understory. In healthy *M. flexuosa* swamp in Brazil the birds also chose taller dead palms (Bianchi 1998). The birds have a weak preference for large diameter palms and use palms in which the core has rotted sufficiently to produce a cavity >1 m deep (Nycander et al. 1995; Bianchi 1998). The choice of isolated trees with deep cavities is presumably an anti-predation strategy (Snyder et al. 1987; Guedes and Harper 1995).

Published clutch sizes for blue-and-yellow macaws (2.1 $\pm$ 0.83, range 1–3, $n = 8$, Nycander et al. 1995 and 2.8 $\pm$ 1.1, range 1–5, $n = 18$, Bianchi 1998) straddle the 2.6 we report here. We found nest success was 50% and fledging was 0.5 $\pm$ 0.52 chicks per nesting attempt. This is nearly identical to previous work in Tambopata where the success was 53% and fledging was 0.53 $\pm$ 0.51 chicks per nest ($n = 19$ nests, Nycander et al. 1995). However, in stands of dead palms in Manu National Park, Peru, nest success was 72% and fledging was 1.0 $\pm$ 0.5 chicks per nest ($n = 18$ nests, Munn 1992). In Brazil, nest success was also 72% and the number of chicks per nest was 0.89 $\pm$ 0.68. Of note is that 28 and 17% of the pairs in Manu and Brazil, respectively raised two chicks while none did in Tambopata. Reasons for the differences between sites are unknown. Combining the data from Peru and Brazil gives an overall nest success of 64% and 0.76 $\pm$ 0.66 chicks fledged per nest. This fledging value is about half the average for parrots as a whole (1.4 $\pm$ 1.0 chicks fledged per nest, $n = 27$ species; Masello and Quillfeldt 2001). This suggests that endangered populations may be slow to recover even with a complete cessation of hunting and collection for the pet trade. However, reproduction may be greater in some instances: wild-caught blue-and-yellow macaws released on the island of Trinidad have produced 1.1 chicks per pair per year (Plair pers, comm.).

Artificial nests

Blue-and-yellow macaw did not use PVC nest boxes even though these boxes were hung in the correct habitat at appropriate heights in isolated *M. flexuosa* palms. This could be because, the birds do not face a shortage of natural nest sites. However, pairs quickly occupied the cut palms and fought over suitable nest sites, suggesting that there were more pairs than suitable nest cavities (Munn 1992; Nycander et al. 1995). Not all cavity nesters, even those that presumably face a shortage of nest sites, recognize artificial structures as suitable nest sites (Snyder et al. 1987). This may be the case in this study. The birds may not have recognized the artificial nests as suitable, because they were hung on live palms while most blue-and-yellow macaw nest in dead palms (Nycander and Bianchi pers. com.). However, Bianchi (1998) hung 18 nest boxes for this species on dead *M. flexuosa* palms in suitable habitat in Brazil and none of them were occupied. This suggests that thermal characteristics, shape, drainage or other basic characteristics of the PVC nests are unacceptable to the blue-and-yellow macaws. My research has also shown that PVC nests are not used by red-and-green macaws (*Ara chloroptera*), but are readily accepted by scarlet macaws (DJB unpubl. data). Perhaps blue-and-yellow macaws would use nests incorporating natural materials with different thermal characteristics that blend more readily in to the surrounding landscape as was found with the Puerto Rican Parrot (*Amazona vittata*; Snyder et al. 1987).

Swamp management

Sustainable management of *M. flexuosa* swamps for nesting macaws would require successful palm regeneration and a long enough rotation length to allow the regrowth and reproduction of adult palms. Developing such a management scheme requires detailed information on the biology of *M. flexuosa* including female palm densities, fruiting schedules, germination requirements, growth rates, age of first fruiting, and life span. The sex ratio of *M. flexuosa* under natural conditions is approximately 1:1, so seed trees would be readily available (Vásquez and Gentry 1989). However, in severely impacted forests where most females have been removed, seed sources could limit regeneration of cut swamps. Fruting is concentrated in the wet season and germination takes from 1 to 6 months, suggesting that cutting palms should be done in the late wet or early dry season (Padoch 1988; Penn 1999). Fruiting, germination, seedling establishment, and seedling growth are apparently best in high light so regeneration should be good in managed areas (Penn 1999). Our data support this contention. In areas cut 8 years earlier seedlings were as dense as in intact swamp, juveniles were twice as dense as in intact swamp and juvenile densities were about 10 times higher than the density of adults in intact swamp (Table 1). Age at first fruiting, while not studied in detail, is apparently less than 20 years (Penn 1999). The lifespan of these palms has not been studied, but in healthy palm swamps about 4% of the trunked palms are dead (Table 1). If naturally dieing palms last about 4 years before falling (like cut palms) about 1% of the trunked palms die per year suggesting that the average trunked *M. flexuosa* in Tambopata lives about 100 years. While the uncertainty of this estimate is great, a 100-year rotation should be long enough to allow adult palms to regrow even if the first regenerating cohort is cut before senescence.

Using the age specific falling rates of cut palms and reproduction by macaws at TRC, we can evaluate possible management schemes to create blue-and-yellow macaw nesting colonies in intact *M. flexuosa* palm swamp. By cutting five palms per year, the number of standing dead palms would stabilize at about 20 by year six. In areas with palm densities similar to healthy TRC swamp, the amount of area cut each year would be about 350 m^2 and the total area under management at any one time would be a clearing of about 26 m radius (assuming that five palms are cut and one female left uncut as a fruit source each year). The entire.management scheme could be carried out on a 100 year rotation in about 3.5 ha. In areas like the healthy BSNP swamp with higher palm densities, the total area cut would be about 110 m^2 per year and the 100-year rotation would use less than 1.5 ha. In other swamps, the densities of *M. flexuosa* range from 46 to 350 per ha suggesting that the entire management scheme could require up to 11 ha (Kahn 1988; Kahn and de Granville 1992). In areas where female tree densities have been reduced by fruit harvesting, only male palms should be cut to maintain all possible seed sources and fruit for wildlife. Truly sustainable extractive activities are rare, as even apparently benign management schemes like the harvest of Brazil nuts often turn out to be unsustainable in the long term (Peres et al. 2003). As a result, additional studies of *M. flexuosa* demography and swamp regeneration are needed before the proposed management scheme could be declared truly sustainable. However, cutting such small numbers of palms on such a long rotation is much closer to sustainable than the fruit harvesting practices being carried out in thousands of hectares annually.

Groups of 20 dead palms produced by the management scheme proposed here should attract about six pairs of blue-and-yellow macaws and produce on average 3.4 chicks per year. However, the number of nesting macaws will depend on local conditions like the density of macaws, the abundance of naturally occurring nest sites, the surrounding vegetation and the presence of competitors. In areas with few macaws or many natural nest sites, few pairs are likely to nest in managed swamps, for example on Trinidad, where reintroduced populations of blue-and-yellow macaws are small and brushfires kill many. *M. flexuosa* palms (Bonadie and Bacon 2000; Oehler et al. 2001; B. Plair pers. com). Reduced palm occupancy may also result when regenerating vegetation grows up around dead palms. The presence of competitors may also reduce the palm occupancy rates. In Tambopata, the only other bird species that used the cut palms was the red-bellied macaw (370 g), which is too small to compete for nests with the larger blue-and-yellow macaw (1125 g, Dunning 1993; Brightsmith 2005). However, in other areas *Amazona* parrots (up to 510 g) and scarlet macaws (1025 g) frequently use dead palms and could compete with blue-and-yellow macaws for nests. We suspect that aggressive interactions among pairs of blue-and-yellow macaws would not limit nesting densities as we found three pairs nested successfully within a 5 m radius area and in Brazil pairs nested within 4 m of each other (Bianchi 1998). Instead, the occupancy rates of cut palms could be significantly greater than those we report because we studied groups of $8.6 + 2.88$ palms per year (range 5–12). With groups of 20 dead palms the percent occupancy and nest success could be higher if macaw pairs are enticed to nest by the presence of other nesting pairs (see also Munn 1992).

The proposed management scheme could be used to boost reproduction of blue-and-yellow macaws and concentrate nesting pairs in protected areas. Many large psittacids, including macaws, face a shortage of suitable nesting sites and not all eligible pairs breed (Munn 1992; Guedes and Harper 1995; Nycander et al. 1995; Marsden and Pilgrim 2003; Murphy et al. 2003). Managing *M. flexuosa* swamps could increase a population's reproductive output and help the species naturally recolonize areas from which they were extirpated. In hostile landscapes, where hunters and poachers take blue-and-yellow macaws from nests, creating nesting colonies through swamp management could concentrate nesting birds in protected areas while enforcement and education campaigns work to reduce the taking of the birds by local people (Forshaw 1989; González 2003; Vaughan et al. 2003; Powell pers. com.).

The proposed management scheme could also create a valuable ecotourism resource. Nature based tourism is a multi billion dollar business worldwide (TIES 2000) and observation and photography of large macaws and parrots is potentially worth thousands of dollars annually (Munn 1992; Christian et al. 1996). The macaws at our site usually begin to defend nest sites in July or August and most chicks fledge by April so managed swamps should have macaw activity for up to 10 months per year (DJB pers. obs). At TRC, Rainforest Expeditions constructed a 15 m scaffolding tower in the middle of the stand of dead palms. The tower was open on top and from here groups of up to 10 people would observed the nesting colony year-round. The macaws nested successfully in dead palms that were within 15 m of the tower in spite of the daily presence of people (DJB unpubl. data). At this site where guests paid approximately $900 for a 5 day visit, up to 11% of the guests considered the macaw colony the highlight of the trip and the more macaws present the higher the level of tourist satisfaction (Figure 2).

The idea of cutting natural palm swamp to provide a tourist attraction may not be acceptable to all. However, there are many scenarios under which a macaw colony could generate enough conservation benefits to justify the costs. *M. flexuosa* fruits and macaw chicks are being unsustainably harvested from thousands of hectares of swamps (Padoch 1988; Vásquez and Gentry 1989; González 2003). Without some intervention these activities will continue to degrade swamp ecosystems throughout the western Amazon basin (Penn 1999). While it is widely acknowledged that ecotourism is not a panacea (Belsky 1999; Snow 2001; López-Espinosa de los Monteros 2002), properly planned and implemented ecotourism projects could help protect large areas of swamp and adjoining forest by funding protected areas, hiring local guards, restoring degraded swamps, sponsoring education campaigns and providing economic alteratives for local people (Menkaus and Lober 1996; Stronza 1999, 2000; Báez 2002; Bouton and Frederick 2003).

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