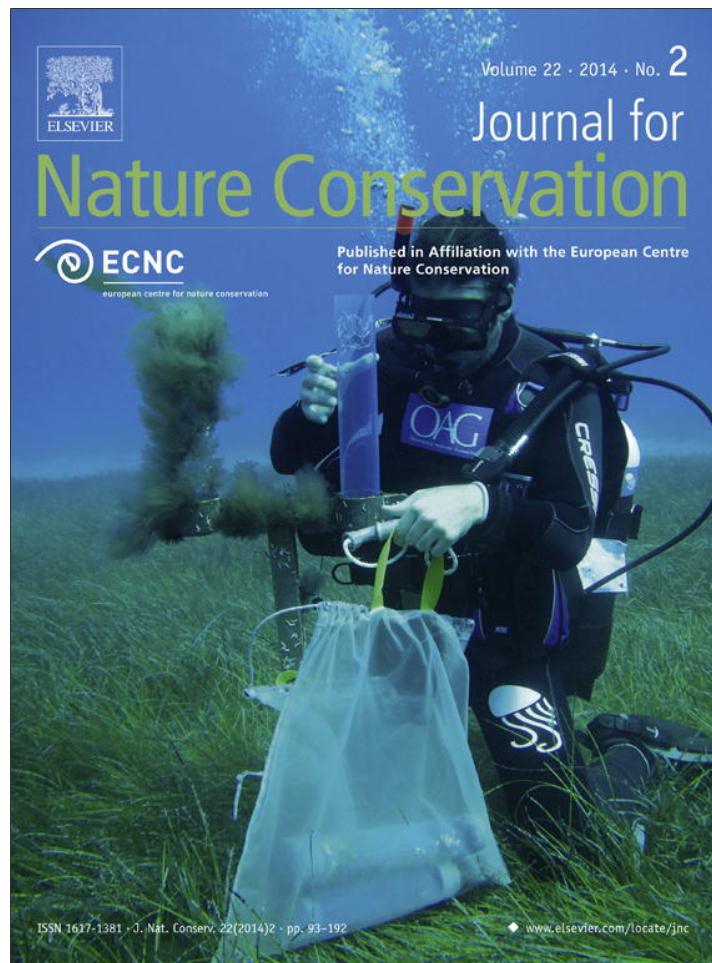


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.de/jnc

Nest site selection and efficacy of artificial nests for breeding success of Scarlet Macaws *Ara macao macao* in lowland Peru

George Olah^{a,d}, Gabriela Vigo^{b,d}, Robert Heinsohn^a, Donald J. Brightsmith^{c,d,*}^a Fenner School of Environment and Society, College of Medicine, Biology & Environment, The Australian National University, Canberra, Australia^b Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX, USA^c Schubot Center at Texas A&M University, Department of Veterinary Pathobiology, College Station, TX, USA^d Tambopata Macaw Project, Madre de Dios, Peru

ARTICLE INFO

Article history:

Received 9 April 2013

Received in revised form

21 November 2013

Accepted 21 November 2013

Keywords:

Nest hollow

Nest site preference

Parrots

Nest box

ABSTRACT

Psittacidae (parrots) have the most threatened species of any bird family in the world. Most parrots are obligate secondary cavity nesters, and can be limited in their breeding success by the availability and quality of nest hollows. However, nesting opportunities for parrots can be increased by provision of artificial nest boxes. The Tambopata Macaw Project has been studying the breeding ecology and natural history of the Scarlet Macaw *Ara macao macao* in the south-eastern Peruvian Amazon for over 20 years by monitoring natural nest hollows and two types of artificial nest (wooden and PVC). We present data for breeding success in natural and artificial nests over 12 consecutive breeding seasons. The aims of this study were to: (a) determine the nesting requirements and reproductive success of breeding macaws; and, (b) compare the efficacy of the two types of artificial nests and natural nest cavities. Our data showed a high rate of reoccupation of successful nests in consecutive years and that nests in artificial and natural nests had very similar reproductive parameters. Our results indicate that artificial nest types can be used by conservation managers seeking to assist *A. macao* populations where nest hollows are in short supply, and that artificial nests can contribute important data to natural history studies of species where access to natural nests is limited.

© 2013 Elsevier GmbH. All rights reserved.

Introduction

Information about nest sites and reproductive success of wild bird populations is necessary for effective conservation and management strategies (Renton 2000). Breeding success is a crucial determinant of recruitment rates, population size and long-term population viability in many avian species (Martin & Geupel 1993). The type of nest used by birds can determine breeding success rates and other aspects of life-history (Paredes & Zavalaga 2001). Most parrots are obligate secondary cavity nesters (Monterrubio-Rico & Escalante-Pliego 2006), thus their breeding success is closely related to the availability and quality of nest hollows (Collar 1997). The number and quality of nest cavities have been shown to be limiting for various parrot species, like Eclectus Parrot *Eclectus roratus* Müller, 1776 (Heinsohn 2008a; Heinsohn et al. 2005), Palm

Cockatoo *Probosciger aterrimus* Gmelin, 1788 (Heinsohn et al. 2003), Swift Parrot *Lathamus discolor* White, 1790 (Stojanovic et al. 2012), Amazona parrots (White et al. 2005), and Blue-throated Macaw *Ara glaucogularis* Dabbene, 1921 (Hesse & Duffield 2000) among others.

Secondary cavity nesters can be assisted by the provision of artificial nest boxes (Brightsmith 2005a). They can be placed in areas where hollow availability is low, and can be supplied in large enough numbers to facilitate statistical inference for scientific research (Major & Kendal 1996). Their characteristics usually mimic the natural nest hollows of the target species, but artificial nests can also be more amenable to experimental manipulation as they reduce variation in nesting circumstances and improve accessibility to the nest (Villard & Pärt 2004). They can be useful tools for supporting reintroduction and translocation of endangered bird species (White et al. 2006), and for enhancing ecotourism by increasing the numbers of nesting birds (Nycander et al. 1995). Nest boxes have made it easier to perform comparative and experimental field investigations, since they can facilitate the installation of electronic monitoring devices (Grenier & Beissinger 1999; White & Vilella 2004). Nevertheless, concerns have been raised about the generality and applicability of data from nest box studies (Lambrechts et al. 2012). For instance, there have been doubts about

* Corresponding author at: Schubot Exotic Bird Health Center, Department of Veterinary Pathobiology, TAMU 4467, College of Veterinary Medicine, Texas A&M University, College Station, TX 77843-4467, USA. Tel.: +1 979 458 0563; fax: +1 979 845 9231.

E-mail address: DBrightsmith@cvm.tamu.edu (D.J. Brightsmith).

whether experimental setups of artificial nests mirror accurately enough the natural systems they attempt to model (Major & Kendal 1996).

The family Psittacidae (parrots) has the highest number of threatened species of any bird family (Bennett & Owens 1997; IUCN 2013). Approximately 30% of all the parrot species are threatened globally and 37% of the Neotropical parrots are threatened (IUCN 2013). Despite the increase in parrot studies in the last decade (Amuno et al. 2007; Berkunsky & Rebores 2009; Boyes & Perrin 2009; Briceño-Linares et al. 2011; Brightsmith & Villalobos 2011; Britt 2011; Downs 2005; Ekstrom et al. 2007; Heinsohn 2008b; Murphy et al. 2007; Stojanovic et al. 2012; Theuerkauf et al. 2009; Vigo et al. 2011; White et al. 2012) more research is required to document basic natural history and determine the effects of processes such as deforestation, habitat fragmentation, hunting by humans for food, and trapping for the pet trade (Laurance et al. 2009).

Macaws (genera *Ara*, *Anodorhynchus*, *Cyanopsitta*, *Primolius*, *Orthopsittaca*, and *Diopsittaca*) are charismatic parrots that remain poorly understood in the wild (Forshaw 1989). Currently five species of macaws are extinct, and of the remaining 17 species, three are critically endangered (CR), four endangered (EN), two vulnerable (VU), and one near threatened (NT). Many of these macaws are found in the Amazon Basin in South America, which also contains a highly diverse and complex globally important ecosystem. Even today, this region that includes 60% of the world's remaining tropical rainforest (Laurance et al. 2002) is little known. The large size and wide-ranging habits of macaws, together with their popularity in human society, make them suitable 'umbrella' species for conservation in the Amazon region (Roberge & Angelstam 2004).

The Tambopata Macaw Project has been studying the breeding ecology and natural history of three large macaw species (Scarlet Macaw *Ara macao macao* Linnaeus, 1758, Red-and-green Macaw *Ara chloropterus* Gray, 1859, and Blue-and-yellow Macaw *Ara ararauna* Linnaeus, 1758) in the south-eastern Peruvian Amazon for over 20 years (Brightsmith 2005a; Brightsmith et al. 2008a; Nycander et al. 1995). In the Tambopata region of Peru *A. macao* is still found in abundance (Renton & Brightsmith 2009). This natural environment provides ideal circumstances for understanding the nest preferences of this bird, which can then be applied in other locations where their populations are declining.

In this paper we examine the long-term nesting success of *A. macao macao* (hereafter *A. macao*) with emphasis on the effectiveness of providing the birds with artificial nest boxes. Our aims are to: (a) determine the natural nesting requirements and reproductive success of the breeding macaws; and, (b) examine the efficacy of two different types of artificial nest (wooden and PVC) and compare their success to natural nest cavities. We anticipate that data from both natural and artificial nest types will have important conservation applications by informing conservation managers seeking to assist macaw populations where nest hollows are in short supply.

Materials and methods

Study area

The study was conducted in the forests surrounding the Tambopata Research Center (TRC) in south-eastern Peru (13° 8.070' S, 69° 36.640' W), in the Department of Madre de Dios, in the Tambopata National Reserve (2747 km²), near the border of the Bahuaja-Sonene National Park (10,914 km²). This area, which receives an average annual rainfall of about 3300 mm (Brightsmith 2004), is located in tropical moist forest adjacent to subtropical wet forest (Tosi 1960) and is surrounded by four main forest types:

terra firme; floodplain; palm swamp; and, a mixture of early and late successional forest. The research centre is located 880 m from a large clay lick, Collpa Colorado, that serves as an important source of sodium rich soil which macaws feed on year round, especially during breeding when they feed it to their chicks (Brightsmith & Villalobos 2011; Brightsmith et al. 2008b, 2010; Powell et al. 2009). All the studied nests were located within 3 km of TRC. The apparently high density of nests is likely due to both the provisioning of artificial nests and the close proximity of the large clay lick (Brightsmith 2004; Brightsmith et al. 2008b). In an effort to document the breeding parameters of the normal wild population, data from the nests of the hand-raised and released individuals of *A. macao* found in the study area (Brightsmith et al. 2005; Nycander et al. 1995) were excluded from the analyses presented in this paper. Data on these birds will be presented elsewhere.

Study species

The breeding of *A. macao* in south-eastern Peru takes place during the wet season (November–April). The species nests in hollows of emergent trees including ironwood tree *Dipteryx micrantha* Harms, 1926 (Fabaceae), *Calycophyllum* sp. Candolle, 1830 (Rubiaceae), *Hymenaea oblongifolia* Huber, 1909 (Fabaceae), *Erythrina* sp. (Fabaceae), and barrigona palm *Iriartea deltoidea* Ruiz and Pavon, 1978 (Arecaceae) (Brightsmith 2005b; Renton & Brightsmith 2009). Birds usually lay 2–4 eggs asynchronously, the incubation period is 26–28 days, and the chicks fledge around 86 ± 4 days post hatching (Forshaw 1989; Vigo et al. 2011). Macaws like other parrots hatch asynchronously (Stoleson & Beissinger 1997). Although three eggs hatch on average, in general only one or two chicks survive until fledging, mainly due to starvation of the youngest siblings (Vigo et al. 2011). We used The Clements Checklist of Birds of the World as source of the nomenclature of avian taxa (Clements et al. 2013), the IUCN Red List database for other animal taxa (IUCN 2013), and the International Plant Names Index for plants (IPNI 2012).

Nest monitoring

We employed data collected from November 1999–March 2011 (12 nesting seasons) to determine factors affecting the nest use and reproductive success of wild *A. macao*. The number of natural nests varied annually as new nests were found and old nests were lost due to takeover by stinging insects or through tree fall. The first artificial macaw nests were installed at the site in the early 1990s (Nycander et al. 1995). The number of artificial nests monitored each year varied as new nests were added, old nests were moved, trees containing nests fell down, and old nests were abandoned by the birds. All artificial nests were hung one per tree although distance between adjacent artificial nests varied greatly: from 31 to 425 m. They were hung at an average height of 26.8 ± 5.7 m.

Wooden nest boxes (Fig. 1B) were about 1.5 m tall and made from tropical hardwoods (*Cedrela odorata*, *Cedrelinga catenaeformis*, *Calophyllum* sp., etc.), with an approximate weight around 70 kg. PVC nests (Fig. 1A) were constructed from 26 to 39 cm diameter PVC pipes lined with wire mesh and weighed 35–60 kg. Both nest types were filled to a depth of 30 cm with a mixture of sawdust, wood, and sand. A single door near to the bottom of each nest allowed investigators access to eggs and young individuals. The artificial nests were fixed to tree trunks with a 2.5 cm wide climbing webbing or 11 mm diameter climbing rope, and they were attached both at the top and bottom to reduce swaying and spinning.

We climbed to the nests using single-rope ascending techniques (Perry 1978; Perry & Williams 1981) and lowered chicks to the ground in buckets (Nycander et al. 1995). Nest visits usually took 30–50 min from arrival until departure. For the safety of the chicks and the researchers, nests were not climbed during rain or high

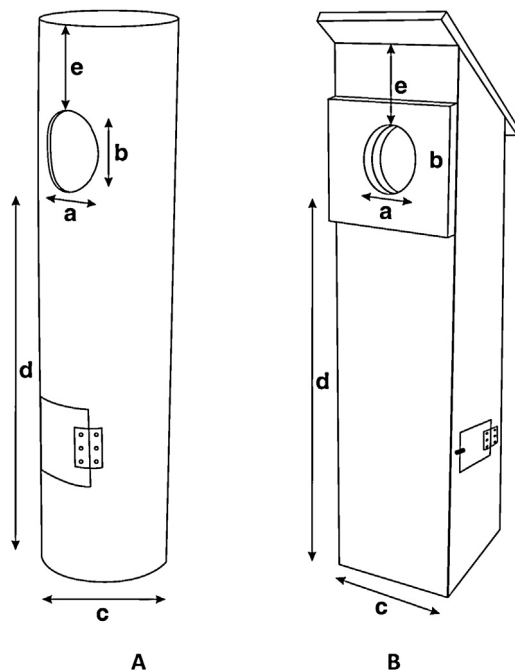


Fig. 1. PVC (A) and wooden (B) nest designs used in the study for *Ara macao*. Main measurements (and their average values) analysed were: (a) horizontal (17.18 cm) and (b) vertical diameter (18.40 cm) of the hole; (c) inside diameter (36.15 cm); (d) maximum depth (100.85 cm); and (e) inside height (23.44 cm).

wind. Over the course of the 12 breeding seasons we monitored a total of 26 natural, 12 wooden and 24 PVC nests. The number of nests monitored per season was 10.1 ± 3.7 SD natural, 3.1 ± 2.2 wooden and 10.3 ± 3.3 SD PVC. Nests were monitored from October to April, and those located closer to TRC were usually monitored more intensely than those further from the centre. Nests where there was no presence of *A. macao* were climbed 1–2 times per week from November to January. However, where macaws were seen defending the nests, climbing frequency increased to every one to two days (on average five climbs before eggs were found at occupied nests). Climbing protocols changed throughout the study: from 2000 to 2002 we climbed every 2–3 days during incubation and from 2003 to 2011 once eggs were found we did not climb the nest again until the estimated hatch date to minimise the effect of human disturbance on nesting. After chicks hatched we measured them daily for the first 15 days, then two or three times per week. Climbs were increased to daily or every other day near the estimated fledging date. Overall, occupied nests were climbed an average of $28.6 (\pm 1.6 \text{ SE})$ times per season. If at least one egg was laid in a nest during the breeding season it was considered a “nesting attempt” and the nest was considered “occupied” for that season. For each nesting attempt we determined the following: (1) whether eggs were damaged, hatched, or did not hatch; and, (2) whether the nest was depredated, taken over by other macaws, fell down, or successful (fledged one or more chicks).

Statistical analysis

To determine the relationship between nesting success and nest characteristics, we analysed four measures of nest use and nesting success as response variables – whether eggs were laid (yes or no), whether ≥ 1 egg hatched (y/n), whether ≥ 1 chick fledged (y/n) and number of chicks fledged. We used combinations of 43 different variables depending on the analysis. The explanatory variables examined fall into four main categories: *Nest monitoring* (10) to test if the actions of the researchers had any effect on

breeding success; *Presence of adult macaws* (4) to test the influence of parental behaviour on nest success; *Nest cavity characteristics* (12) to test the importance of nest measurements on reproductive success; and *Nest site characteristics* (12) to test the effects of visibility, habitat type and distance to other nests (Table 1).

We used a statistical modeling approach with all analyses carried out in GenStat 13.2 (Payne et al. 2009). Whenever the data included repeated measures of the same nest over multiple years we assigned nest identity as a random effect, while the other factors were examined as fixed effects of interest.

We fitted generalised linear mixed models (GLMM) with a binary response (yes/no) to determine which factors influenced: (a) whether eggs were laid; (b) hatching success (one or more eggs hatched); and, (c) fledging success (one or more chicks fledged). We determined with linear mixed models (LMM) which factors affected the number of chicks fledged (continuous response variable), using all nests where eggs were laid. Due to the risk of over-parameterisation, the variables of interest were tested in four separate blocks: (1) nest site characteristics; (2) nest cavity characteristics; (3) macaws present at nest; and, (4) the extent of researcher monitoring activity. Once the significant variables were obtained from each block we combined these variables into a final model and reran it.

In order to determine success at the most occupied nests we performed a generalised linear model (GLM) analysis on nests that were occupied for at least five seasons over the study period. We used the number of years a nest was occupied as the response variable, which we compared to the total years the same nest was observed (as binomial total of the model). We started each analysis with a full model and progressively dropped non-significant terms until the most parsimonious model containing all significant terms was obtained. Unless otherwise stated, we present data as mean \pm standard error.

Results

Characteristics of nest trees and nest hollows

We analysed data from a total of 147 nesting attempts ($n=8$ in 1999–2000, $n=9$ in 2000–2001, $n=15$ in 2001–2002, $n=12$ in 2002–2003, $n=10$ in 2003–2004, $n=11$ in 2004–2005, $n=14$ in 2005–2006, $n=12$ in 2006–2007, $n=14$ in 2007–2008, $n=15$ in 2008–2009, $n=8$ in 2009–2010, $n=19$ in 2010–2011) that occurred in 42 different nest sites (18 natural, 8 wooden nest boxes and 16 PVC nest boxes) over the 12 years of the study. Most of the available nests were located in floodplain forest (55%), with the remainder in upland or terra firme forest (28%) and successional forest (17%). The distribution of the occupied nests among habitats did not differ significantly from the distribution of available nest sites ($\chi^2_2 = 0.32$, $P=0.850$, Fig. 2).

Of the occupied nests, 44% successfully fledged ≥ 1 chick, 55% failed, and 1% had unknown outcome. Among the 81 nest failures, 37% were lost because the eggs were broken or disappeared before the hatch date. In 32% the eggs were cracked or failed to hatch after the anticipated hatch date. Most of these cases (18 of 26) were in PVC nests with only four in wooden nests and four in natural nests. In 15% of failed nests we found chicks which were killed by parasites, sickness, and bee or wasp attacks but without any sign of predation. For only 7.5% of failed nests ($n=6$) did we suspect loss to predators. Of these six predation events, four occurred in natural nests, one in a wooden nest and one in a PVC nest. At least six clutches (7.5% of failed nests) failed due to fights with other pairs of macaws over nest ownership (two in artificial and four in natural nest). We suspect some of the nests where eggs were cracked or did not hatch may have also failed due to fights over nest ownership.

Table 1
Variables used in the regression analyses for testing the nest site selection of *Ara macao* in the lowlands of south-eastern Peru.

Category	Variable name	Variable description
Breeding effort	# Eggs	Number of eggs in clutch
	# Hatched	Number of chicks hatched
	# Fledged	Number of chicks fledged
	Outcome last year	The outcome of the nest the year before: (0) no activity or no eggs; (1) eggs hatched; (2) young fledged; (3) predation; (4) fight or takeover; (5) disappeared or cracked eggs after hatch date; (6) nest flooded; (7) nest (tree) fell; (8) unknown; (9) chick found dead in nest without any sign of predation; and, (10) eggs broken or disappeared before hatch date
	Occupancy rate	% of all years nest was occupied (calculated only for nests monitored ≥ 5 years)
Nest monitoring	# Climbs per season	Number of times nest was climbed in the season
	Before eggs	Number of climbs before eggs were laid
	1–10 days	Number of climbs during first 10 days of incubation
	11–20 days	Number of climbs during second 10 days of incubation
	21–26 days	Number of climbs during last 6 days before expected hatching
	1st week chick age	Number of climbs during first 7 days after first chick hatched
	1–2 weeks chick age	Number of climbs from day 8 to 14 after first chick hatched
	2–4 weeks chick age	Number of climbs from day 15 to 28 after first chick hatched
Presence of adult macaws	4–8 weeks chick age	Number of climbs during the 2nd four weeks after first chick hatched
	8–12 weeks chick age	Number of climbs during the 3rd four weeks after first chick hatched
	% birds present	Percentage of climbs macaws were present
Presence of adult macaws	Min dist	The average minimal distance between the climber and the macaws
	% birds called	Percentage of climbs macaws made an alarm call at the nest
	% birds left	Percentage of climbs macaws left the nest area
Nest cavity characteristics	Nest type	(1) Artificial wooden, (2) artificial PVC, (3) natural hole in tree, (4) natural palm hollow
	Nest position	Nest orientation: (1) horizontal, (2) vertical
	# Natural in tree	Number of additional natural nests in the same tree
	# Artificial in tree	Number of additional artificial nests in the same tree
	Hole vert	Vertical diameter of the hole entrance (if there is more than one hole the largest one) in cm
	Hole horiz	Horizontal diameter of the hole (if there is more than one hole the largest one) in cm
	Diameter inside	Internal diameter of cavity 30 cm from entrance in cm
	Max depth	Bottom of hole to base of the nest in cm
	Inside height	Top of hole to the roof in cm
	Hole height ^a	Height of hole entrance from ground in cm
Nest site characteristics	Direction hole faces	The compass bearing of the hole entrance
	Vertical angle the hole faces	Positive angle faces above horizontal (+90 straight up; -90 straight down)
	Dist to 1st	Distance (m) to the nearest nest occupied by Scarlet Macaws
	Dist to 2nd	Distance (m) to the second nearest nest occupied by Scarlet Macaw
	Macaw 1st	Distance (m) to the nearest nest occupied by either Scarlet or Red-and-green Macaw
	Macaw 2nd	Distance (m) to the second nearest nest occupied by either Scarlet or Red-and-green Macaw
	Collpa (clay lick)	Distance (m) of nest from Collpa Colorado clay lick
	Habitat	(1) Terra firme forest, (2) floodplain forest, (3) palm swamp forest, (4) successional forest
	Tree height	Total height of the tree where the nest is situated
	Tree circumference	Circumference (at 150 cm above ground or above the buttresses) of the nest tree
Canopy major axis	Maximum width of the canopy of the nest tree	
Lowest leaf	Height of the lowest leaf (from the ground level) of the nest tree	
Canopy minor axis	The width of the canopy measured perpendicular the maximum canopy width of the nest tree	
Tree species	Species of the nest tree	

^a The nest height is defined as the hole height.

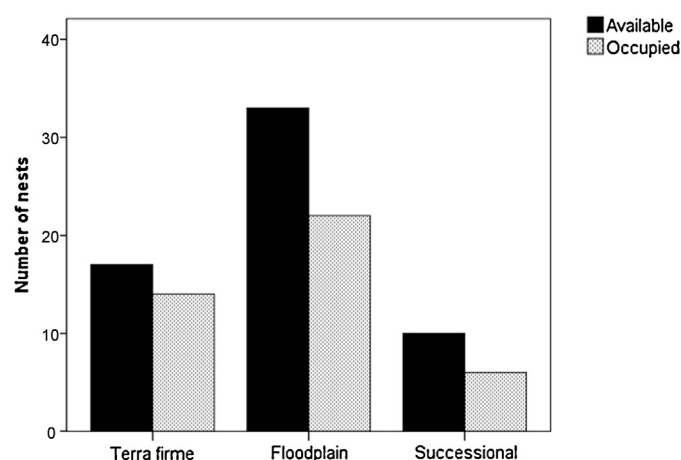


Fig. 2. Distribution of available and occupied (natural and artificial) *Ara macao* nests by habitat types in the lowlands of south-eastern Peru. Differences were not significant.

One nest (1% of failed nests) was lost because the bottom of the PVC nest box fell off. No nests were lost due to the nesting tree falling down.

Determinants of reproductive success: (1) clutch initiation

Over the 12 seasons, 37% of the occupied nests were in natural cavities and 63% were in artificial (15% wooden and 48% PVC). Nearly half (49%) of the clutches had three eggs, 12% had one egg, 25% had two eggs, and 14% had four eggs. The mean number of eggs laid per clutch was 2.70 (± 0.08 SE) with no significant difference between natural and artificial nests (GLMM_{Nest type}: $\chi^2_2 = 1.66$, $P = 0.441$; Table 3).

A. macao laid eggs significantly more often in nests which were successful the year before (GLMM_{Outcome last year}: $\chi^2_7 = 21.2$, $P = 0.030$). In total 85% of nests successful one year were re-occupied the next year, while only 41% of nests which were not successful (no activity or failed) were occupied the subsequent year. We found no significant effect on occupancy of the distance to the nearest nest occupied by the same species (Mean_{occupied nest} = 192 m \pm 18

SE; Mean_{unoccupied nest} = 193 m ± 22 SE; GLMM_{Distance to nearest nest}: $\chi_1^2 = 0.74$, $P = 0.39$). However, we found that the distance to the second nearest nest had a significant positive effect on occupancy (Mean_{occupied nest} = 321 m ± 22 SE, Mean_{unoccupied nest} = 375 m ± 29 SE; GLMM_{Distance to second nearest nest}: $\chi_1^2 = 4.84$, $P = 0.029$).

The proportion of years a hollow was occupied was dependent on the nest's inside diameter (GLM_{Diameter inside}: $\chi_1^2 = 8.89$, $P = 0.003$). The highest occupancy rate was for nests with 40–50 cm inside diameter (69% occupancy over the period each nest was monitored), while the lowest occupancy was for nests with >50 cm diameter (26%). All other variables tested were not significant ($\chi_1^2 < 1.84$, $P > 0.175$; Table 1).

Determinants of reproductive success: (2) hatching success

A. macao hatching success did not differ significantly between natural and artificial nests (GLMM_{Nest type}: $\chi_2^2 = 1.79$, $P = 0.421$; Table 3). The likelihood of hatching one or more egg increased with the number of eggs in the clutch (GLMM_{Number of eggs}: $\chi_1^2 = 14.63$, $P < 0.001$). The mean number of eggs at nests where one or more eggs hatched was 3.04 ± 0.08 SE compared with 2.21 ± 0.14 SE at nests where no eggs hatched (ANOVA $F_{1,1136} = 32.44$, $P < 0.001$). Hatching success was higher in nests with larger internal diameters (Mean_{chicks hatched} = 38.5 cm ± 0.9 SE, Mean_{chicks did not hatch} = 34.4 cm ± 0.94 SE; GLMM_{Diameter inside}: $\chi_1^2 = 4.24$, $P = 0.048$). Hatching success was also higher in nests with a larger canopy minor axis (Mean_{chicks hatched} = 22.50 m ± 0.58 SE, Mean_{chicks did not hatch} = 19.80 m ± 1.1 SE; GLMM_{Canopy minor axis}: $\chi_1^2 = 6.5$, $P = 0.017$). Hatching success was not related to any of the other physical characteristics of the nests or nest trees (GLMM: $\chi_1^2 < 2.63$, $P > 0.150$). However, nests where eggs hatched had adults which were more likely to be present at the nest during nest inspections (Mean_{eggs hatched} = 84% birds present ± 1.3 SE; Mean_{eggs did not hatch} = 66% ± 2.9 SE; GLMM_{% of birds present}: $\chi_1^2 = 8.07$, $P = 0.005$). Hatching success was not related to any of the measures of nest monitoring intensity (GLMM: $\chi_1^2 < 2.65$, $P > 0.106$).

Determinants of reproductive success: (3) fledging

For nests that successfully fledged young, the mean number of fledged chicks was 1.44 ± 0.06 SE, with no significant difference between natural and artificial nests (LMM_{Nest type}: $\chi_2^2 = 0.51$, $P = 0.783$; Table 3). The number of fledglings was significantly positively related to the number of eggs laid (LMM: $\chi_1^2 = 14.9$, $P < 0.001$; Fig. 3). Fledging success did not vary significantly with any of the nest cavity characteristics measured (GLMM: $\chi_1^2 < 3.24$, $P > 0.078$).

Nests where chicks fledged had adults which were more likely to be present at the nest during nest inspections (Mean_{fledged} = 85% ± 1.5 SE presence, $n = 65$; Mean_{no fledge} = 70% ± 2.4 SE presence, $n = 81$; GLMM_{% of birds present}: $\chi_1^2 = 10.22$, $P = 0.002$). The probability of fledging did not vary with the number of times nests were checked during the breeding season (GLMM: $\chi_1^2 < 1.91$, $P > 0.172$).

Discussion

To date most reproductive information on wild *A. macao* has been based on only a few long-term studies in the field (Nycander et al. 1995; Vaughan et al. 2003, 2009). Our long-term data provides more insights into their reproductive biology and also allows important comparisons between natural and artificial nests, and an evaluation of the latter as a potential tool for enhancing macaw conservation.

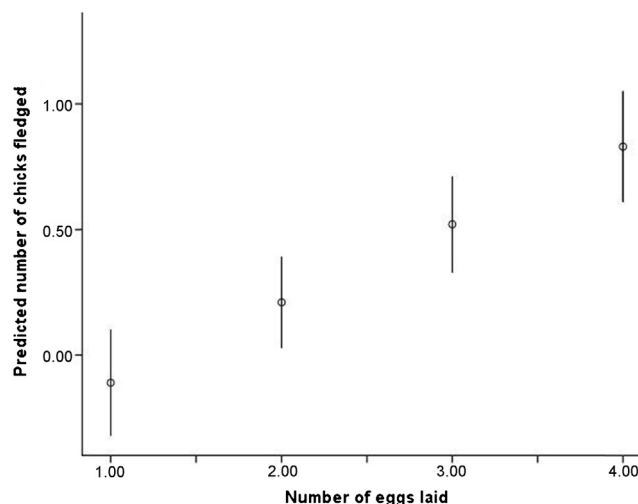


Fig. 3. Predicted number (\pm SE) of fledged chicks versus the number of eggs at laying per *Ara macao* nests in southeastern Peru. Data from 147 nesting attempts between 1999 and 2012. We used predictions of linear mixed modes (LMM) to build this graph.

Nesting preferences

A. macao are secondary cavity nesters (Renton & Brightsmith 2009) and use high and deep hollows with relatively large entrances in emergent canopy trees (*Dipteryx*, *Hymenaea*), isolated trees in broken canopy successional forest (*Erythrina*), and occasionally live or dead palms (*Iriartea*) (Brightsmith 2005b). During the 12 years of this study we monitored a total of 62 nests and not all were used every year. A major determinant of nest use was whether the nest had been successful in the previous year. A similar observation was made by Berkunsky and Reboreda (2009) for Blue-fronted Amazon (*Amazona aestiva* Linnaeus, 1758) and by White et al. (2005) for Puerto Rican Amazon (*Amazona vittata* Boddaert, 1783). We found that macaws preferred to use nests with larger internal diameters, but this was the only physical characteristic that we found that affected their preference.

Our analysis occurred over a fairly small area (<9 km²) and this may have hampered our attempts to detect significant effects of the spatial distribution of nests. In addition, the study site was quite close to the Collpa Colorado, which serves as an important sodium source for the birds at this site (Brightsmith 2004; Brightsmith et al. 2008b, 2010) and may have encouraged nest site clumping. However, the distance to the second nearest nest was significant with occupied nests having a closer second nearest neighbour. This variable may act as a proxy for local nest density, which may suggest that good nests are clustered in good habitat (e.g. near fruiting trees) or that the macaws prefer to breed close to each other at high density. Our anecdotal observations suggest that the latter may hold true and that there may be anti-predation benefits of nesting in close proximity. For example, neighbouring macaws were observed to respond in unison when predators (e.g. eagles, monkeys, tayras) or humans approached nests. Other parrot species are also known to nest in close proximity to each other when nest locations are available, thereby improving predator detection (Eberhard 2002).

Reproductive success

A. macao, like other birds, often lay more eggs than they raise, which may act as a form of insurance in case of hatching failure or other loss during incubation (Stinson 1979). The mean clutch size in this study was 2.70 (± 0.08 SE), similar to previous data for this species (Forshaw 1989; Nycander et al. 1995) and similar to other

parrots of similar body size. The average clutch size for *A. macao*, *A. chloropterus*, and *A. ararauna* (body mass 1015–1250 g) is 2.5–2.8 (Nycander et al. 1995), whereas in large cockatoos of the genera *Calyptorhynchus*, *Cacatua*, *Lophochroa*, and *Probosciger* (275–841 g) mean clutch size ranges from 1.0, e.g. *P. aterrimus* (Murphy et al. 2003), to 3.3, e.g. Pink Cockatoo *Lophochroa leadbeateri* Vigors, 1831 (Rowley & Chapman 1991).

Eggs hatched in 61% of occupied nests (Table 3), and 50% of eggs hatched successfully (hatching success). This compares to a 56% hatching success for Monk Parakeet *Myiopsitta monachus* Boddaert, 1783 (Navarro et al. 1992), 64% for Red-tailed Black-Cockatoo *Calyptorhynchus banksii* Latham, 1790 (Saunders 1984), 72% for Red-lored Amazon *Amazona autumnalis* (Enkerlin-Hoeflich 1995), 81% for Thick-billed Parrot *Rhynchopsitta pachyrhyncha* Swainson, 1827 (Enkerlin-Hoeflich et al. 1999), and 90% for Horned Parakeet *Eunymphicus cornutus* Gmelin, 1788 (Robinet & Salas 1999). Our 61% hatching rate (% of occupied nests that produced hatchlings) is very similar to the 60% rate previously described by Nycander et al. (1995) for *A. macao* in the same study site in Peru. Nearly 70% of breeding failures occurred during incubation even though this represents only one third of the total nesting period (Vigo et al. 2011).

Hatching success was higher in nests with larger inside diameter suggesting that females do better while incubating eggs if they have more space. In support of this result, PVC nests with smaller inside diameters also had a higher rate of apparently infertile or cracked eggs. Similar results were also reported from Costa Rica, where *A. macao* preferred to nest in tubes with larger diameters (Vaughan et al. 2003).

Among the occupied nests, 44% successfully fledged at least one young (Table 3), and 49% of the hatchlings fledged (fledging success). This is an intermediate result compared to other parrots, e.g. 27% of active *E. roratus* nests were successful (Heinsohn & Legge 2003), 22% for *P. aterrimus* (Murphy et al. 2003), 40% for *A. macao cyanoptera* Wiedenfeld, 1995 in Guatemala (Boyd & McNab 2008). Nycander et al. (1995) described a higher rate of successful fledging for *A. macao* at the same Tambopata site but with a much smaller sample size: 9 of 14 (64%) occupied nests fledged one or more young. Fledging success (percentage of hatchlings that fledged) was 91% for Burrowing Parrots *Cyanoliseus patagonus* Vieillot, 1818 (Masello & Quillfeldt 2002), 88% for Hyacinth Macaw *Anodorhynchus hyacinthinus* Latham, 1790 (Guedes 1995), 63% for *E. cornutus* (Robinet & Salas 1999), and 50% for Pacific Parakeet *Aratinga strenua* Ridgway, 1915 (Wermundsen 1998).

Adults are usually absent more from their nest during the nestling stage because parents need to obtain more food for their rapidly growing chicks and because the chicks can thermoregulate on their own (Iñigo-Elias 1996; Vaughan et al. 2009). Our results show that nesting success increased with the proportion of time the adults were present during nest inspections. It is unclear how this influences nesting success, but a variety of interpretations are possible. Parents that spend more time near the nest during nest inspections may be less afraid of the investigators, and by spending less time off their nests, the nest visits may not affect them. Alternatively, parents that are more efficient foragers may benefit by both bringing more food to the nest and by having more time to spend in nest attendance (Persson & Göransson 1999; Rensel et al. 2010). This suggests that social factors, parental quality, and food availability may be important features determining reproductive success for the species. Such factors may be even more important where predation risk from diurnal predators (like *Micrastur* sp. forest-falcons) threaten macaw chicks (Garcia, R., pers. com).

Our research and those of others show that brood reduction takes place in *A. macao* as in many other parrot species (Krebs 1999; Masello & Quillfeldt 2002; Nycander et al. 1995; Brightsmith & Vigo, unpublished data). Regardless of the number of chicks which

hatch, *A. macao* pairs using natural hollows never fledged more than two chicks during our study. The fact that natural pairs did not fledge more than two young begs the question of why the birds continue to lay up to four eggs. Our results show that the average number of chicks fledged is greater with clutches of three and four eggs than with only two eggs. This presumably provides the selective pressure to maintain the average clutch size above 2.0.

The limitation of tree cavities on the reproductive rate of this and other large parrot species (Beissinger & Bucher 1992; Heinsohn et al. 2003; Legge et al. 2004; Newton 1994; Nycander et al. 1995; Wiley et al. 2004) can result in intense conflict over nest sites. We confirmed nest loss by nest fights in only six cases. However, we did not systematically monitor nests for conflict during this study, and recent observations suggest we may have underestimated the impact on nesting success from this source. Preliminary analysis of nest observation data suggests that increased frequency of intruding pairs of *A. macao* at nests correlates with reduced hatching success (Brightsmith & Vigo, unpublished data).

Nest predation for *A. macao* in this study was relatively low with only six (4%) of the occupied nests suspected of being predated (7.5% of all failed nests). This was in spite of a diverse community of birds, reptiles, and mammals capable of taking both adults and young, and may reflect the ability of macaws to defend their nests due to their large body size (1015 g; Dunning 2008) and strong beaks. Other smaller parrots have higher predation rates, e.g. 45% in *E. roratus* (Heinsohn & Legge 2003) and 23% in Rose-ringed Parakeets *Psittacula krameri* Scopoli, 1769 (Shwartz et al. 2009). Known nest predators of *A. macao* are Black Spider Monkey (*Ateles paniscus* Linnaeus, 1758), Bolivian Squirrel Monkey (*Saimiri sciureus* Linnaeus, 1758), White-throated Toucan (*Ramphastos tucanus cuvieri* Linnaeus, 1758), Chestnut-eared Aracari (*Pteroglossus castanotis* Gould, 1834), rodents including *Rattus* spp., and insects like cockroaches (Nycander et al. 1995). Other potential predators are Brown Capuchin Monkey (*Cebus paella* Linnaeus, 1758), Tayra (*Eira barbara* Linnaeus, 1758), Common Opossum (*Didelphis marsupialis* Linnaeus, 1758), Crested Eagle (*Morphnus guianensis* Daudin, 1800), forest-falcons (*Micrastur* spp.), and snakes including *Oxybelis fulgidus* Daudin, 1803, *Leptodeira annulata* Linnaeus, 1758, and *Tripanurgos compressus* Daudin, 1803.

In 37% of failed nesting attempts eggs were found broken or disappeared from nests before the anticipated hatch date, and these were probably the consequences of fights for nest possession or predation. At 32% of failed nests, the eggs remained intact but failed to hatch by the hatch date. In these cases, the eggs were probably infertile, cracked during incubation, or were not incubated continuously (possibly due to nest takeover attempts in some cases). Most of these clutches occurred in PVC nests where higher internal temperatures (Brightsmith, unpublished data) and smaller internal diameters could have been important contributing factors. In 15% of failed nests we found dead chicks probably resulting from parasites, starvation, or unknown diseases (Olah et al. 2013). Further and more detailed investigations are needed to better evaluate the causes of nest failures.

The asynchronous nesting of *A. macao* makes it difficult to estimate the developmental stages of nestlings (Myers & Vaughan 2004). We therefore climbed nest trees at a high frequency to determine the exact date of hatching, and to examine nestlings to determine the timing and causes of death. We did not find any significant effect of climbing rate on reproductive success at any stage of breeding. To date few studies have explicitly tested the hypothesis that researcher activities impact on reproductive success of the study species (Grier 1969; MacCivor et al. 1990; Major 1990), although such knowledge is clearly important especially where researchers are studying the nests of species of high conservation concern.

Table 2
Characteristics of occupied natural and artificial *Ara macao* nests in the lowlands of south-eastern Peru.

Variables	Nest type	N	Minimum	Maximum	Mean (\pm SE)
Extra natural hollows per tree	Natural	12	0	2	1.08 \pm 0.19
	Artificial	17	0	1	0.12 \pm 0.08
Extra artificial nests per tree	Natural	12	0	0	0.00 \pm 0.00
	Artificial	17	0	0	0.00 \pm 0.00
Entrance hole vertical measurement (cm)	Natural	10	14	77	35.30 \pm 6.18
	Artificial	17	14	30	18.40 \pm 0.92
Entrance hole horizontal measurement (cm)	Natural	10	6	34	19.45 \pm 2.60
	Artificial	17	13	37	17.18 \pm 1.29
Inside diameter (cm)	Natural	9	17	66	38.56 \pm 5.07
	Artificial	17	32	42	36.15 \pm 0.79
Maximum depth (cm)	Natural	10	45	213	109.20 \pm 20.10
	Artificial	17	14	176	100.85 \pm 9.74
Inside height (cm)	Natural	10	0	155	69.60 \pm 17.32
	Artificial	17	0	38	23.44 \pm 2.71
Entrance hole height from the ground (m)	Natural	10	8.8	36.3	26.57 \pm 2.75
	Artificial	17	19	36.1	29.34 \pm 1.18
Angle the entrance hole faces	Natural	10	40	358	194.10 \pm 32.09
	Artificial	17	20	340	183.18 \pm 29.40
Vertical angle the entrance hole faces	Natural	11	-11	90	22.18 \pm 11.50
	Artificial	17	0	0	0.00 \pm 0.00
Distance to the clay lick (m)	Natural	12	450	2039	1180.50 \pm 103.43
	Artificial	17	536	1927	1083.94 \pm 105.40
Tree height (m)	Natural	12	28.6	58.7	44.94 \pm 2.67
	Artificial	17	21.7	61.9	43.57 \pm 2.75
Tree circumference (m)	Natural	12	2.8	5	3.72 \pm 0.21
	Artificial	17	2	5.3	3.28 \pm 0.20
Lowest leaf height from the ground (m)	Natural	12	19.6	35.6	27.51 \pm 1.56
	Artificial	17	21.2	31.2	27.13 \pm 0.75
Canopy major axis (m)	Natural	12	11.2	40.3	26.24 \pm 2.73
	Artificial	17	15	44.9	25.28 \pm 2.00
Canopy minor axis (cm)	Natural	12	2.3	32.4	18.75 \pm 2.03
	Artificial	17	12	29.1	20.98 \pm 1.58

Nest boxes versus natural cavities

There were no significant differences in success rates between artificial nest boxes and natural nest hollows at any stage of reproduction. In addition we did not observe differences between wooden boxes and PVC tube nests. Other studies of birds have found that natural nests had higher success than artificial nests [e.g. Barrow's Goldeneyes *Bucephala islandica* Gmelin, 1789 (Evans et al. 2002), Eastern Yellow Robins *Eopsaltria australis* Shaw, 1790

(Zanette 2002), or Bufflehead *Bucephala albeola* Linnaeus, 1758 (Evans et al. 2002)]. Our results have important implications for conservation of macaws (Nycander et al. 1995; Vaughan et al. 2003; White et al. 2006), and follow other studies demonstrating the high value of artificial nests (Vaughan et al. 2003; Lambrechts et al. 2012; Libois et al. 2012). Our current designs with small modifications as outlined below could be useful for *A. macao* in other geographic locations where the status of the local population is of concern (e.g. in Costa Rica Vaughan et al. 2003), or with modifications for other

Table 3
Nest occupancy and breeding success of *Ara macao* in the lowlands of south-eastern Peru.

	Artificial wooden nests	Artificial PVC nests	Natural nests	Combined data for all nests
Number of occupied nests (number of available nests) ^a	22 (37)	70 (123)	55 (NA)	147
Clutch size (N) ^b	2.73 \pm 0.21 (22)	2.8 \pm 0.11 (69)	2.55 \pm 0.13 (47)	2.7 \pm 0.08 (138)
% of occupied nests that hatch ^c	73	51	67	61
% of eggs that hatched ^d	60	42	58	50
Number of chicks which hatch per successful clutch (N) ^e	2.25 \pm 0.23 (16)	2.28 \pm 0.16 (36)	1.97 \pm 0.12 (36)	2.15 \pm 0.09 (88)
% of occupied nests that fledged ^f	50	43	44	44
% of hatchlings that fledged ^g	39	52	51	49
Number of chicks which fledged per successful nest (N) ^h	1.27 \pm 0.14 (11)	1.43 \pm 0.09 (30)	1.52 \pm 0.12 (23)	1.44 \pm 0.06 (64)

^a Number of occupied nest years over the study period (number of total nest year where available).

^b Average number (\pm SE) of eggs laid in occupied nests.

^c Percentage of occupied nests in which hatched one or more eggs.

^d Percentage of laid eggs that hatched (hatching success).

^e Average number (\pm SE) of hatchlings for each nest which hatched one or more eggs.

^f Percentage of occupied nests that fledged one or more chicks.

^g Percentage of hatchlings that fledged (fledging success).

^h Average number (\pm SE) of fledglings for each nest which fledged at least one chick.

macaw species. However, the occupancy of these artificial nests may be highly variable among different study sites even for the same species. Our project has also hung similar artificial nests in a tourist lodge and a local community within 60 km of TRC and none of these nests were occupied over the two nesting seasons they were monitored, probably due to a lower ratio of macaws to natural nest sites (Brightsmith, unpublished data). Further studies are needed to determine the variation of acceptance of these artificial nests.

PVC nests may be preferred by researchers as they are more durable and require less maintenance than wooden nest boxes that quickly rot in humid tropical environments. In addition, the destruction of wooden nests is hastened by the incubating female macaws which chew on the inside of the box. PVC nests are not only durable for macaws but also immune to attacks by woodpeckers, termites, bees and fungi, and are relatively light, easy to make, transport, and erect (Nycander et al. 1995). Considering the preferences of *A. macao* at our site, we suggest that the diameter of artificial nests should be larger than 40 cm in future applications. However, the artificial nests in this study had smaller entrance sizes than natural nest cavities (Table 2), and this design feature should be maintained as it may help to deter predators as found in other studies (White et al. 2005; Zanette 2002).

Artificial nests can also enhance scientific research. The low side doors on the artificial nests provide easy access to eggs and chicks for the researchers facilitating morphological studies (Vigo et al. 2011). This is in contrast to natural nests where it can be difficult to reach to the bottom and extract the chicks. Furthermore, artificial nests also facilitate the installation of electronic monitoring devices like microphones, sensors, and cameras (Grenier & Beissinger 1999; White & Vilella 2004).

In both a previous study (Nycander et al. 1995) and this one, many *A. macao* appeared to become accustomed to researchers climbing to check the nests. The presence of artificial nests where macaws and other species are predictable and habituated to human presence can increase the value of each bird to ecotourism (Brightsmith & Bravo 2006; Munn 1992; Nycander et al. 1995). So in areas where macaws are protected, the use of artificial nests and other methods to attract nesting macaws can be important for ecotourism operations (Vaughan et al. 2005).

Conclusion

Even with 12 years of data we were unable to isolate the attributes of *A. macao* nest trees and holes that are best for reproductive success. There are probably many factors that the birds consider each time they choose a nest cavity. Renton and Brightsmith (2009) suggest that *A. macao* might be less able to successfully compete for high-quality nests with the sympatric *A. chloropterus* leading to greater flexibility in their choice of nest sites. Our sample of known nests is useful for describing their broad choice of nest site but clearly does not provide enough variation to isolate the factors that most affect breeding success. However, our data showed a high rate of reoccupation of successful nests in the consecutive years and anecdotal observations suggest that many of these consecutive reoccupations were by the same pairs of birds (Boyd & Brightsmith 2010; Brightsmith 2009). Others found that *Amazona* parrots re-used successful nests in consecutive breeding seasons (Berkunsky & Rebores 2009; Enkerlin-Hoeflich 1995).

We showed that artificial and natural nests had similar reproductive parameters, suggesting that artificial nests can also contribute important data to natural history studies of species where access to natural nests is limited. This finding also supports the use of artificial nests for conservation management especially in regions where the large emergent canopy trees with the best

nest hollows have been removed (e.g. due to logging) but habitat has otherwise been maintained (Munn 1992).

Acknowledgments

We thank Rainforest Expeditions and the staff of TRC for the logistical support at the research centre and all the volunteer field assistants for their enormous help in data collection. We thank our field leaders during the study period: Adrian Sanchez; Adriana Bravo; Aida Figari; Carlos Huamani; Carolina Caillaux; Caterina Cosmópolis; Fernando Takano; Gustavo Martinez; Jerico Solis; Jesus Zumaran; Marc Dragiewicz; Nancy Carlos; Oscar Gonzalez; and, Robert Wilkerson. We also thank Linda Alpern for making the nest box drawings in this article. This research was supported by Duke University, Earthwatch Institute, Schubot Exotic Bird Health Center at Texas A&M University, Raleigh Durham Caged Bird Society, Rufford Small Grant Foundation, Idea Wild, and The Australian National University. INRENA and the Servicio Nacional de Áreas Naturales Protegidas (SERNANP) in Peru granted research permits for the studies.

References

- Amuno, J. B., Massa, R., & Dranzoa, C. (2007). Abundance, movements and habitat use by African Grey Parrots (*Psittacus erithacus*) in Budongo and Mabira forest reserves, Uganda. *Ostrich*, 78, 225–231.
- Beissinger, S. R., & Bucher, E. H. (1992). Sustainable harvesting of parrots for conservation. In S. R. Beissinger, & N. F. R. Snyder (Eds.), *New world parrots in crisis* (pp. 73–115). Washington, DC: Smithsonian Institution Press.
- Bennett, P. M., & Owens, I. P. F. (1997). Variation in extinction risk among birds: Chance or evolutionary predisposition? *Proceedings of the Royal Society, London B: Biological Sciences*, 264, 401–408.
- Berkunsky, I., & Rebores, J. C. (2009). Nest-site fidelity and cavity reoccupation by blue-fronted parrots *Amazona aestiva* in the dry Chaco of Argentina. *Ibis*, 151, 145–150.
- Boyd, J., & Brightsmith, D. (2010). *Large macaw satellite telemetry: 2010*. College Station, TX, USA: Schubot Exotic Avian Health Center, Texas A&M University.
- Boyd, J. D., & McNab, R. B. (2008). The Scarlet Macaw in Guatemala and El Salvador: 2008 status and future possibilities. In *Findings and recommendations from a species recovery workshop 9–15 March 2008* Guatemala City and Flores, Petén, Guatemala. Wildlife Conservation Society.
- Boyes, R. S., & Perrin, M. R. (2009). The feeding ecology of the Meyer's Parrot *Poi-cephalus meyeri* in the Okavango Delta, Botswana. *Ostrich*, 80, 153–164.
- Briceno-Linares, J. M., Rodríguez, J. P., Rodríguez-Clark, K. M., Rojas-Suárez, F., Millán, P. A., Vittori, E. G., et al. (2011). Adapting to changing poaching intensity of yellow-shouldered parrot (*Amazona barbadensis*) nestlings in Margarita Island, Venezuela. *Biological Conservation*, 144, 1188–1193.
- Brightsmith, D. J. (2004). Effects of weather on parrot geophagy in Tambopata, Peru. *Wilson Bulletin*, 116, 134–145.
- 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). Parrot nesting in southeastern Peru: Seasonal patterns and keystone trees. *Wilson Bulletin*, 117, 296–305.
- Brightsmith, D. J. (2009). *Satellite telemetry of large macaws in Tambopata, Peru*. College Station, TX, USA: Unpublished Report to the Wildlife Protection Foundation, Schubot Exotic Avian Health Center, Texas A&M University.
- Brightsmith, D. J., & Bravo, A. (2006). Ecology and management of nesting blue-and-yellow macaws (*Ara ararauna*) in Mauritia palm swamps. *Biodiversity and Conservation*, 15, 4271–4287.
- Brightsmith, D. J., Hilburn, J., del Campo, A., Boyd, J., Frisius, M., Frisius, R., et al. (2005). The use of hand-raised psittacines for reintroduction: A case study of scarlet macaws (*Ara macao*) in Peru and Costa Rica. *Biological Conservation*, 121, 465–472.
- Brightsmith, D. J., Matsufuji, D., McDonald, D., & Bailey, C. A. (2010). Nutritional content of free-living Scarlet Macaw chick diets in southeastern Peru. *Journal of Avian Medicine and Surgery*, 24, 9–23.
- Brightsmith, D. J., Stronza, A., & Holle, K. (2008). Ecotourism, conservation biology and volunteer tourism: A mutually beneficial triumvirate. *Biological Conservation*, 141, 2832–2842.
- Brightsmith, D. J., Taylor, J., & Phillips, T. D. (2008). The roles of soil characteristics and toxin adsorption in avian geophagy. *Biotropica*, 40, 766–774.
- Brightsmith, D. J., & Villalobos, E. M. (2011). Parrot behavior at a Peruvian clay lick. *Wilson Journal of Ornithology*, 123, 595–602.
- Britt, C. R. (2011). *Nest survival and nest-site selection of Scarlet Macaws (Ara macao cyanoptera) in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize*. Las Cruces, New Mexico, USA: New Mexico State University.
- Clements, J. F., Schulenberg, T. S., Iliff, M. J., Sullivan, B. L., Wood, C. L., & Roberson, D. (2013). *The eBird/Clements checklist of birds of the world: Version 6.8*.

- Downloaded from <http://www.birds.cornell.edu/clementschecklist/download/> (accessed 1.10.13)
- Collar, N. J. (1997). Family *psittacidae* (parrots). In J. del Hoyo, A. Elliott, & J. Sargatal (Eds.), *Handbook of the birds of the world* (vol. 4) (pp. 280–477). Barcelona: Linx Edicions.
- Downs, C. T. (2005). Abundance of the endangered Cape parrot *Poicephalus robustus* in South Africa: Implications for its survival. *African Zoology*, 40, 15–24.
- Dunning, J. B. (2008). *CRC handbook of avian body masses*. Boca Raton, Florida: CRC Press, Taylor & Francis Group.
- Eberhard, J. R. (2002). Cavity adoption and the evolution of coloniality in cavity nesting birds. *Condor*, 104, 240–247.
- Ekstrom, J. M. M., Burke, T., Randrianaina, L., & Birkhead, T. R. (2007). Unusual sex roles in a highly promiscuous parrot: The Greater Vasa Parrot *Caracopsis vasa*. *Ibis*, 149, 313–320.
- Enkerlin-Hoeflich, E. C. (1995). *Comparative ecology and reproductive biology of three species of Amazona parrots in northeastern Mexico*. College Station, TX, USA: Texas A&M University.
- Enkerlin-Hoeflich, E. C., Macias Caballero, C., Monterrubio Rico, T., Cruz Nieto, M. A., Snyder, N. F. R., Venegas Holguin, D., et al. (1999). *Status, distribución, ecología y conservación de las cotorras serranas (Rhynchopsitta terrisi y Rhynchopsitta pachyrhyncha) en el norte de México: 4a parte*. México: Comisión Nacional para el uso y conocimiento de la biodiversidad – CONABIO.
- Evans, M. R., Lank, D. B., Boyd, W. S., & Cooke, F. (2002). A comparison of the characteristics and fate of Barrow's Goldeneye and Bufflehead nests in nest boxes and natural cavities. *Condor*, 104, 610–619.
- Forshaw, J. M. (1989). *Parrots of the world Melbourne*. Melbourne, Australia: Landdowne Editions.
- Grenier, J. L., & Beissinger, S. R. (1999). Variation in the onset of incubation in a neotropical parrot. *Condor*, 101, 752–761.
- Grier, J. W. (1969). Bald eagle behavior and productivity responses to climbing to nests. *Journal of Wildlife Management*, 33, 961–966.
- Guedes, N. M. R. (1995). Algunos aspectos sobre o comportamento reprodutivo da arara-azul *Anodorhynchus hyacinthinus* e a necessidade de manejo para a conservação da espécie. *Anais de Ecologia*, 13.
- Heinsohn, R. (2008a). The ecological basis of unusual sex roles in reverse-dichromatic eclectus parrots. *Animal Behaviour*, 76, 97–103.
- Heinsohn, R. (2008b). Ecology and evolution of the enigmatic eclectus parrot (*Eclectus roratus*). *Journal of Avian Medicine and Surgery*, 22, 146–150.
- Heinsohn, R., & Legge, S. (2003). Breeding biology of the reverse-dichromatic, cooperative parrot *Eclectus roratus*. *Journal of Zoology (London)*, 259, 197–208.
- Heinsohn, R., Legge, S., & Endler, J. A. (2005). Extreme reversed sexual dichromatism in a bird without sex role reversal. *Science*, 309, 617–619.
- Heinsohn, R., Murphy, S., & Legge, S. (2003). Overlap and competition for nest holes among eclectus parrots, palm cockatoos and sulphur-crested cockatoos. *Australian Journal of Zoology*, 51, 81–94.
- Hesse, A. J., & Duffield, G. E. (2000). The status and conservation of the Blue-Throated Macaw *Ara glaucogularis*. *Bird Conservation International*, 10, 255–275.
- Iñigo-Elias, E. E. (1996). *Ecology and breeding biology of the Scarlet Macaw (Ara macao) in the Usumacinta drainage basin of Mexico and Guatemala*. Gainesville, Florida, USA: University of Florida.
- (2012). *International plant names index – IPNI*. Published online: <http://www.ipni.org> (accessed 1.10.13).
- International Union for Conservation of Nature – IUCN. (2013). *The IUCN red list of threatened species*. UK: IUCN.
- Krebs, E. A. (1999). Last but not least: Nestling growth and survival in asynchronously hatching crimson rosellas. *Journal of Animal Ecology*, 68, 266–281.
- Lambrechts, M., Wiebe, K., Sunde, P., Solonen, T., Sergio, F., Roulin, A., et al. (2012). Nest box design for the study of diurnal raptors and owls is still an overlooked point in ecological, evolutionary and conservation studies: A review. *Journal of Ornithology*, 153, 23–34.
- Laurance, W. F., Albernaz, A. K. M., & Schroth, G. (2002). Predictors of deforestation in the Brazilian Amazon. *Journal of Biogeography*, 29, 737–748.
- Laurance, W. F., Goosem, M., & Laurance, S. G. W. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution*, 24, 659–669.
- Legge, S., Heinsohn, R., & Garnett, S. (2004). Availability of nest hollows and breeding population size of eclectus parrots *Eclectus roratus* on Cape York Peninsula, Australia. *Wildlife Research*, 31, 149–161.
- Libois, E., Gimenez, O., Oro, D., Mínguez, E., Pradel, R., & Sanz-Aguilar, A. (2012). Nest boxes: A successful management tool for the conservation of an endangered seabird. *Biological Conservation*, 155, 39–43.
- MaCivior, L. H., Melvin, S. M., & Griffin, C. R. (1990). Effects of research activity on piping plover nest predation. *Journal of Wildlife Management*, 54, 443–447.
- Major, R. E. (1990). The effect of human observers on the intensity of nest predation. *Ibis*, 132, 608–612.
- Major, R. E., & Kendal, C. E. (1996). The contribution of artificial nest experiments to understanding avian reproductive success: A review of methods and conclusions. *Ibis*, 138, 298–307.
- Martin, T. E., & Geupel, G. R. (1993). Nest-monitoring plots: Methods for locating nests and monitoring success (métodos para localizar nidos y monitorear el éxito de estos). *Journal of Field Ornithology*, 64, 507–519.
- Masello, J. F., & Quillfeldt, P. (2002). Chick growth and breeding success of the burrowing parrot. *Condor*, 104, 574–586.
- Monterrubio-Rico, T. C., & Escalante-Pliego, P. (2006). Richness distribution and conservation status of cavity-nesting birds in Mexico. *Biological Conservation*, 128, 67–78.
- Munn, C. A. (1992). Macaw biology and ecotourism, or when a bird in the bush is worth two in the hand. In S. R. Beissinger, & N. F. R. Snyder (Eds.), *New world parrots in crisis: Solutions from conservation biology* (pp. 47–72). Washington and London: Smithsonian Institution Press.
- Murphy, S., Double, M., & Legge, S. (2007). The phylogeography of palm cockatoos, *Probosciger aterrimus* in the dynamic Australo-Papuan region. *Journal of Biogeography*, 34, 1534–1545.
- Murphy, S., Legge, S., & Heinsohn, R. (2003). The breeding biology of palm cockatoos (*Probosciger aterrimus*): A case of a slow life history. *Journal of Zoology (London)*, 261, 327–339.
- Myers, M. C., & Vaughan, C. (2004). Movement and behavior of scarlet macaws (*Ara macao*) during the post-fledging dependence period: Implications for in situ versus ex situ management. *Biological Conservation*, 118, 411–420.
- Navarro, J. L., Martella, M. B., & Bucher, E. H. (1992). Breeding season and productivity of monk parakeets in Cordoba, Argentina. *Wilson Bulletin*, 104, 413–424.
- Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation*, 70, 265–276.
- Nycander, E., Blanco, D. H., Holle, K. M., Campo, A. D., Munn, C. A., Moscoso, J. I., et al. (1995). Manu and Tambopata: Nesting success and techniques for increasing reproduction in wild macaws in southeastern Peru. In B. L. S. J. Abramson, & J. B. Thomsen (Eds.), *The large macaws: Their care, breeding and conservation* (pp. 423–443). Fort Bragg: Raintree Publications.
- Olah, G., Vigo, G., Ortiz, L., Rozsa, L., & Brightsmith, D. J. (2013). *Philornis* sp. bot fly larvae in free living scarlet macaw nestlings and a new technique for their extraction. *Veterinary parasitology*, 196(1–2), 246–249.
- Paredes, R., & Zavalaga, C. B. (2001). Nesting sites and nest types as important factors for the conservation of Humboldt penguins (*Spheniscus humboldti*). *Biological Conservation*, 100(2), 199–205.
- Payne, R. W., Murray, D. A., Harding, S. A., Baird, D. B., & Soutar, D. M. (2009). *GenStat for windows: Introduction* ((12th ed.)). Hemel, Hempstead: VSN International.
- Perry, D. R. (1978). A method of access into the crowns of emergent and canopy trees. *Biotropica*, 10, 155–157.
- Perry, D. R., & Williams, J. (1981). The tropical rain forest canopy: A method providing total access. *Biotropica*, 13, 283–285.
- Persson, I., & Göransson, G. (1999). Nest attendance during egg laying in pheasants. *Animal Behaviour*, 58(1), 159–164.
- Powell, L. L., Powell, T. U., Powell, G., & Brightsmith, D. (2009). Parrots take it with a grain of salt: Available sodium content may drive collpa (clay lick) selection in Southeastern Peru. *Biotropica*, 41, 279–282.
- Rensel, M. A., Wilcoxon, T. E., & Schoech, S. J. (2010). The influence of nest attendance and provisioning on nestling stress physiology in the Florida scrub-jay. *Hormones and Behavior*, 57(2), 162–168.
- Renton, K. (2000). Scarlet macaw. In R. P. Reading, & B. Miller (Eds.), *Endangered animals: A reference guide to conflicting issues* (pp. 253–257). Westport: Greenwood Press.
- Renton, K., & Brightsmith, D. (2009). Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru. *Journal of Field Ornithology*, 80, 1–8.
- Roberge, J.-M., & Angelstam, P. E. R. (2004). Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology*, 18, 76–85.
- Robinet, O., & Salas, M. (1999). Reproductive biology of the endangered Ouvea parakeet *Eunymphicus cornutus uvaensis*. *Ibis*, 141, 660–669.
- Rowley, I., & Chapman, G. (1991). The breeding biology, food, social organisation, demography and conservation of the Major Mitchell or Pink Cockatoo *Cacatua leadbeateri* on the margin of the Western Australia wheat-belt. *Australian Journal of Zoology*, 39, 211–261.
- Saunders, D. A. (1984). Egg shape within the Australian Psittaciformes with comments on eggs of *Nymphicus hollandicus*. *Emu*, 84, 36–37.
- Shwartz, A., Strubbe, D., Butler, C. J., Matthyssen, E., & Kark, S. (2009). The effect of enemy-release and climate conditions on invasive birds: A regional test using the rose-ringed parakeet (*Psittacula krameri*) as a case study. *Diversity and Distributions*, 15, 310–318.
- Stinson, C. H. (1979). On the selective advantage of fratricide in birds. *Evolution*, 33, 1219–1225.
- Stojanovic, D., Webb, M., Roshier, D., Saunders, D., & Heinsohn, R. (2012). Ground-based survey methods both overestimate and underestimate the abundance of suitable tree-cavities for the endangered Swift Parrot. *Emu*, 112, 350–356.
- Stoleson, S. H., & Beissinger, S. R. (1997). Hatching asynchrony, brood reduction, and food limitation in a neotropical parrot. *Ecological Monographs*, 67, 131–154.
- Theuerkauf, J., Rouys, S., Mériot, J. M., Gula, R., & Kuehn, R. (2009). Cooperative breeding, mate guarding and nest sharing in two parrot species of New Caledonia. *Journal of Ornithology*, 150, 791–797.
- Tosi, J. A. (1960). *Zonas de vida natural en el Perú. Memoria explicativa sobre el mapa ecológico del Perú*. Lima, Peru: Instituto Interamericano de las Ciencias Agrícolas de la Organización de los Estados Americanos.
- Vaughan, C., Bremer, M., & Dear, F. (2009). Scarlet Macaw (*Ara macao*) (Psittaciformes: Psittacidae) Parental Nest Visitation in Costa Rica: Implications for Research and Conservation. *Revista de Biología Tropical*, 57, 395–400.
- Vaughan, C., Nemeth, N. M., Cary, J., & Temple, S. (2005). Response of a Scarlet Macaw *Ara macao* population to conservation practices in Costa Rica. *Bird Conservation International*, 15, 119–130.
- Vaughan, C., Nemeth, N., & Marineros, L. (2003). Ecology and management of natural and artificial Scarlet Macaw (*Ara macao*) nest cavities in Costa Rica. *Ornitología Neotropical*, 14, 381–396.
- Vigo, G., Williams, M., & Brightsmith, D. J. (2011). Growth of Scarlet Macaw (*Ara macao*) chicks in southeastern Peru. *Ornitología Neotropical*, 22, 143–153.

- Villard, M. A., & Pärt, T. (2004). Don't put all your eggs in real nests: A sequel to Faaborg. *Conservation Biology*, 18, 371–372.
- Wermundsen, T. (1998). Colony breeding of the Pacific Parakeet *Aratinga strenua* Ridgway 1915 in the Volcán Masaya National Park, Nicaragua. *Tropical Zoology*, 11, 241–248.
- White, T. H., Abreu-Gonzalez, W., Toledo-Gonzalez, M., & Torres-Baez, P. (2005). Artificial nest cavities for *Amazona* parrots. *Wildlife Society Bulletin*, 33, 756–760.
- White, T. H., Brown, G. G., & Collazo, J. A. (2006). Artificial cavities and nest site selection by Puerto Rican Parrots: A multiscale assessment. *Avian Conservation and Ecology*, 1, 5.
- White, T. H., Collar, N. J., Moorhouse, R. J., Sanz, V., Stolen, E. D., & Brightsmith, D. J. (2012). Psittacine reintroductions: Common denominators of success. *Biological Conservation*, 148, 106–115.
- White, T. H., & Vilella, F. J. (2004). Nest management for the Puerto Rican Parrot (*Amazona vittata*): Gaining the technological edge. *Ornitología Neotropical*, 15, 467–476.
- Wiley, J. W., Gnam, R. S., Koenig, S. E., Dornelly, A., Glvez, X., Bradley, P. E., et al. (2004). Status and conservation of the Family Psittacidae in the West Indies. *Journal of Caribbean Ornithology*, 17, 94–154.
- Zanette, L. (2002). What do artificial nests tells us about nest predation? *Biological Conservation*, 103, 323–329.