Tree-cavity availability and selection by a large-bodied secondary cavity-nester: the Military Macaw

Sylvia Margarita de la Parra-Martínez, Katherine Renton, Alejandro Salinas-Melgoza & Luis Guillermo Muñoz-Lacy

Journal of Ornithology

ISSN 2193-7192
Volume 156
Number 2

J Ornithol (2015) 156:489-498
DOI 10.1007/s10336-014-1150-9

Springer

Tree-cavity availability and selection by a large-bodied secondary cavity-nester: the Military Macaw

SYLVIA MARGARITA DE LA PARRA-MARTÍNEZ[1], KATHERINE RENTON[2,*], ALEJANDRO SALINAS-MELGOZA[1,3], AND LUIS GUILLERMO MUÑOZ-LACY[1]

[1]Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, México D.F.

[2]Estación de Biología Chamela, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 21, San Patricio-Melaque, Jalisco, México.

[3]Current address: Centro Tlaxcala de Biología de la Conducta, Universidad Autónoma de Tlaxcala-CONACyT, Km. 1.5. Carr. Fed. Tlaxcala-Puebla, Tlaxcala de Xicohténcatl, Tlaxcala, México.

*Corresponding author: krenton@ib.unam.mx

Telephone & Fax: 52-315-3510202

Summary

Large-bodied secondary cavity-nesters are constrained to use cavities of sufficient size to permit access, while also selecting characteristics to reduce predation. However, no information exists on nest-site availability for large-bodied secondary cavity-nesters in tropical forests. We located 12 tree-cavity nests of the threatened Military Macaw (*Ara militaris*) in tropical dry semi-deciduous forest in Jalisco, Mexico. For each nest we determined cavity characteristics, and compared the structure of nest-trees with nearest-neighbor trees. We also established four 100x50 m transects in each of deciduous, semi-deciduous, and oak forest to determine tree-cavity availability over 6 ha. Military Macaw nest-sites occurred most frequently in cavities of live *Enterolobium cyclocarpum* trees. Nest-trees had significantly larger diameter and ramification height than the four nearest-neighbor trees, indicating that macaws selected tall emergent trees as nest-sites. Cavities used as nest-sites by Military Macaws were also in significantly larger trees, at a greater height, and had larger entrance diameter and depth than all accessible cavities. Height above the ground was the main criteria predicting nest-cavity selection, possibly as this may reduce predation risk. There was also a negative correlation of nest-cavity height with depth suggesting a trade-off where Military Macaws may select a nest-cavity high above the ground regardless of depth, but when using lower cavities these tend to be deeper. We found a low density of cavities with characteristics suitable for nesting, and these were concentrated in semi-deciduous forest. Our results demonstrate that the Military Macaw exhibits species-specific selection of nest-cavities, with a low density of cavities suitable for large-bodied secondary cavity-nesters in tropical forests.

Key words: *Ara militaris*; cavity characteristics; Mexico, Psittacidae; tree-cavity availability, tropical dry forest

Introduction

Breeding habitat and nest-site selection are important determinants of the population dynamics of birds (Citta and Lindberg 2004). Finding adequate nest-sites may be a limiting factor for secondary cavity nesters as they rely on pre-existing cavities, and hence the availability of suitable nest-sites may be a constraint on the number of breeding pairs (Newton 1994). Secondary cavity nesting birds may select nest-sites based on cavity characteristics such as height from the ground, entrance width, and depth (Li and Martin 1991; Cockle et al. 2008), which may serve to limit the access of predators or competitors to the nest (Newton 1994). Hence, the selection of cavities with specific characteristics could limit the availability of adequate nest-sites for secondary-cavity nesters (Cockle et al. 2008, 2011).

The family Psittacidae has the greatest number and proportion of species that are obligate cavity nesters (Monterrubio-Rico and Escalante-Pliego 2006), and includes more threatened species than any other bird family (Bennett and Owens 1997). Psittacines frequently use nest-sites with specific characteristics of tree species and size, cavity height, entrance width, and cavity depth (Renton and Salinas-Melgoza 1999; Heinsohn et al. 2003; Monterrubio-Rico and Enkerlin-Hoeflich 2004; Selman et al. 2004; Walker et al. 2005). Three species of Amazon parrot in Mexico were found to select nest cavities with narrow entrance widths and at a greater height above the ground that could reduce the risk of predation (Enkerlin-Hoeflich 1995). However, very few studies have determined whether psittacines select cavities with specific characteristics for nesting, and most studies of nest-cavity use have been conducted on small or medium-sized psittacines, while little is known of the nest-cavity requirements of large psittacines.

Body size may impose stronger constraints in large-bodied secondary-cavity nesters, where the need for a cavity of sufficient size to accommodate the nest contents may reduce the availability of suitable sized cavities. Cockatoos in Australia demonstrated species-specific requirements for entrance dimensions and internal diameter of cavities used for nesting, with larger species using cavities of greater dimensions (Saunders et al. 1982). In the case of large macaws, there is limited information available, with only a few studies providing information on the use of specific nesting substrates of tree or palm species (Renton and Brightsmith 2009), and nest-cavity characteristics (Pinho and Nogueira 2003; Vaughan et al. 2003; Berkunsky et al. 2014; Olah et al. 2014). However, no studies have evaluated nest-site availability for large macaws, or whether macaws may select nest-sites based on cavity characteristics.

The Military Macaw (*Ara militaris*) is the most northerly distributed macaw species in the Americas, ranging from northern Mexico to Argentina (Forshaw 1989). In Mexico, the Military Macaw is considered endangered (SEMARNAT 2010), and presents a fragmented distribution along the Pacific slope from Sonora to Guerrero, and on the Atlantic slope from Nuevo Leon to San Luis Potosi. The species has mainly been reported nesting in cavities in cliffs (Forshaw 1989). However, along the coast of Jalisco the Military Macaw nests in cavities in large trees (Carreón-Arroyo 1997). As one of the larger macaw species at 75 cm length and 900-1100 g weight (Forshaw 1989), the Military Macaw would require large cavities in trees of sufficient girth. Hence, there may be a limited availability of cavities of sufficient size for Military Macaw nesting and reproduction, but no information exists on the availability of adequate nest-sites for large-bodied, threatened psittacines in tropical forests.

In the present study, we determined tree-cavity nesting requirements of the Military Macaw, and evaluated whether the Military Macaw selects nest-sites based on cavity characteristics. As found for other secondary cavity nesting birds, we expected that macaws would select nest-cavities based on height from the ground and entrance diameter. Furthermore, given the large size of Military Macaws we hypothesize that there would be a low density of cavities of suitable size for nesting by large-bodied psittacines. Finally, we also aimed to provide information on habitat variation in tree-cavity availability for birds, enabling comparisons with other studies in tropical and temperate forests.

METHODS

Study area

The study was conducted in the forests on the south-east side of the 10 x 2 km Cajón de Peñas dam (19° 58´to 20° 03´ N and 105° 01´ to 105° 05´ W) in Jalisco, Mexico. Annual rainfall at Cajón de Peñas is 1,433 mm, with mean annual temperature of 28°C (García-Oliva et al. 1991, Ortega-Reyes 2004). We searched for Military Macaw nests in an area of 58 km^2 along the south-eastern edge of the dam, at 200-500 m asl. Vegetation in this study area was mainly semi-deciduous forest on the low-lying slopes around the dam, with deciduous forest on the ridges, and reaching oak forest at the far eastern edge of the dam. Tropical semi-deciduous forest was characterized by trees of 15-30 m canopy height, where most trees retain leaf-cover during the dry season (Rzedowski 2006), with dominant tree species of *Brosimum alicastrum*, *Bursera* *simaruba, Enterolobium cyclocarpum*, *Hura polyandra* and *Tabebuia* spp. (Ortega-Reyes 2004). Deciduous forest on ridge-tops has a canopy height of 8-12 m, where the majority of trees drop their leaves for 5-8 months in the dry season, and was characterized by tree species of *Caesalpinia* spp, *Ceiba aesculifolia*, *Bursera instabilis*, *Jatropha* spp, *Lonchocarpus* spp., and *Lysiloma microphyllum* (Rzedowski 2006). Oak forest at the eastern edge of the dam was dominated by *Quercus glauscens* (Ortega 2004). The western, down-stream area of the dam has been extensively cleared for agriculture, whereas in the relatively conserved forest along the southern and eastern edges of the dam the main human activity was that of free-range cattle-grazing within the forest.

Nest-site characteristics

We located 12 Military Macaw nests in the January to April 2013 breeding season. Nest trees were identified by direct observation of nesting pairs, and information on nest locations supplied by local residents, some of whom were former nest poachers. We confirmed use of the cavity as a nest-site by Military Macaws using a wireless tree-peeper camera (www.ibwo.org) affixed to the top of a 15 m extendable tree-measuring pole. Where a nest had failed or been poached we confirmed the presence of Military Macaw feathers and egg-shells in the base. For each nest located, we determined characteristics of the nest tree, considering tree species, total height, tree diameter at breast height (dbh), and condition (live or dead). We also measured characteristics of the cavity used for nesting: 1) height of entrance from the ground; 2) entrance width; 3) support diameter; and 4) cavity depth (Saunders 1979; Saunders et al. 1982).

Nest area vegetation structure

We characterized nesting habitat of the Military Macaw by sampling vegetation structure around the nest tree (Cameron 2006). We estimated the percent canopy cover around the nest, and measured the four nearest trees with dbh >10 cm, at each of the cardinal compass points around the nest tree (N, S, E, W). We determined tree species, dbh, total height, and height to first ramification, as well as distance from the nest tree for each of the four nearest-neighbor trees. Trees that ramify at more than half their total height may be considered primary or conserved forest trees, whereas those that ramify below the midway section of the trunk may be indicative of disturbed forests (Marsden and Fielding 1999).

Cavity availability

To determine the availability of cavities as potential nest sites for the Military Macaw, we established four transects of 100 x 50 m (Gibbs et al. 1993) in each of the main vegetation types of tropical deciduous, semi-deciduous, and oak forest. This represented a sampling area of 2 ha per vegetation type and a total of 6 ha for the study area. We distributed survey transects at random in each of the three forest types within the study area, so as to evaluate habitat variation in cavity availability for the avian community of secondary cavity-nesters. In this way, we aimed to avoid potential bias of locating survey transects around macaw nests, as parrots may select nesting areas with a high abundance of cavities (Carniero et al. 2009), that they can use as nest-sites in any given year (Salinas-Melgoza et al. 2009).

In each transect, we checked all trees with binoculars (10x40) to determine the presence of cavities. On locating a cavity we recorded the tree species, dbh, height of the cavity from the ground, entrance width, and cavity depth. We used a 15 m extendable tree-measuring pole to measure cavity height, with a graded measuring tube affixed horizontally to the top of the pole to measure entrance width. We measured cavity depth using a lead weight attached to a fishing line and reel running through the top of the measuring pole, and determined the depth of the cavity by the distance with which the weight descended within the cavity. For cavities above 15 m height, we used a Criterion RD 1000 digital dendrometer to measure cavity height and entrance width. We characterized cavities by tree condition as live or dead, and origin as natural or excavated (Aitken and Martin 2007). Cavities excavated by birds can be distinguished by the symmetrical, round shape of the entrance, while naturally formed cavities are irregularly shaped, and may be located at the site of tree damage (Aitken and Martin 2007). We measured all cavities with an entrance diameter ≥2 cm encountered in the transects. To permit comparisons with other studies on tree-cavity availability for the avian community of secondary cavity-nesters, we considered cavities that could potentially be used by birds (≥2 cm entrance diameter, ≥8 cm depth; Cockle et al. 2008), and also determined the density of cavities with characteristics most suitable for use by birds (≥2.5 m height, ≥13 cm depth; Cockle et al. 2011).

To determine the minimum cavity entrance diameter that would be accessible by Military Macaws we took body measurements of four Military Macaw specimens in the Colección Nacional de Aves of the Instituto de Biología at the Universidad Nacional Autónoma de México. Military Macaw specimens had a frontal diameter of mean 12 ± 0.41 cm (range 11.6 – 12.4 cm), and mean front-back depth of 8.4 ± 0.34 cm (range 8.1 – 8.9 cm). We therefore considered as accessible by Military Macaws those cavities with an entrance width of at least 8 cm. Dimensions of museum specimens may not exactly represent those of live birds, however, this minimum entrance diameter is similar to the smallest 9 cm entrance diameter reported for nest-sites of the similar-sized Blue-throated Macaw, *Ara glaucogularis* (Berkunsky et al. 2014). Finally, to determine the density of adequate nesting resources for Military Macaws in each vegetation type, we considered only those cavities with characteristics within the range of values for those used as nests by Military Macaws.

Statistical analysis

Normality of data was determined using Kolmogorov-Smirnov normality tests, and transformed by logarithm to improve normality for parametric statistical analysis. Where data did not conform to a normal distribution we applied non-parametric statistics (Zar 1999). Cavity characteristics presented a normal distribution following log transformation, therefore we applied ANOVA to compare characteristics of all cavities potentially available to the avian secondary cavity-nesting community among the three vegetation types.

To determine resource selection of nest-sites by Military Macaws we compared the characteristics of trees and cavities used for nesting with those of accessible cavities registered in the transects (Manly et al. 2002). We applied chi-square test with simultaneous Bonferroni 95% confidence intervals to determine whether use of tree species as nest-sites differed from the proportional availability of cavities accessible to macaws (entrance diameter ≥ 8cm) in those tree species. We considered the observed proportion of use as significantly different when the expected proportion of use based on availability falls outside the 95% confidence interval for observed use, having a $P < 0.05$ probability of usage (Neu et al. 1974; Byers et al.1984). Data on dbh of nearest-neighbor trees presented a normal distribution after log transformation, therefore we applied two-sample *t*-tests to compare dbh of nest-trees with that of nearest-neighbor trees. By comparison, height to first ramification did not present a normal distribution and this was not improved by data transformation, therefore we applied Mann-Whitney *U* test to compare nearest-neighbor and nest-trees.

To evaluate whether Military Macaws selected cavities based on their characteristics we applied two-sample *t*-tests to compare the characteristics of cavities used as nest-sites with those of all cavities accessible to macaws (entrance diameter ≥ 8cm). We also modelled the probability that a cavity would be selected as a nest-site by Military Macaws using multiple logistic regression (nest = 1, unused = 0), comparing the characteristics of nest-cavities with those of all accessible cavities. Tree dbh was significantly correlated with cavity height ($r = 0.35$, $P = 0.031$) and entrance width ($r = 0.40$, $P = 0.014$), therefore we excluded tree dbh from the initial multiple logistic regression model (Quinn and Keough 2002). We applied the Wald statistic to determine which of the variables of cavity height, entrance width, or cavity depth best predicted whether a cavity was used as a nest by macaws (Quinn and Keough 2002). We also determined the odds ratio, and inflection point of the probability model for significant variables to identify the value above which there is a greater than 50% probability of selection as a nest-site. Finally, we conducted Pearson's correlation matrix on the characteristics of the 12 Military Macaw nest-sites to determine whether negative correlations exist between the variables of cavity dimensions that could indicate a trade-off in characteristics of cavities used as nest-sites by Military Macaws (Agrawal et al. 2010). Descriptive statistics are presented with mean and standard deviation, and we considered $P < 0.05$ as significant for statistical analyses.

RESULTS

Nest-site characteristics

We located 12 Military Macaw nests, with a mean distance of 1.3 ± 0.92 km ($n = 9$ non-repeated pairs, range 0.33 – 3.4 km) between nearest-neighboring nests, with nests having a 25-75% interquartile range of 709 - 1,738 m from the nearest neighbor. All nest-cavities occurred in live trees, and were principally in naturally-formed cavities. Military Macaw nest-cavities occurred in five tree species, though 58% of nest-sites were located in cavities in live trees of *Enterolobium cyclocarpum*, followed by *Astronium graveolens* (17%), with one nest cavity each in live trees of *Brosimum alicastrum*, *Tabebuia rosei*, and *Ficus* sp. (Fig. 1). These tree species all present growth traits of tall, straight trunks, with mean ramification at 11.2 ± 4.2 m (range = 7 – 22 m, n =11), which is half the total tree height (mean = 22.9 ± 4.7 m, range = 15 – 30 m, n =12), indicative of primary or conserved forest trees (Marsden and Fielding 1999). In particular, nest-trees of *E. cyclocarpum* were large canopy trees of mean 156 ± 92 cm (range = 70.3 – 249.4, n =7) diameter and total height of 24 ± 4.8 m (range = 16-30, n = 7).

Military Macaws used nest-cavities in large trees (Table 1), with tree dbh ranging from 56.1 – 348 cm, and a support diameter at the cavity entrance of 78.6 ± 29.0 cm (range = 50 - 150 cm; *n* = 11). Nest-cavities were located high above the ground (Table 1), with the lowest nest-cavity occurring at 7.5 m and the highest at 17 m above the ground. Cavity height was also the nest-cavity characteristic with least variation around the mean (coefficient of variation = 25.5%). Cavity entrances were relatively wide (Table 1), ranging from 11 to 40 cm, where the 25-75% interquartile range of nest-cavities had an entrance width of 12 to 21 cm. Nest-cavities had a mean 62.8 cm depth (Table 1; range = 18 – 198 cm), though 60% of nests had a depth of less than 40 cm.

Nest sites of Military Macaws were located in conserved forest habitat with mean 64 ± 21.9% (range = 40-91%, *n* = 12) canopy cover around nest sites, and a mean distance of 16 ± 16.7 m (range 8.5 – 11.8 m, *n* = 48) to nearest neighboring trees. We registered 15 tree species around Military Macaw nests, of which the dominant species were *Hura polyandra* and *Brosimum alicastrum* each comprising 22.9% of nearest neighbor trees, and together representing almost half of all nearest-neighbor trees. The next most frequently registered nearest-neighbor tree species were *Tabebuia rosei* (10.4%) and *Bursera simaruba* (8.3%), with all these tree species being characteristic of mature semi-deciduous forest (Rzedowski 2006).

Tree-cavity availability

We registered a total of 47 cavities with entrance diameter ≥2 cm in 6 ha of tropical dry and oak forest around the Cajón de Peñas dam. However, 11 cavities did not meet the minimum criteria of 8 cm depth specified by Cockle et al. (2008), giving a density of 6 cavities/ha. These were concentrated in tropical semi-deciduous forest (21 cavities), with 10 cavities in tropical deciduous forest, and 5 cavities in oak forest. Cavities were located in 12 tree species, with the majority of cavities in live trees of *Tabebuia* sp (22% of cavities). Overall, cavities occurred in large trees of mean dbh 69.2 ± 57.9 cm (range = 18.4 – 316 cm, *n* = 33), at a mean height of 7.2 ± 3.1 m (range = 3 – 16 m, *n* = 36) above the ground, with mean 9.8 ± 5.4 cm (range = 2 – 30 cm, *n* = 35) entrance diameter, and mean depth of 50.4 ± 51.5cm (range = 10 – 212 cm, *n* = 24). There were more cavities per transect in semi-deciduous forest, though this was not significantly different (Table 2). However, cavities in semi-deciduous forest occurred in significantly larger trees (Table 2). Likewise, cavities in oak forest tended to occur at a lower height and with narrower entrance diameters, but this was not significant

(Table 2). Of the 47 cavities recorded in the survey plots, 27 (57%) had dimensions suitable for cavity-nesting birds (≥2.5 m height, ≥13 cm depth; Cockle et al. 2011), with a density of 4.5 suitable bird cavities/ha.

Considering only cavities accessible to Military Macaws that had an entrance diameter ≥8 cm, irrespective of depth, 19 of the original 47 cavities did not meet the criteria of minimum entrance diameter, and were excluded from analysis of cavity resources accessible to macaws. Hence, a total of 28 (60%) cavities were potentially accessible to Military Macaws, with an overall 4.7 accessible cavities/ha in the tropical dry and oak forest of Cajon de Peñas. However, cavities were concentrated in semi-deciduous forest (8.5 accessible cavities/ha), with only 4 and 1.5 accessible cavities/ha in deciduous and oak forest respectively. Nevertheless, very few cavities had characteristics within the range of those used as nest-sites by Military Macaws (height ≥7.5 m, entrance diameter ≥11 cm, depth ≥18 cm), with only 0.7 adequate cavities/ha for macaws in the tropical dry forest of Cajón de Peñas, none of which occurred in oak forest.

Nest-site selection by Military Macaws

Use of tree species as nest sites by the Military Macaw differed significantly from their availability in providing cavities accessible to macaws ($G_4 = 16.9$, $P < 0.005$). Bonferroni comparison of use and availability of tree species with accessible cavities demonstrated that Military Macaws selected *Enterolobium cyclocarpum* as nest-trees, with observed use of this tree species as a nest-site and 95% confidence intervals being significantly greater than the expected use based on availability (Observed proportion = 0.58, CI: 0.22 – 0.95, Expected proportion = 0.13; Fig. 1). By comparison, macaws used *Tabebuia rosei* as a nest-tree significantly less than expected by the proportional availability of accessible cavities in this tree species (Observed proportion = 0.08, CI: 0 – 0.29, Expected proportion = 0.63; Fig. 1).

Nest-trees used by Military Macaws were also significantly larger than nearest-neighbor trees ($t_{53} = 9.4$, $P < 0.001$; Fig. 2a), and had a greater height to initial trunk ramification ($U_{55} = 118$, $P = 0.009$; Fig. 2b), indicating that Military Macaws selected large, emergent trees with tall, straight trunks as nest sites. Furthermore, characteristics of tree-cavities used as nest-sites by Military Macaws differed significantly from characteristics of accessible cavities (Table 3). Macaws selected as nest-sites cavities in significantly larger trees, at a greater height from the ground, with larger entrance diameters, and greater depth than all accessible cavities (Table 3).

The initial multiple logistic regression model, excluding tree dbh, demonstrated that cavity height from the ground significantly predicted nest-cavity selection by Military Macaws (Wald $\chi^2_1 = 8.2$, $P = 0.004$). The other variables of entrance width (Wald $\chi^2_1 = 2.8$, $P = 0.092$) and cavity depth ($P = 0.97$) were not significant in the initial multiple logistic regression model. When tested by logistic regression individually, tree dbh also predicted nest-cavity selection by macaws (Wald $\chi^2_1 = 5$, $P = 0.025$). The odds ratio demonstrated that a cavity was 1.6 times as likely to be selected as a nest-site with each 1 m increase in height (odds ratio = 1.56; 95% CI = 1.15–2.11), and 1.0 times as likely to be selected with each increase in tree diameter (odds ratio = 1.02; 95% CI = 1.00–1.04). Calculation of probability values for cavity height and tree dbh found that the inflection point of the probability curve occurred at a cavity height of 10.7 m and tree dbh of 134 cm, above which there was a greater than 50% probability that a cavity would be selected as a nest-site.

The correlation matrix for characteristics of cavities used as nest-sites by Military Macaws demonstrated a negative correlation between the variables of cavity height and depth ($r_{10} = -0.611$, $P = 0.06$), which was not significant due to sample size but had a high power of 0.63. Given that cavity height was the main criteria predicting selection as a nest-site, this may suggest that where possible Military Macaws will select cavities high above the ground as nest-sites, but when lower cavities are used there may be a tendency to use deeper cavities (Fig. 3).

DISCUSSION

Characteristics of Military Macaw nest-sites

Military Macaw nest-sites occurred in large, mature trees characteristic of primary semi-deciduous forest, and used predominantly one tree species for nesting. Most observations of the Military Macaw report the species nesting in cavities in cliffs (Forshaw 1989; Rivera-Ortiz et al. 2008). However, tree-cavity nesting is the ancestral trait for psittacines, and most taxa that use alternative substrates for nesting have retained the tree-cavity nesting trait (Brightsmith 2005). Hence, Military Macaws along the coast of Jalisco may have retained this ancestral trait due to the existence of suitable tree-cavity nesting sites, and a potential lack of appropriate nesting cliffs.

Nest studies of other parrot species have recorded a tendency to use only a few species of tree for nesting (Saunders et al. 1982; Snyder et al. 1987; Renton and Salinas-Melgoza 1999; Monterrubio-Rico and Enkerlin-Hoeflich 2004; Monterrubio-Rico et al. 2009; Renton and Brightsmith 2009), though few of these studies have evaluated whether parrots select particular tree species as nest-sites based on their structural characteristics. In the present study, we found that Military Macaws selected cavities in *Enterlobium cyclocarpum* more than may be expected by the availability of accessible cavities in this tree species. This may be due to the large size and structural characteristic of this tree species, which can reach 3 m dbh and 20 to 30 m height (Pennington and Sarukhán 1998). Tree dbh is an important indicator of tree size and age, with larger, older trees more likely to have cavities suitable for use as nest-sites (Lindenmayer et al. 1991).

Tree-cavities used as nest-sites by the Military Macaw had large mean entrance diameters, and were of moderate depth. This differs from most medium-sized parrot species, particularly of the genus *Amazona*, which use cavities with narrower mean entrance diameters of between 7.9 cm and 15 cm, and greater mean depth of between 66.2 cm and 149 cm than the Military Macaw (Lanning and Shiflet 1983; Snyder et al. 1987; Renton and Salinas-Melgoza 1999; Fernandez-Sexais and Miranda-Mouroa 2002; Rodriguez-Castillo and Eberhard 2006; Rodriguez-Ferraro and Sanz 2007; Berkunsky and Reboreda 2009). Entrance diameters of cavities used as nest-sites by Military Macaws were similar to those of the similar-sized Blue-throated Macaw (Berkunsky et al. 2014). Only the larger-bodied Scarlet (*Ara macao*) and Hyacinth Macaw (*Anodorhynchus hyacinthinus*) and Australian cockatoos use cavities with larger mean entrance diameters (Saunders et al. 1982; 2014; Marsden et al. 2001; Heinsohn et al. 2003; Pinho and Nogueira 2003; Vaughan et al. 2003; Olah et al. 2014). Most macaw species use relatively shallow nests, and the mean cavity depth of 62.8 cm for Military Macaw nests is within the median range for mean depth of natural tree-cavities used for nesting by other macaw species (Gonzalez 2003; Pinho and Nogueira 2003; Vaughan et al. 2003; Berkunsky et al. 2014; Olah et al. 2014). The use of shallow nest-cavities with large entrance diameters may make Military Macaw nests more vulnerable to access by predators. Evaluations of nest success of Military Macaws would indicate whether macaw nests have a high risk of predation.

Finally, though we located only 12 nests of the Military Macaw, this is actually within the high range of natural tree-cavity nest-sites reported in other studies of macaws. On average, studies of macaws have measured cavity characteristics of a mean 9 ± 5.7 natural nests, ranging from studies of 3 natural nest-sites to the highest number of 18 natural nests (Berkunsky et al. 2014), with the majority of studies providing data on 3-14 natural nest-sites (Gonzalez 2003; Pinho and Nogueira 2003; Vaughan et al. 2003; Brightsmith and Bravo 2006; Olah et al. 2014). The generally low sample-sizes in studies of natural tree-cavity nests used by macaws is probably a reflection of the low density of nesting macaws, and the spatial scale at which such large-bodied canopy-dwelling birds may operate.

Tree-cavity availability and selection by the Military Macaw

We found a low density of 6 cavities/ha in the tropical dry and oak forest of Cajón de Peñas, most of which were concentrated in semi-deciduous forest, with 4.5 cavities/ha fitting the criteria as suitable for use by cavity-nesting birds (Cockle et al. 2011). This is a much lower density than the 12.3 cavities/ha recorded in temperate forests (Aitken and Martin 2007), and the 16 cavities/ha recorded in the dry forest of Australia (Saunders et al. 1982), and the Atlantic forest of Argentina (Cockle et al. 2008). However, the density of cavities suitable for birds was similar to the 4.5 suitable cavities/ha in primary Atlantic forest of Argentina, with only 0.5 suitable bird cavities/ha in logged forest (Cockle et al. 2010). Furthermore, 4.7 cavities/ha were accessible to Military Macaws, but there were only 0.7 adequate cavities/ha which presented characteristics within the range of those used as nest-sites by macaws. Hence, the great majority of cavities did not have the suite of characteristics selected by Military Macaws for nesting resulting in a very low density of cavities suitable for nesting by macaws.

The Military Macaw has been reported using a variety of habitats (Forshaw 1989); however, as determined in the present study, most tree-cavity nesting resources were concentrated in semi-deciduous forest. In particular, oak forest at the study site offered no cavities suitable for use as nest-sites by Military Macaws, given that few cavities were located in this forest type, and they were generally of small entrance diameters and at a low height above the ground. Therefore, while the Military Macaw may be reported in oak forest, this is unlikely to provide nesting resources for macaws. Furthermore, the concentration of nesting resources in semi-deciduous forest where cavities occur in significantly larger trees, highlights the importance of this habitat for macaw reproduction, which depends on the maintenance of large, mature trees in this forest type.

The nesting requirements of Military Macaws for large cavities in mature, primary semi-deciduous forest trees could be a limiting factor for their reproduction. Added to the low density of adequate cavities for nesting, there may also be intra- and inter-specific competition for nest-sites. During the present study, we recorded a Collared Forest Falcon (*Micrastur semitorquatus*) which had taken over a previous Military Macaw nest-site, and was incubating three eggs. As well as being a potential nest-predator, this large raptor is also an inter-specific nest-site competitor (Lopez-Lanus 2000; Aguiar-Carrara et al. 2007), reducing even further the availability of adequate cavities for nesting.

Military Macaws selected nest-cavities in larger trees, at a greater height above the ground, and with larger entrance diameters and depth than most of the accessible cavities. Height above the ground was the main criteria for nest-cavity selection, and is a selection criteria for other cavity-nesting birds that may reduce the risk of predation (Nilsson 1984; Wilcove 1985; Li and Martin 1991; Newton 1994; Cockle et al. 2011). The fact that Military Macaws select nest-cavities with wide entrance diameters may be due to their body size, though on average macaws used cavities with entrance diameters greater than that required to permit access by the nest owners, potentially providing access to a wider range of predators. The negative correlation of height with depth in cavities used as nest-sites by Military Macaws may suggest a trade-off in nest-cavity selection whereby macaws may preferentially select a nest-cavity high above the ground, regardless of depth, but when using lower cavities, the preference may be for these to be deeper. Whether or not this has fitness consequences for nesting macaws could be determined by evaluating the influence of nest-cavity characteristics on outcome of the nesting attempt.

Conservation implications

Understanding the nesting requirements of large, threatened psittacines such as the Military Macaw is essential to develop strategies to preserve habitat features that influence breeding productivity and survival. The fact that Military Macaw populations along the coast of Jalisco use tree-cavity nest-sites makes them highly vulnerable to human nest-poaching, compared with other populations nesting in relatively inaccessible cliffs. Nest poaching is intense in the region, making it imperative to implement environmental outreach with local communities in macaw nesting areas, and establish alternative economic activities such as ecotourism based on observation of Military Macaw nests that may provide incentives for conservation of the macaws and their nesting habitat (Muñoz Lacy 2014).

Tree-cavities with adequate characteristics for nesting macaws occurred at extremely low densities, and may be a limiting resource for Military Macaw reproduction. Most Military Macaw nest-cavities occurred in large trees of ~1 m diameter, and all macaw nests were located in semi-deciduous forest, which contained larger cavity-bearing trees. Selective forestry practices tend to establish a minimum girth for extraction promoting the removal of larger trees from semi-deciduous forest. This therefore brings into conflict macaw conservation with forestry practices aimed at extraction of large valuable-wood trees. Therefore adaptive strategies need to be devised to reconcile the two potentially conflicting aims of macaw conservation and selective forestry. These may include the establishment of set-aside conservation areas, and long-term replanting programs with native trees to ensure maintenance of semi-deciduous as valuable macaw nesting habitat. Selective forestry practices could also establish a quota of large trees >1 m diameter to be exempt from extraction to preserve the forest structure of large emergent canopy trees. While excessive capture for the pet trade is the most visible threat to parrot populations in the study area, the loss of essential nesting habitat would have implications for persistence of the wild population in the long-term. Therefore, a landscape management strategy to maintain breeding habitat for the Military Macaw should focus on conservation of primary semi-deciduous forest.

ACKNOWLEDGMENTS

The study was conducted in partial fulfillment of a Doctoral thesis by SMPM at the Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México (UNAM), who was supported by a student grant from the Consejo Nacional de Ciencia y Tecnología (CONACyT 220278). ASM was supported by a Postdoctoral grant from CONACyT (98294), and LGML was supported by a CONACyT Masters student grant. The research was funded by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT grant IN203012) of UNAM, and the Loro Parque Fundación A.C., both to KR. The Dirección General de Vida Silvestre of the Secretaria del Medio Ambiente y Recursos Naturales provided permits for the study, and the research complies with Mexican law. We are grateful to the Cajon de Peñas local community for permission to work on their lands, and thank Bonnie Jauregui for logistical support.

Assistance in the field was provided by Christian A. Montes Medina, while Patricia Escalante and Miguel De Labra Hernández assisted with measurements of Military Macaw specimens in the Colección Nacional de Aves, of the Instituto de Biología, UNAM. Kristina Cockle and an anonymous reviewer provided constructive suggestions for improvement of the manuscript.

REFERENCES

Agrawal AA, Conner JK, Rasmann S (2010) Tradeoffs and adaptive negative correlations in evolutionary ecology. In: Bell M, Eanes W, Futuyma D, Levinton J (eds) Evolution after Darwin: the first 150 years. Sinauer Associates, Sunderland, pp 243-268.

Aguiar-Carrara L, Zuquim-Antas PT, Souza-Yabe R (2007) Nidificação do gavião-relógio *Micrastur semitorquatus* (Aves: Falconidae) no Pantanal Mato-grossense: dados biométricos, dieta dos ninhegos e disputa com araras. Rev Bras Ornitol 15:85-93.

Aitken KEH, Martin K (2007) The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forest in western Canada. J Ornithol 148:S425-S434.

Bennet PM, Owens IPF (1997) Variation in extinction risk among birds: chance or evolutionary predisposition?. Proc R Soc B 264:401–408.

Berkunsky I, Reboreda JC (2009) Nest-site fidelity and cavity reoccupation by Blue-fronted Parrots *Amazona aestiva* in the dry Chaco of Argentina. Ibis 151:145-150.

Berkunsky I, Daniele G, Kacoliris FP, Dıaz-Luque JA, Silva Frias CP, Aramburu RM, Gilardi JD (2014) Reproductive parameters in the critically endangered Blue-throated Macaw: limits to the recovery of a parrot under intensive management. Plos One 9: doi: 10.1371/journal.pone.0099941.

Brightsmith DJ (2005) Competition, predation and nest niche shifts among tropical cavity nesters: phylogeny and natural history evolution of parrots (Psittaciformes) and trogons (Trogoniformes). J Avian Biol 36:64-73.

Brightsmith D, Bravo A (2006) Ecology and management of nesting Blue-and-yellow Macaws (*Ara ararauna*) in *Mauritia* palm swamps. Biodivers Conserv 15:4271-4287.

Byers CR, Steinhorst RK, Krausman PR (1984) Clarification of a technique for analysis of utilization-availability data. J Wildl Manage 48:1050-1053.

Cameron M (2006) Nesting habitat of the Glossy Black Cockatoo in central New South Wales. Biol Conserv 127:402-410.

Carneiro APB, Jiménez JE, Vergara PM, White TW Jr (2013) Nest-site selection by Slender-billed Parakeets in a Chilean agricultural-forest mosaic. J Field Ornithol 84:13–22.

Carreón-Arroyo G (1997) Estimación poblacional, biología reproductiva y ecología de la nidificación de la Guacamaya verde (*Ara militaris*) en una selva estacional del oeste del estado de Jalisco. B.Sc. Dissertation, Universidad Nacional Autónoma de México.

Citta JJ, Lindberg MS (2004) Nest site selection of passerines: effects of geographic scale and public and personal information. Ecology 88:2034-2046.

Cockle K, Martin K, Wiebe K (2008) Availability of cavities for nesting birds in the Atlantic forest, Argentina. Ornitol Neotrop 19:269-278

Cockle KL, Martin K, Drever MC (2010) Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biol Conserv 143:2851-2857.

Cockle K, Martin K, Wiebe K (2011) Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic forest. Biotropica 43:228-236.

Enkerlin-Hoeflich EC (1995) Comparative ecology and reproductive biology of three species of *Amazona* parrots in northeastern Mexico. Ph.D. Dissertation. Texas A&M University.

Fernandes Seixas GH, Miranda Mourão G (2002) Nesting success and hatching survival of the Blue-fronted Amazon (*Amazona aestiva*) in the Pantanal of Mato Grosso do Sul, Brazil. J Field Ornithol 73:399-409.

Forshaw JM (1989) Parrots of the world. Landsdown Editions, Australia.

Garcia-Oliva F, Ezcurra E, Galicia L (1991) Pattern of rainfall distribution in the central Pacific coast of Mexico. Geogr Ann A 73:179-186.

Gibbs JP, Hunter Jr ML, Melvin SM (1993) Snag availability and communities of cavity nesting birds in tropical versus temperate forests. Biotropica 25:236-241.

Gonzalez JA (2003) Harvesting, local trade, and conservation of parrots in the northeastern Peruvian Amazon. Biol Conserv 114: 437-446.

Heinsohn R, Murphy S, Legge S (2003) Overlap and competition for nest holes among Eclectus Parrots, Palm Cockatoos and Sulphur-crested Cockatoos. Aust J Zool 51:81-94.

Lanning DV, Shiflett JT (1983) Nesting ecology of Thick-billed Parrots. Condor 85:66-73.

Li P, Martin TE (1991) Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405-418.

Lindenmayer DB, Cunningham RB, Nix HA, Tanton MT, Smith AP (1991) Predicting the abundance of hollow-bearing trees in montane forests of southeastern Australia. Aust J Ecol 16:91-98.

López-Lanus B (2000) Collared Forest-Falcon *Micrastur semitorquatus* courtship and mating, with take-over of a macaw nest. Cotinga 14:9-11.

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource Selection by Animals: Statistical Design and Analysis for Field Studies. 2nd edn. Dordrecht: Kluwer Academic Publishers.

Marsden S, Fielding A (1999) Habitat association of parrots on the Wallacean islands of Buru, Seram and Sumba. J Biogeogr 26:439-446.

Marsden S, Pilgrim JD, Wilkinson R (2001) Status, abundance and habitat use of Blue-eyed Cockatoo *Cacatua ophthalmica* on New Britain, Papua New Guinea. Bird Conserv Int 11:151–160

Monterrubio-Rico TC, Enkerlin-Hoeflich E (2004) Present use and characteristics of Thick-billed Parrot nest sites in Northwestern Mexico. J Field Ornithol 75:96-103.

Monterrubio-Rico TC, Escalante-Pliego LP (2006) Richness, distribution and conservation status of cavity nesting birds in Mexico. Biol Conserv 128:67-78.

Muñoz Lacy LG (2014) Uso del hábitat y recursos alimenticios por la guacamaya verde (*Ara militaris*) en la costa de Jalisco y su potencial para el ecoturismo. Masters Dissertation, Universidad Nacional Autónoma de México.

Newton I (1994) The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biol Conserv 70:265-276.

Nilsson SG (1984) The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand 15:167-175.

Neu CW, Byers CR, Peek JM (1974) A technique for analysis of utilization-availability data. J Wildl Manage 38:541-545

Olah G, Vigo G, Heinsohn R, Brightsmith D.J. (2014) Nest site selection and efficacy of artificial nests for breeding success of Scarlet Macaws *Ara macao macao* in lowland Peru. J Nat Conserv 22:176-185.

Ortega-Reyes J (2004) Composición de la fauna mastozoológica de la presa Cajón de Peña, Tomatlán, Jalisco. Rev Mex Mastozool 8:9-20.

Pennington TD, Sarukhán J (1998) Árboles Tropicales de México. 2nd Edition. Mexico City: Fondo de Cultura Económica.

Pinho JB, Nogueira FMB (2003) Hyacinth Macaw (*Anodorhynchus hyacinthinus*) reproduction in the northern Pantanal, Mato Grosso, Brazil. Ornitol Neotrop 14:29-38.

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Renton K, Salinas-Melgoza A (1999) Nesting behavior of the Lilac-crowned Parrot. Wilson Bull 111:488-493.

Renton K, Brightsmith D (2009) Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru. J Field Ornithol 80:1-8.

Rivera-Ortiz FA, Contreras-Gonzalez AM, Soberanes-Gonzalez CA, Valiente-Banuet A, Arizmendi MC (2008) Seasonal abundance and breeding chronology of the Military Macaw (*Ara militaris*) in a semi-arid region of Central Mexico. Ornitol Neotrop 19:255–263.

Rodríguez-Castillo A, Eberhard, JR (2006) Reproductive behavior of the Yellow-crowned Parrot (*Amazona ochrocephala*) in Western Panama. Wilson J Ornithol 118:225-236.

Rodríguez-Ferraro A, Sanz V (2007) Natural history and population status of the Yellow-shouldered Parrot on La Blanquilla Island, Venezuela. Wilson J Ornithol 119:602-609.

Rzedowski J (2006) Vegetación de México, digital edition. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. http://www.biodiversidad.gob.mx/publicaciones/librosDig/pdf/VegetacionMx_Cont.pdf. Accessed 8 October 2014.

Salinas-Melgoza A, Salinas-Melgoza V, Renton K (2009) Factors influencing nest spacing of a secondary cavity nesting parrot: habitat heterogeneity and proximity of conspecifics. Condor 111:305-313.

Saunders DA (1979) The availability of tree hollows for use as nest sites by White-tailed Black Cockatoos. Aus Wildl Res 6:205-216.

Saunders DA, Mawson PR, Dawson R (2014) Use of tree hollows by Carnaby's Cockatoo and the fate of large hollow-bearing trees at Coomallo Creek, Western Australia 1969–2013. Biol Conserv 177:85–193.

Saunders DA, Smith GT, Rowley I (1982) The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. Aust Wildl Res 9:541–556.

Selman R, Perrin M, Hunter M (2004) Characteristics and competition for nest sites by the Rüppell´s Parrot, *Poicephalus rueppelli*. Ostrich 75:89-94.

SEMARNAT (2010) Norma Oficial Mexicana NOM-059-SEMARNAT-2010. Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. Diario oficial 30 de diciembre de 2010: 1-78. http://www.biodiversidad.gob.mx/especies/pdf/NOM_059_SEMARNAT_2010.pdf Accessed 8 October 2014.

Snyder NFR, Wiley JW, Kepler CB (1987) The Parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles.

Vaughan C, Nemeth N, Marineros L (2003) Ecology and management of natural and artificial Scarlet Macaw (*Ara macao*) nest cavities in Costa Rica. Ornitol Neotrop 14:381-396.

Walker JS, Cahill AJ, Marsden SA (2005) Factors influencing nest-site occupancy and low reproductive output in the critically endangered Yellow-crested Cockatoo *Cacatua sulphurea* on Sumba, Indonesia. Bird Conserv Int 15:347-359.

Wilcove DS (1985) Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Zar JH (1999) Biostatistical analysis, 4th edition. Prentice Hall Inc, New Jersey.

Table 1. Characteristics (mean ± SD) of tree-cavities used as nest-sites by Military Macaws and those accessible to macaws (≥8cm entrance diameter), with two-sample *t*-test significance values.

Variable	Nest-cavities (n = 12)	Accessible cavities (n = 28)	Significance value
Tree diameter at breast height (cm)	145.8 ± 101.5	67.9 ± 39.4	$t_{37} = 3.5$, $P = 0.002$
Cavity height from the ground (m)	11.1 ± 2.82	7.0 ± 2.9	$t_{38} = 4.9$, $P < 0.001$
Entrance width (cm)	17.5 ± 8.25	12.7 ± 5.1	$t_{37} = 2.3$, $P = 0.032$
Cavity depth (cm)	62.8 ± 55.8	41.8 ± 54.4	$t_{32} = 2.3$, $P = 0.028$

Table 2. Comparison of cavity (≥2 cm entrance diameter, ≥8 cm depth; Cockle et al. 2008) characteristics (mean ± SD) among three forest types at Cajon de Peñas, Jalisco.

Variable	Deciduous (n = 10)	Semi-deciduous (n = 21)	Oak (n = 5)	Significance test
Cavities / transect	2.5 ± 3.3	5.3 ± 2.6	1.3 ± 0.96	$F_{2,9}$= 2.7 , ns
Tree DBH (cm)	50.7 ± 34.4	90.2 ± 67.7*	30.8 ± 5.8	$F_{2,30}$= 6.0, P = 0.006
Cavity height (m)	7.3 ± 2.6	7.7 ± 3.4	5.2 ± 1.6	$F_{2,33}$= 1.4, ns
Entrance width (cm)	10.6 ± 4.6	10.2 ± 6.1	6.8 ± 3.4	$F_{2,32}$= 1.4, ns
Cavity depth (cm)	88 ± 77.8	34.8 ± 28.2	35.4 ± 21.0	$F_{2,21}$= 2.1, ns

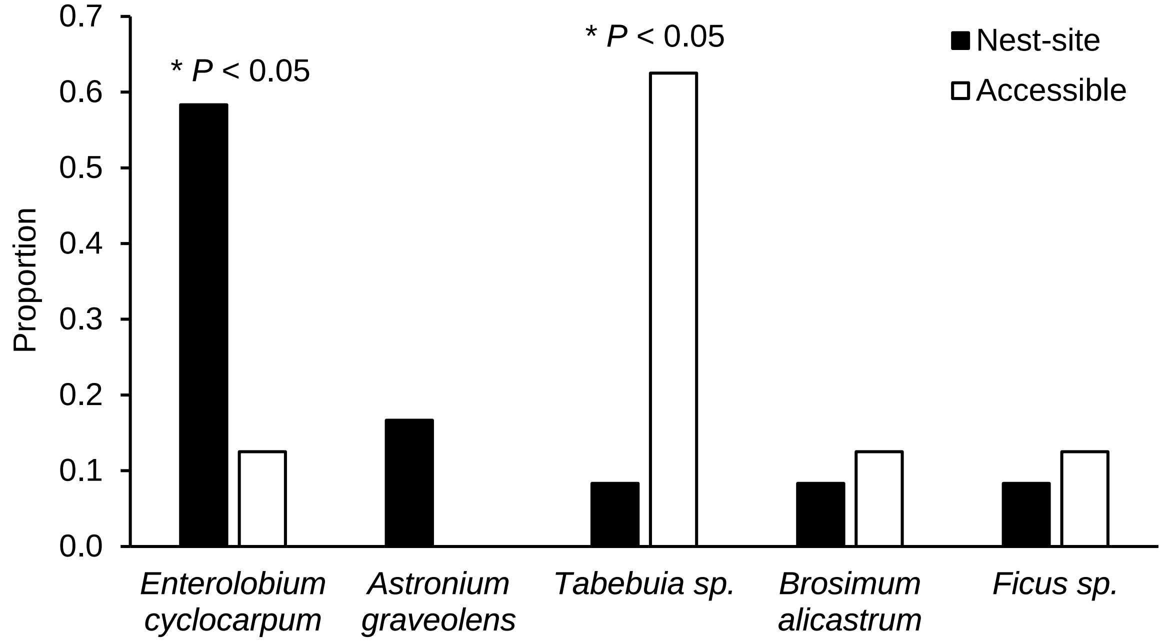
* Tukey post-hoc comparison $P < 0.05$

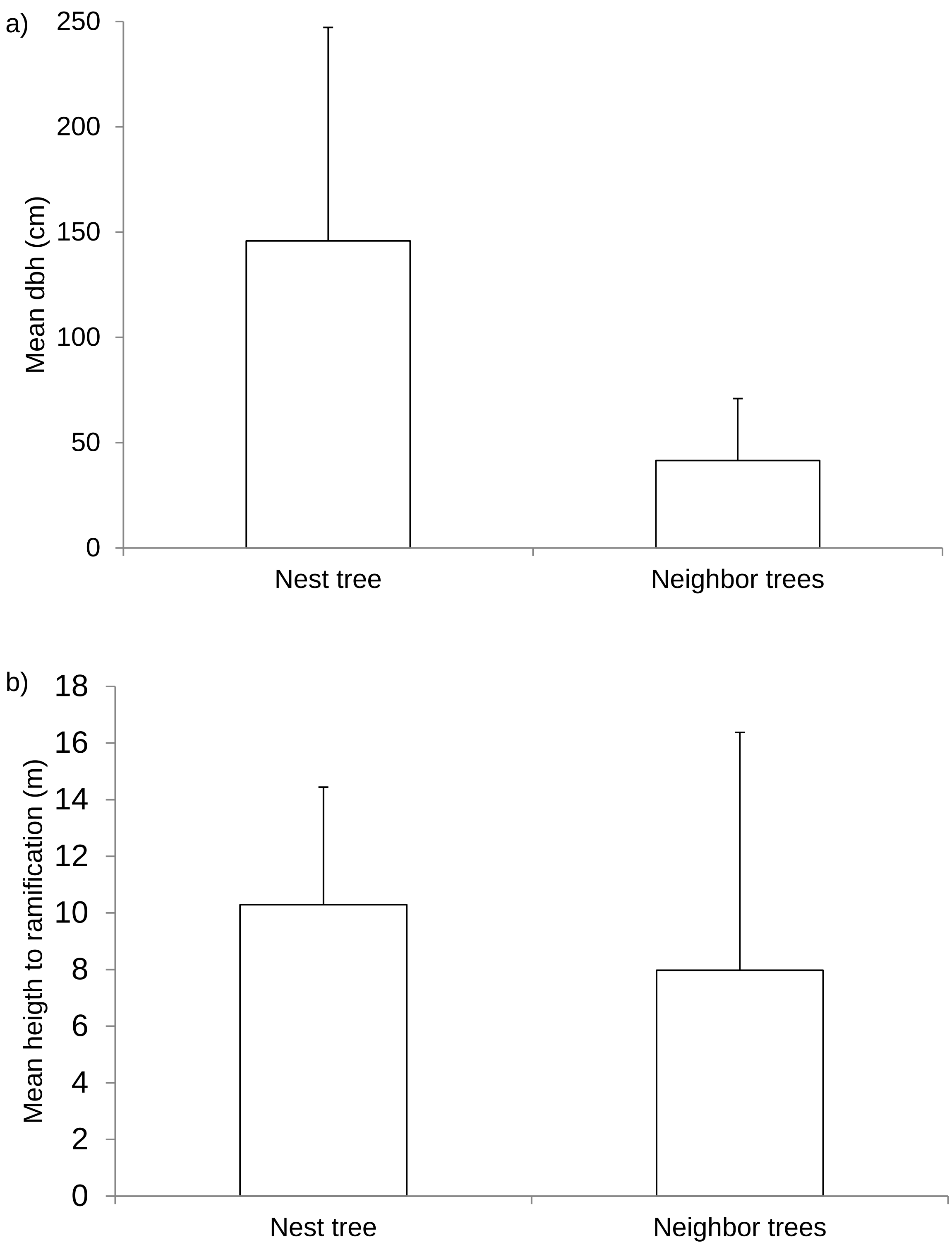
FIGURE LEGENDS

Figure 1. Proportion of tree species used as nest-sites by the Military Macaw, and of tree species with accessible cavities (≥8 cm entrance diameter). * Bonferroni 95% confidence intervals of observed use differ significantly from proportional availability.

Figure 2. Mean (±SD) dimensions of Military Macaw nest-trees and nearest-neighbor trees for a) diameter at breast height and b) height to first ramification.

Figure 3. Correlation of cavity height and depth for 10 Military Macaw nest-cavities (r = -0.611, P = 0.061; power = 0.63).


* P < 0.05
* P < 0.05
Nest-site
Accessible
Proportion
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Enterolobium cyclocarpum
Astronium graveolens
Tabebuia sp.
Brosimum alicastrum
Ficus sp.


a)
250
200
150
100
50
0
Mean dbh (cm)
Nest tree
Neighbor trees
b)
18
16
14
12
10
8
6
4
2
0
Mean heigth to ramification (m)
Nest tree
Neighbor trees