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Source: Tropical Conservation Science, 9(4)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082916680361

Research Article

Tropical Conservation Science
October-December 2016: 1–10
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DOI: 10.1177/1940082916680361
journals.sagepub.com/home/trc
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Importance of Large, Old Primary Forest Trees in Nest-Site Selection by the Northern Mealy Amazon (*Amazona guatemalae*)

Miguel Ángel De Labra-Hernández[1] and Katherine Renton[2]

Abstract

The increasing conversion of primary tropical moist forest to secondary forest may have consequences for threatened, large-bodied cavity-nesters, such as the Northern Mealy Amazon (*Amazona guatemalae*). We determined availability and characteristics of tree-cavities in 24 1-ha survey plots in Los Chimalapas, southeast Mexico, with 9 plots in evergreen forest, 7 in riparian, and 8 in secondary forest. We compared these with 40 parrot nest-trees to determine whether parrots select cavities with specific characteristics for nesting. Over half of Northern Mealy Amazon nests occurred in live trees of *Terminalia amazonia* (32.5%) and *Dialium guianense* (20%). Compared with available cavities, the Northern Mealy Amazon selected nest-cavities in significantly larger trees, at a greater height above the ground, with larger internal diameter, and greater depth. In particular, internal diameter and cavity depth predicted whether a cavity was selected as a nest-site by parrots. We found a low density of 2.3 available cavities/ha in the study site, although only 1.6 cavities/ha had characteristics suitable for use as nest-sites by parrots. Cavities in secondary forest occurred in smaller trees, at a lower height, and with shallower depth, where only 0.75 cavities/ha were suitable for nesting by parrots. Our results demonstrate that the Northern Mealy Amazon requires nest-cavities in large, old trees able to form large cavities, the majority of which occur in primary forest. The low density of suitable nest-sites for parrots in secondary forest suggests that increased degradation of primary tropical moist forest may have long-term implications for reproduction of this threatened species.

Keywords

Los Chimalapas, Psittaciformes, resource use and availability, secondary cavity-nesters, tree-cavity characteristics, tropical moist forest

Introduction

A large proportion of threatened avian species are secondary cavity-nesters that do not construct their own nest-cavities but depend on the availability of existing cavities (Monterrubio-Rico & Escalante-Pliego, 2006; Newton, 1994). Tropical moist forests are reported to have a high density of tree-cavities (Boyle, Ganong, Clark, & Hast, 2008) and support a variety of cavity-nesting bird species (Monterrubio-Rico & Escalante-Pliego, 2006). However, not all cavities have characteristics suitable for use as nest-sites by birds (Cockle, Martin, & Drever, 2010; Politi, Hunter, & Rivera, 2010; Vázquez & Renton, 2015), and there may be a low density of tree-cavities suitable for large-bodied secondary cavity-nesters (de la Parra-Martínez, Renton, Salinas-Melgoza, & Muñoz-Lacy, 2015). Secondary cavity-nesting birds may also select tree-cavities with specific characteristics of

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Received 12 August 2016; Revised 18 October 2016; Accepted 29 October 2016

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height from the ground, entrance diameter, and cavity depth (Cockle, Martin, & Wiebe, 2011; Politi, Hunter, & Rivera, 2009), which could restrict access by predators increasing the likelihood of nest success (Cockle, Bodrati, Lammertink, & Martin, 2015). Furthermore, tropical moist forests are increasingly being converted to secondary forests, having a high biomass loss of primary forest, and the highest increment rate of secondary forest (de Jong et al., 2010). This may have consequences for secondary cavity-nesting birds, as human-managed forests have been found to have a lower availability of tree-cavities for use by birds (Cockle et al., 2010; Politi et al., 2010).

The majority of Psittaciformes (parrots) are secondary cavity-nesters, where medium- to large-bodied species use tree-cavity nesting substrates (Renton, Salinas-Melgoza, De Labra-Hernández, & de la Parra-Martínez, 2015). The greatest diversity of tree-cavity nesting Psittaciformes occurs in the Neotropics, almost half of which are considered internationally threatened (Renton et al., 2015), with the greatest number and proportion of threatened parrot species worldwide occurring in the Neotropics (Olah et al., 2016). Only a few studies have evaluated nest-site availability and selection by Psittaciformes, and these demonstrate that parrots select nest-sites in large trees, based on cavity characteristics of height from the ground, entrance diameter, and cavity depth (Brightsmith & Bravo, 2006; de la Parra-Martínez et al., 2015; Enkerlin-Hoeflich, 1995; Snyder, Wiley, & Kepler, 1987; Stojanovic, Webb, Roshier, Saunders, & Heinsohn, 2012). Furthermore, many parrots are large-bodied secondary cavity-nesters that may be limited by the availability of tree-cavities with suitable dimensions for nesting (de la Parra-Martínez et al., 2015).

The Northern Mealy Amazon (*Amazona guatemalae*) is the largest Amazon parrot in continental America (Forshaw, 1989) and inhabits tropical moist forests of Mesoamerica (Bjork, 2004). The species is internationally considered Near Threatened (BirdLife International, 2016) and has recently been split from the more widely distributed Southern Mealy Amazon (*Amazona farinosa*) in South America (Wenner, Russello, & Wright, 2012). However, almost nothing is known of the species' nesting requirements, or how this may be affected by the increasing conversion of tropical moist forest to secondary forest. Only one study in the Petén of Guatemala determined that the Northern Mealy Amazon uses nest-sites in large trees of 22 species (Bjork, 2004). Therefore, in the present study, we aimed to determine nest-site requirements of the Northern Mealy Amazon, and the availability of tree-cavities for use by parrots in primary and secondary tropical moist forest. We further aimed to determine whether parrots select cavities based on their characteristics for use as nest-sites and evaluate the consequences of primary forest conversion for nest-site availability and selection by the Northern Mealy Amazon.

Methods

Study Area

We conducted the study in a 56-km^2 region of Los Chimalapas in northeastern Oaxaca, Mexico, comprising three main areas of Chalchijapa (17° 03′ 15″N; 94° 39′ 23″W), San Antonio Nuevo Paraíso (17° 09′ 38″N; 94° 21′ 9″W), and La Fortaleza (17° 09′ 32.2″N; 94° 13′ 45.3″W) within the municipality of Santa Maria Chimalapa. Mean annual temperature in the region is 22°C to 26°C, with high annual rainfall of 2,000 to 4,500 mm, presenting a short dry season from March to June (Trejo, 2004). The dominant vegetation in the region is tropical moist forest, comprised of primary evergreen forest that covers 45.7% of the landscape (Martínez-Pacheco, 2012), with common tree species of *Dialium guianense*, *Terminalia amazonia*, *Brosimum alicastrum*, and *Cojoba arborea* (Rzedowski, 2006; Torres Colín, 2004). Riparian forest occurs along permanent rivers, with common tree species of *Ficus* sp., *Garcinia macrophylla*, *Vochysia guatemalensis*, and *Inga vera* (Torres Colín, 2004). Nevertheless, in Santa Maria Chimalapa over the last few decades, a total of 2,046.8 km^2 of primary tropical evergreen forest has been degraded, with a current rate of loss of 5.8% of primary forest per year (Martínez-Pacheco, 2012), mainly due to increased cattle-grazing and selective logging. This contrasts with the 6.8% increase in secondary forest recorded in the region from 2000 to 2003 (Martínez-Pacheco, 2012). Research permits for the study were provided by the Secretaria del Medio Ambiente y Recursos Naturales in Mexico.

Nest-Site Characteristics

We located nests of the Northern Mealy Amazon during the months of February to May over four consecutive breeding seasons in 2013 to 2016, by observation of the behavior of nesting pairs, and with the assistance of local guides. We used single-rope tree-ascending techniques (Houle, Chapman, & Vickery, 2004; Perry & Williams, 1981) to confirm nesting activity by the presence of eggs or chicks in the nest and take measurements of the nest cavity. For each nest-tree located, we recorded tree species, diameter at breast height (dbh), condition (live or dead), and GPS location. We also noted cavity origin as formed by decay processes (decayed) or excavated by primary cavity-nesters (Aitken & Martin, 2007). Finally, we measured cavity characteristics of height from the ground, entrance width and length, cavity depth, internal diameter, and diameter of the supporting structure (trunk or branch) where the cavity was located (Cockle, Martin, & Wiebe, 2008).

We located a total of 48 Northern Mealy Amazon nests in 40 distinct nest-trees, where 8 nest-trees were reused by parrots between seasons. However, we considered only individual nest-trees as the nest-site for all analyses. Of the 40 nest-trees, 11 occurred in primary forest (evergreen = 9 nest-trees, riparian = 2 nest-trees), with an additional 17 nest-sites located in remnant trees in areas cleared for cattle grazing at the edge of primary forest, and 12 nest-trees occurred in secondary forest.

Cavity Availability

To determine the availability of tree-cavities in tropical moist forest, we established 24 1-ha survey plots (100 × 100 m) distributed among the three study areas, with 9 tree-cavity survey plots in evergreen forest, 7 in riparian, and 8 in secondary forest. In each survey plot, we conducted an intensive search for cavities inspecting all trees with 10 × 40 binoculars. On locating a tree-cavity, we measured the same variables as for the parrot nests. We used a 15-m extendible tree-measuring pole to measure cavity height from the ground and entrance length. A 50-cm length, horizontal plastic tube, with 1 cm graduated markings, was attached to the top of the tree-measuring pole to measure cavity entrance width and internal diameter. Finally, we used a weighted fishing-line that passed through the top of the tree-measuring pole to determine cavity depth by the length the line descended within the cavity (Vázquez & Renton, 2015). This enabled us to measure the dimensions of the majority of cavities; however, for 10 cavities >16 m above the ground, we used a digital dendrometer (Criterion RD 1000) to estimate cavity height, entrance width and length, and support diameter (Cockle et al., 2010) but were unable to measure internal diameter and depth of these cavities.

To be comparable with other studies of tree-cavity availability in tropical forests, we measured all tree-cavities with ≥2 cm entrance diameter and ≥8 cm cavity depth (Cockle et al., 2008). However, we defined a cavity as available for use by parrots based on measurements (Saunders, Smith, & Rowley, 1982) of five specimens of the Northern Mealy Amazon collected in Mexico and located in the Colección Nacional de Aves of the Instituto de Biología at Universidad Nacional Autónoma de Mexico in Mexico City. These Northern Mealy Amazon specimens had a mean diameter at the widest point (shoulder-to-shoulder) of 10.2 ± 1.2 cm (range 8.9–11.5 cm, $n = 5$), with a breast-to-back measurement of mean 7.5 ± 0.2 cm (range 7.3–7.8 cm, $n = 5$). Therefore, it is unlikely that Northern Mealy Amazons could enter a cavity with an entrance diameter less than 7 cm, and we considered as available to parrots only cavities with ≥7.0 cm entrance diameter. We also estimated the density of cavities suitable for nesting by Northern Mealy Amazons considering the minimum characteristics of cavities used as nest-sites by parrots.

Statistical Analyses

Although we measured all tree-cavities found in survey plots, we conducted statistical analysis only on cavities accessible to parrots (entrance diameter ≥7 cm) that were considered as available for parrots. Kolmogorov–Smirnov analysis of normality determined that data on tree dbh, cavity height above the ground, entrance width, and internal diameter had a normal distribution. Therefore, we applied one-way analysis of variance (ANOVA) to compare these characteristics of available cavities among the three vegetation types of evergreen, riparian, and secondary forest. Data on number of available cavities in each survey plot, cavity entrance length, cavity depth, and support diameter did not present a normal distribution; therefore, we applied Kruskal–Wallis ANOVAs to compare these characteristics of available cavities among vegetation types. We conducted Tukey post hoc analyses for one-way ANOVAs and Dunn post hoc analyses for Kruskal–Wallis ANOVAs (Zar, 1999).

We calculated the standardized Levins' (1968) niche breadth index for tree species used as nest-sites by Northern Mealy Amazons, where a value close to 0 indicates that nesting is concentrated on only a few tree species, whereas a value close to 1 indicates a broad use of tree species as nest-sites (Colwell & Futuyma, 1971). We also applied G-test to determine whether use of tree species as nest-sites by the Northern Mealy Amazon corresponded to the availability of accessible cavities in each tree species. Finally, we generated simultaneous confidence intervals with Bonferroni adjusted alpha for the proportional use of each tree species as a nest-site (Byers, Steinhorst, & Krausman, 1984; Nue, Byers, & Peek, 1974). Use of a tree species as a nest-site is considered significantly different when the expected proportion of use based on availability falls outside the confidence interval of observed use (Byers et al., 1984).

We first compared characteristics of Northern Mealy Amazon nest-sites among vegetation types in the modified landscape using one-way ANOVAs with Tukey post hoc comparisons for nest-tree dbh, entrance length, cavity depth, internal diameter, and support diameter, and applied Kruskal–Wallis ANOVAs with Dunn post hoc comparisons for cavity height and entrance width. We determined no significant differences in nest-site characteristics and therefore combined nest-site data in comparisons with available cavities. Combined data did not present a normal distribution; therefore, to determine whether Northern Mealy Amazons selected nest-sites based on cavity characteristics, we used Mann–Whitney U test to compare characteristics of cavities used as nests by parrots with those of all available cavities (entrance diameter ≥7.0 cm) recorded in survey plots.

Finally, we applied multiple logistic regression to determine whether cavity characteristics predicted use of a cavity as a nest-site by Northern Mealy Amazons (nest = 1, available cavity = 0). As cavity entrance diameter would limit access by parrots and potential predators, we considered the smallest entrance dimension (length or width) for multiple logistic regression, although in 95% of cases, the smallest diameter was entrance width. Support diameter was strongly correlated with internal cavity diameter ($r = 0.82$, $p < 0.001$); therefore, we excluded the variable of support diameter from the initial logistic regression model. We used the Wald statistic (Quinn & Keough, 2002) to determine which variable (tree dbh, cavity height, smallest entrance diameter, cavity depth, and internal cavity diameter) predicted selection of a cavity as a nest-site by the Northern Mealy Amazon. We also evaluated the odds ratio and the inflection point of the probability curve for significant variables to determine the value above which there is a greater than 50% probability that a cavity would be selected as a nest-site by parrots. Descriptive statistics are presented as mean values with standard deviation, and we considered a value of $p = .05$ as significantly different for statistical analyses.

Results

Nest-Site Characteristics

The 40 Northern Mealy Amazon nest-trees comprised 13 tree species (Figure 1), although parrots exhibited a narrow 0.39 niche-breadth of tree species used for nesting with over half of all Northern Mealy Amazon nest-sites occurring in live trees of *T. amazonia* (32.5%; $n = 13$ nest-trees), and *D. guianense* (20%; $n = 8$ nest-trees). The majority of nest-sites occurred in cavities in live trees (75%; $n = 30$), located either on the main trunk or secondary branch (50%; $n = 20$ in both cases), and all were formed by decay processes. Overall, Northern Mealy Amazon nest-sites occurred in large trees with mean 101.1 ± 28.6 cm dbh (range 50–184 cm), in cavities located 18 ± 5.1 m above the ground (range 8.1–29.5 m), with a wide 23.5 ± 12.7 cm entrance diameter (range 8–73 cm), and large 45.5 ± 17.6 cm internal diameter (range 14–81 cm), that were on average about a meter deep (mean 93 ± 65.1 cm; range 5–280 cm; Table 1).

Tree-Cavity Availability

We recorded a total of 57 cavities in 24 ha of tropical moist forest; however, two cavities had entrance diameters <7 cm and therefore were not available for use by parrots. Of the 55 available cavities, 30 were located in primary evergreen forest, 15 in primary riparian forest, and 10 in secondary forest. The majority of available cavities were formed by decay (85.5%; $n = 47$) and occurred in live trees (78.2%; $n = 43$), with most cavities located on the main trunk (77.8%; $n = 35$).

There was an overall density of 2.3 cavities/ha available for use by Northern Mealy Amazons in tropical moist forest, but number of available cavities per survey plot differed significantly among vegetation types (Table 2). In particular, survey plots in primary evergreen forest had significantly more cavities than survey plots in secondary forest ($q = 2.8$, $p < .01$). Furthermore, cavities

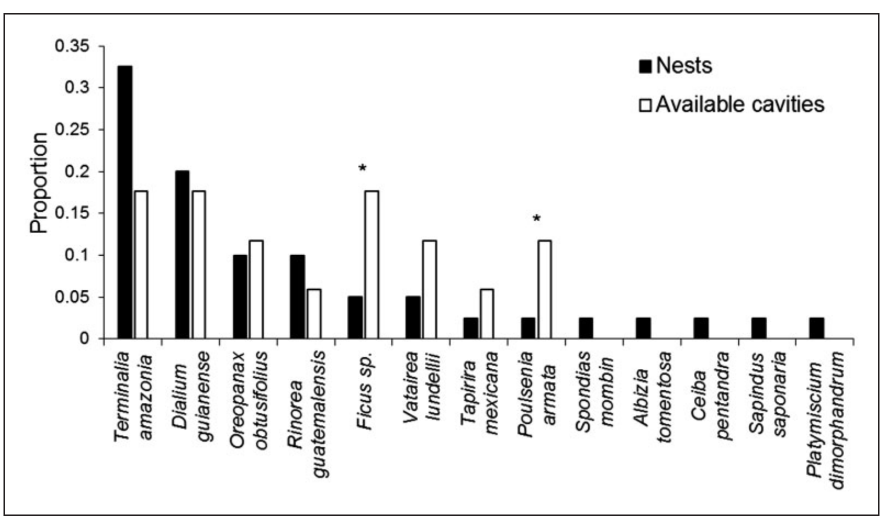

Figure 1. Proportion of tree species used as nests by the Northern Mealy Amazon (Amazona guatemalae), and available cavities (entrance ≥7 cm) in each tree species in the tropical moist forest of Los Chimalapas, Oaxaca. *Expected proportion based on availability falls outside the confidence intervals for observed use of each tree species.

Table 1. Characteristics (mean ± SD) of tree-cavities used as nests by the Northern Mealy Amazon (*Amazona guatemalae*) and all available cavities (≥7.0 cm entrance diameter) in tropical moist forest of Los Chimalapas, Mexico, with Mann-Whitney U test of significance.

Variable	Nest cavities ($n = 40$)	Available cavities ($n = 55$)	Significance values
Tree diameter at breast height (cm)	101.1 ± 28.6	64.9 ± 29.3	$U(40, 52) = 415.5$, $p < .001$*
Cavity height above the ground (m)	18.0 ± 5.1	12.4 ± 5.0	$U(40, 55) = 458.0$, $p < .001$*
Entrance width (cm)	23.5 ± 12.7	17.4 ± 6.9	$U(39, 51) = 689.0$, $p = .013$
Entrance length (cm)	42.1 ± 20.2	29.8 ± 17.9	$U(35, 51) = 545.5$, $p = .001$*
Cavity depth (cm)	93 ± 65.1	22.7 ± 14.9	$U(40, 45) = 278.0$, $p < .001$*
Internal diameter (cm)	45.5 ± 17.6	19.3 ± 8.1	$U(40, 45) = 137.0$, $p < .001$*
Support diameter (cm)	70.6 ± 26.6	38.2 ± 17.5	$U(40, 51) = 285.5$, $p < .001$*

*Significant after Bonferroni adjustment to $p = .007$.

Table 2. Mean (± SD) characteristics of cavities available for the Northern Mealy Amazon (≥7 cm entrance diameter) in three forest types at Los Chimalapas, Mexico, with parametric (one-way ANOVA) and non-parametric (Kruskal-Wallis ANOVA) test of significance. Letters indicate significantly different post hoc pairwise comparisons among forest types.

Variables	Evergreen ($n = 30$)	Riparian ($n = 15$)	Secondary ($n = 10$)	Significance values
Cavities/1-ha survey plot	3.3 ± 1.1^{a}	$2.1 \pm 1.8^{a,b}$	1.3 ± 1.0^{b}	$H(2, 24) = 8.2$, $p = .016$
Tree diameter at breast height (cm)	66.3 ± 30.2^{a}	76.8 ± 26.4^{a}	40.6 ± 15.3^{b}	$F(2, 49) = 5.1$, $p = .01$
Cavity height above the ground (m)	12.3 ± 6.0	14.2 ± 3.1	10.4 ± 3.3	$F(2, 52) = 1.8$, $p = .18$
Entrance length (cm)	$29.7 \pm 14.7^{a,b}$	38.5 ± 26.6^{a}	20.4 ± 10.7^{b}	$H(2, 51) = 6.0$, $p = .049$
Entrance width (cm)	17.5 ± 5.3	19.6 ± 10.7	14.6 ± 6.1	$F(2, 48) = 1.4$, $p = .26$
Cavity depth (cm)	22.5 ± 15.3	29.4 ± 17.2	15.8 ± 6.6	$H(2, 45) = 3.6$, $p = .17$
Internal diameter (cm)	17.5 ± 5.6	23.3 ± 12.7	19.3 ± 5.5	$F(2, 42) = 2.0$, $p = .15$
Support diameter (cm)	$37.6 \pm 16.3^{a,b}$	49.2 ± 21.4^{a}	27.8 ± 8.2^{b}	$H(2, 51) = 6.7$, $p = .035$

in secondary forest occurred in significantly smaller trees compared with cavities in primary evergreen (tree dbh: $q = 3.5$, $p < .05$) and riparian forest (tree dbh: $q = 4.5$, $p < .01$; support diameter: $q = 2.6$, $p < .01$; Table 2). Cavities in secondary forest also had smaller entrance dimensions than cavities in primary riparian forest (entrance length: $q = 2.4$, $p < .02$; Table 2).

Only 38 cavities had characteristics within the range of those used as nest-sites by Northern Mealy Amazons (height above the ground ≥8.1 m, entrance diameter ≥8 cm, internal diameter ≥14 cm, and depth ≥5 cm), giving an overall density of 1.6 cavities/ha with characteristics suitable for nesting by Northern Mealy Amazons. These suitable cavities were concentrated in primary evergreen (2.1 suitable cavities/ha) and riparian forest (1.9 suitable cavities/ha), with only 0.75 suitable cavities/ha in secondary forest.

Nest-Site Selection by Northern Mealy Amazons

Overall, the use of tree species as nest-sites by Northern Mealy Amazons did not differ significantly from that expected by the availability of accessible cavities in those tree species ($G_{12} = 15.5$, $p = .23$). Only in the case of *Ficus* sp. and *Poulsenia armata*, Northern Mealy Amazons used these tree species as nest-sites less than may be expected by their cavity availability (Figure 1). However, in both cases, the expected proportion only marginally fell outside the confidence intervals (CI) for the observed proportion of use (*Ficus* sp.: expected = 0.18, observed CI = [0, 0.15]; *P. armata*: expected = 0.12, observed CI = [0, 0.10]).

On the other hand, use and availability comparisons determined that Northern Mealy Amazons selected nest-sites based on cavity characteristics. Univariate analyses found significant differences in each cavity characteristic variable between cavities used as nests by Northern Mealy Amazons and available cavities (Table 1). Cavities used as nests by Northern Mealy Amazons occurred in significantly larger trees, at a greater height above the ground, and with larger internal diameter, and greater depth than most of the cavities available for parrots (Table 1). These variables were significantly different even after Bonferroni alpha adjustment to $p < .007$.

The multiple logistic regression model determined that cavity characteristics explained nest-site use by parrots, where cavity depth (Wald $X^2_1 = 3.9$, $p = .047$), and internal diameter (Wald $X^2_1 = 5.2$, $p = .022$) significantly predicted selection of a cavity as a nest-site by the Northern Mealy Amazon. The odds that a cavity would be selected as a nest were raised by 1.4 for each increase in internal diameter and 1.1 for each increase in cavity depth. Calculation of the inflection point for the probability curve demonstrated that a cavity had a greater than 50% chance of being selected as a nest-site if this had >29.5 cm internal diameter and was >45.9 cm deep.

Discussion

Nest-Site Requirements of the Northern Mealy Amazon

The Northern Mealy Amazon nested in a variety of tree species in Los Chimalapas, Mexico, but demonstrated a narrow niche-breadth of nesting tree species, using predominantly nest-cavities in live trees of *T. amazonia* and *D. guianense*. This is similar to the variety of 22 tree species used as nest-sites by the Northern Mealy Amazon in the Petén of Guatemala, where *T. amazonia* was also the tree species most frequently used for nesting (Bjork, 2004). Other species of Psittaciformes also use predominantly one to three tree species for nesting (Cameron, 2006; de la Parra-Martínez et al., 2015; Monterrubio-Rico, Ortega-Rodríguez, Marín-Togo, Salinas-Melgoza, & Renton, 2009; Renton & Brightsmith, 2009; Renton et al., 2015; Robinet & Salas, 1999; Symes & Perrin, 2004). However, although Northern Mealy Amazons nested most frequently in cavities in *T. amazonia* and *D. guianense*, they used these tree species for nesting according to their availability of cavities for parrots. This is similar to the Yellow-crowned Amazon (*Amazona ochrocephala*) in Panama, which uses tree species for nesting according to the availability of cavities in those trees (Rodríguez Castillo & Eberhard, 2006), but contrasts with the large Military Macaw (*Ara militaris*), which selects large emergent tree species for nesting (de la Parra-Martínez et al., 2015).

Nevertheless, Northern Mealy Amazons used cavities in *Ficus* sp. and *P. armata* slightly less than may be expected by the availability of cavities in these trees. Similarly, the Northern Mealy Amazon in Guatemala rarely used these tree species as nest-sites (Bjork 2004). Both these species are softwood trees in the Moraceae family of latex producing plants (Pennington & Sarukhan, 1998) and may have structural properties that make them less desirable as a nest-site. The Blue-fronted Parrot (*Amazona aestiva*) was more likely to reuse deep cavities with thick walls (Berkunsky & Reboreda, 2009), and cavities in large, living trees with thick walls tend to maintain more stable temperatures (Maziarz & Wesołowski, 2013; Wiebe, 2001), although microclimatic condition of cavities does not have a large effect on reproductive output (Wiebe, 2001). Nevertheless, we did not evaluate the internal condition of available cavities; therefore, there may be other microclimatic factors making cavities less suitable for use as a nest-site by the Northern Mealy Amazon.

We found that the Northern Mealy Amazon used nest-cavities in large trees of mean 1 m dbh, at a mean 18 m height above the ground, with large mean 23.5 cm entrance diameter, and mean 45.5 cm internal diameter, that were of mean 93 cm deep. Characteristics of nest-sites did not vary among primary and secondary forest or in pastures at the forest edge, as Northern Mealy Amazon nests generally occurred in remnant canopy trees characteristic of primary forest. Most Amazon parrots use nest-cavities of a lower mean height and of smaller mean entrance and internal diameters (Berkunsky & Reboreda, 2009; Enkerlin-Hoeflich, 1995; Renton & Salinas-Melgoza, 1999; Rivera, Politi, & Bucher, 2012; Rodríguez Castillo & Eberhard, 2006; Snyder et al., 1987) than that found for the Northern Mealy Amazon in our study. In fact, the mean nest-site characteristics of tree dbh, height above the ground, entrance diameter, and internal diameter place the Northern Mealy Amazon among the upper quartile of species of Psittaciformes that require large nest-cavities, located high above the ground in large, mature canopy trees (Renton et al., 2015). In particular, the large entrance and internal diameters of Northern Mealy Amazon nests were more similar to those used by large macaws and cockatoos (Berkunsky et al., 2014; Heinsohn, Murphy, & Legge, 2003; Olah, Vigo, Heinsohn, & Brightsmith, 2014; Saunders, Mawson, & Dawson, 2014). Indeed, only about 10% of studied Psittaciformes used nest-cavities with larger mean entrance and internal diameters (Renton et al., 2015). The Northern Mealy Amazon may need to use large nest-cavities to contain the brood. However, the use of nest-cavities with large entrance diameters may permit access by a greater variety of predators, increasing the risks of nest predation for the Northern Mealy Amazon.

Nest-Site Selection by the Northern Mealy Amazon

As found for other parrot species (Renton et al., 2015), the Northern Mealy Amazon selected nest-sites based on cavity dimensions. Parrots selected as nest-sites cavities in larger trees, at a greater height above the ground, and with larger entrance and internal diameters, and greater depth, from the resource of cavities available to them in the landscape. Height of the cavity entrance from the ground is an important criterion for nest-site selection for many cavity-nesting birds (Cockle et al., 2011; Li &

Martin, 1991; Nilsson, 1984) and is a key factor influencing predation rate of nests (Li & Martin, 1991; Nilsson, 1984; Wilcove, 1985). Furthermore, cavity height above the ground is a significant predictor of nest success for some parrot species (Berkunsky & Reboreda, 2009; Cockle et al., 2015). Hence, the selection of nest-cavities high above the ground by the Northern Mealy Amazon may be a strategy to reduce predation risk and increase the probability of nest success.

In particular, cavity depth and internal diameter predicted selection of a cavity as a nest-site by the Northern Mealy Amazon. Cavity depth was found to influence nest success of the Eclectus Parrot (*Eclectus roratus*), with deeper nests producing a greater number of fledglings (Heinsohn, 2008). The importance of internal diameter of the cavity as a criterion predicting nest-site selection may reflect the requirement for a large nest chamber able to accommodate the nest contents for this large-bodied parrot. The Northern Mealy Amazon is the largest Amazon parrot in continental America, only exceeded in size by two Caribbean island parrot species (Forshaw, 1989). Internal diameter of the nest-cavity was found to significantly influence hatching success of the Scarlet Macaw (*Ara macao*) in Peru, with eggs more likely to hatch in nests with larger internal diameters (Olah et al., 2014). Therefore, the selection of deep cavities with larger internal diameters may increase the probability of nest-success and reproductive output for large-bodied parrots such as the Northern Mealy Amazon.

Cavity Availability for Northern Mealy Amazons

As found for other tropical forests (Cockle, Martin, & Wesołowski, 2011; Vázquez & Renton, 2015), the majority of tree-cavities in the tropical moist forest of Los Chimalapas were formed by decay processes. We found a low overall density of 2.4 cavities/ha in the tropical moist forest of Los Chimalapas, with 2.3 cavities/ha available for Northern Mealy Amazons. Even considering just conserved evergreen and riparian forest, there were only 2.9 cavities/ha (2.8 available cavities/ha). This is much lower than cavity densities recorded in other tropical moist forests of continental America, ranging from 16.8 to 111.7 cavities/ha (Boyle et al., 2008; Saunders et al., 1982), with a density of 4.5 cavities/ha suitable for nesting by birds (Cockle et al., 2010).

Furthermore, in Los Chimalapas, only 1.6 cavities/ha had characteristics suitable for nesting by Northern Mealy Amazons. Studies of smaller bodied Amazon parrot species have found higher densities of 4.6 to 11.3 suitable cavities/ha (Rivera et al., 2012; Snyder et al., 1987). Only in the case of large-bodied macaws or cockatoos have lower densities of 0.3 to 0.7 suitable cavities/ha been recorded (de la Parra-Martínez et al., 2015; Marsden & Pilgrim, 2003; Walker, Cahill, & Marsden, 2005). This low density of tree-cavities suitable for nesting by the Northern Mealy Amazon may be a limiting factor on the number of nesting pairs, creating competition for nest-sites (Heinsohn et al., 2003; Newton, 1994). During the present study, we observed agonistic interactions among four pairs of Northern Mealy Amazons for occupancy of a suitable nest-cavity. Interspecific competition may also limit the availability of nest-cavities for the Northern Mealy Amazon as during the parrot nesting seasons of 2014 to 2016, we found potential nest-cavities occupied by other secondary cavity-nesters, including the Guatemalan Screech Owl (*Megascops guatemalae*), Bat Falcon (*Falco rufigularis*), Keel-billed Toucan (*Ramphastos sulfuratus*), and Kinkajou (*Potus flavus*).

We found the lowest density of 1.3 available cavities/ha in secondary forest, where only 0.75 cavities/ha were suitable for nesting by Northern Mealy Amazons. Other studies have also found a generally low density of 0.5 to 1.64 cavities/ha suitable for birds in disturbed or human-managed forests (Cockle et al., 2008, 2010; Politi et al., 2010). As determined in the present study, available tree-cavities in secondary forest occurred in smaller trees and had smaller dimensions than in primary forest. Therefore, the increasing transformation of primary tropical moist forest to secondary forest (de Jong et al., 2010) is likely to have consequences in reducing the availability of suitable nest-sites for large-bodied secondary cavity-nesters. Furthermore, as highlighted by Marsden and Pilgrim (2003), long-lived parrots may be able to utilize food resources in disturbed or managed forests, but the reduction in density of suitable nest-sites in modified forests puts at risk the persistence of wild populations in the long-term.

Implications for Conservation

Our study demonstrated a low density of suitable nest-sites for the Northern Mealy Amazon, which were concentrated in primary tropical moist forest. Secondary forest provided few nest-site resources for this large-bodied threatened parrot species. Furthermore, the Northern Mealy Amazon was highly selective in use of nest-sites, with suitable nest-cavities having characteristics indicative of large, old primary forest trees. Given these specific nest-site requirements of the Northern Mealy Amazon, long-term persistence of the species in Mesoamerica depends in part on maintaining the availability of suitable nest-sites through appropriate forestry practices.

The Northern Mealy Amazon depends on the maintenance of large, mature trees that can provide the large cavity dimensions required for nest-sites, most of which occur in emergent tree species of *T. amazonia* and *D. guianense*. However, these hardwood tree species are frequently cut for use in heavy construction (Pennington & Sarukhán, 1998). Incentives should be provided to maintain large trees (>1 m dbh) in agricultural landscapes as these are more susceptible to selective logging (Gibbons et al., 2008). Compensation or gratification schemes paid to local landowners who protect Northern Mealy Amazon nests on their land could also be implemented to promote the protection of active parrot nests.

Existing legislation may be employed to limit deforestation along watercourses. The 1992 National Water Law in Mexico establishes 10 m either side of watercourses as federal land, while the NOM-152-SEMARNAT-2006 regulation specifies that forestry management programs should maintain riparian vegetation 20 m either side of permanent rivers. This could provide the basis for local land-use strategies to maintain riparian forest within a 20- to 50-m band along permanent rivers thereby preserving some large, cavity-bearing trees. Riparian forests have an added contribution as corridors connecting forest patches in modified landscapes and maintaining animal movements (Gillies & St. Clair, 2008; Lees & Peres, 2008). However, given that our study determined the greatest density of available cavities in tropical moist evergreen forest, and that the most frequently used nest-tree species were characteristic of evergreen forest (Rzedowski, 2006; Torres Colín, 2004), it would still be important to implement strategies to conserve primary evergreen forest to provide adequate nest-sites for large-bodied, threatened secondary cavity-nesters.

Strategies such as conservation set-aside schemes could be implemented in Los Chimalapas and focused on conserving extensive areas of primary evergreen forest. Old growth forests provide a greater number of hollow-bearing trees, with older trees able to form larger cavities (Lindenmayer, Cunningham, Nix, Tanton, & Smith, 1991). Large mature trees are a key resource in forest ecosystems but are rapidly being lost worldwide (Gibbons et al., 2008; Lindenmayer, Laurance, & Franklin, 2012). Therefore, the implementation of a suite of strategies to promote the maintenance of large, mature trees would not only be of benefit for reproduction of the Northern Mealy Amazon but would also contribute to maintaining biodiversity and ecosystem integrity.

Acknowledgments

The study was conducted in partial fulfillment of a PhD degree by MADLH at the Posgrado en Ciencias Biologicas, of the Universidad Nacional Autónoma de México (UNAM). The authors are grateful to Idea Wild who provided field equipment and to Alvaro Campos who assisted with taxonomic identification of tree species. The Secretaria del Medio Ambiente y Recursos Naturales in Mexico provided research permits for the study. The authors are grateful to the authorities of the Santa María Chimalapa municipality for permission to work on their community lands and to the local people of San Francisco La Paz, La Fortaleza, San Antonio Nuevo Paraíso, and Chalchijapa who provided assistance in the field.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This work was supported by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (UNAM-DGAPA-PAPIIT grant IN205716) to KR. MADLH received a Doctoral studies grant from the Consejo Nacional de Ciencia y Tecnología (Conacyt 215549).

References

Aitken, K. E. H., & Martin, K. (2007). The importance of excavators in hole-nesting communities: Availability and use of natural tree-holes in old mixed-forest of western Canada. *Journal of Ornithology*, *148*, S425–S434.

Berkunsky, I., Daniele, G., Kacoliris, F. P., Díaz-Luque, J. A., Silva Frias, C. P., Aramburu, R. M., ... Gilardi, J. D. (2014). Reproductive parameters in the critically endangered Blue-throated Macaw: Limits to the recovery of a parrot under intensive management. *PLoS ONE*, *9*(6): e99941. doi:10.1371/journal.pone.0099941.

Berkunsky, I., & Reboreda, 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.

BirdLife International. (2016). *Species factsheet*: *Amazona guatemalae*. Retrieved from http://www.birdlife.org/datazone/species/factsheet/45430583

Bjork, R. (2004). *Delineating pattern and process in tropical lowlands: Mealy Parrot migration dynamics as a guide for regional conservation planning* (PhD thesis), Oregon State University, Corvallis, OR. Retrieved from http://ir.library.oregonstate.edu/xmlui/handle/1957/10842

Brightsmith, D., & Bravo, A. (2006). Ecology and management of nesting blue-and-yellow macaws (*Ara ararauna*) in *Mauritia* palm swamps. *Biodiversity and Conservation*, *15*, 4271–4287.

Boyle, W. A., Ganong, C. N., Clark, D. B., & Hast, M. A. (2008). Density, distribution, and attributes of tree cavities in old-growth tropical rain forest. *Biotropica*, *40*, 241–245.

Byers, C. R., Steinhorst, R. K., & Krausman, P. R. (1984). Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management*, *48*, 1050–1053.

Cameron, M. (2006). Nesting habitat of the Glossy Black-Cockatoo in central New South Wales. *Biological Conservation*, *127*, 402–410.

Cockle, K.L., Bodrati, A., Lammertink, M., & Martin, K. (2015). Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic forest. *Biological Conservation*, *184*, 193–200.

Cockle, K. L., Martin, K., & Drever, M. C. (2010). Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biological Conservation*, *143*, 2851–2857.

Cockle, K. L., Martin, K., & Wesołowski, T. (2011). Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Frontiers in Ecology and Environment*, *9*, 377–382.

Cockle, K., Martin, K., & Wiebe, K. (2008). Availability of cavities for nesting birds in the Atlantic forest, Argentina. *Ornitologia Neotropical*, *19*, 269–278.

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

Colwell, R. K., & Futuyma, D. J. (1971). On the measurement of niche breadth and overlap. *Ecology*, *52*, 567–576.

de Jong, B., Anaya, C., Masera, O., Olguín, M., Paz, F., Etchevers, J., . . . Balbontín, C. (2010). Greenhouse gas emissions between 1993 and 2002 from land-use change and forestry in Mexico. *Forest Ecology and Management*, *260*, 1689–1701.

de la Parra-Martínez, S. M., Renton, K., Salinas-Melgoza, A., & Muñoz-Lacy, L. G. (2015). Tree-cavity availability and selection by a large-bodied secondary cavity-nester: The Military Macaw. *Journal of Ornithology*, *156*, 489–498. doi:10.1007/s10336-014-1150-9.

Enkerlin-Hoeflich, E. C. (1995). *Comparative ecology and reproductive biology of three species of Amazona parrots in northeastern Mexico* (PhD Thesis), Texas A&M University, College Station, TX.

Forshaw, J. M. (1989). *Parrots of the world* 3rd ed. Melbourne, Australia: Lansdowne Editions.

Gibbons, P., Lindenmayer, D. B., Fischer, J., Manning, A. D., Weinberg, A., Seddon, J., . . . Barrett, G. (2008). The future of scattered trees in agricultural landscapes. *Conservation Biology*, *22*, 1309–1319.

Gillies, C., & St. Clair, C. C. (2008). Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Science USA*, *105*, 19774–19779.

Heinsohn, R. (2008). The ecological basis of unusual sex roles in reverse-dichromatic Eclectus Parrots. *Animal Behaviour*, *76*, 97–103.

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.

Houle, A., Chapman, C. A., & Vickery, W. L. (2004). Tree climbing strategies for primate ecological studies. *International Journal of Primatology*, *25*, 237–260.

Lees, A. C., & Peres, C. A. (2008). Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation Biology*, *22*, 439–449.

Levins, R. (1968). *Evolution in changing environments*. Princeton, NJ: Princeton University Press.

Li, P., & Martin, T. E. (1991). Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. *Auk*, *108*, 405–418.

Lindenmayer, D. B., Cunningham, R. B., Nix, H. A., Tanton, M. T., & Smith, A. P. (1991). Predicting the abundance of hollow-bearing trees in montane forests of southeastern Australia. *Australian Journal of Ecology*, *16*, 91–98.

Lindenmayer, D. B., Laurance, W. F., & Franklin, J. F. (2012). Global decline in large old trees. *Science*, *338*, 1305–1306.

Marsden, S. J., & Pilgrim, J. D. (2003). Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests on New Britain. *Ibis*, *145*, 45–53.

Martínez-Pacheco, A. I. (2012). Monitoreo del cambio de uso de suelo en Los Chimalapas 2000–2003 [Monitoring land-use change in Los Chimalapas 2000–2003]. In D. Ortega del Valle, T. Carranza López, & J. Martínez Pérez (Eds.). *Una mirada desde el corazón de la jícara de oro. Experiencias de conservación en la Selva Zoque de Los Chimalapas* [A look from the heart of the golden gourd. Conservation experiences in the Zoque forest of Los Chimalapas] (pp. 86–94). Oaxaca, Mexico: WWF-Mexico.

Maziarz, M., & Wesołowski, T. (2013). Microclimate of tree cavities used by Great Tits (*Parus major*) in a primeval forest. *Avian Biology Research*, *6*, 47–56.

Monterrubio-Rico, T. C., & Escalante-Pliego, P. (2006). Richness, distribution and conservation of cavity nesting birds in Mexico. *Biological Conservation*, *128*, 67–78.

Monterrubio-Rico, T. C., Ortega-Rodríguez, J., Marín-Togo, M. C., Salinas-Melgoza, A., & Renton, K. (2009). Nesting habitat of the Lilac-crowned Parrot in a modified landscape in Mexico. *Biotropica*, *41*, 361–368.

Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation*, *70*, 265–276.

Nilsson, S. G. (1984). The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. *Ornis Scandinavica*, *15*, 167–175.

Nue, A. W., Byers, C. R., & Peek, J. M. (1974). A technique for analysis of utilization-availability data. *Journal of Wildlife Management*, *38*, 541–545.

Olah, G., Butchart, S. H. M., Symes, A., Medina Guzmán, I., Cunningham, R., Brightsmith, D. J., . . . Heinsohn, R. (2016). Ecological and socio-economic factors affecting extinction risk in parrots. *Biodiversity and Conservation*, *25*, 205–223.

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. *Journal for Nature Conservation*, *22*, 176–185.

Pennington, T. D., & Sarukhán, J. (1998). *Árboles tropicales de México* [Tropical trees of Mexico] 2nd ed. Mexico City, Mexico: Fondo de Cultura Económica.

Perry, D. R., & Williams, J. (1981). The tropical rain forest canopy: A method providing total access. *Biotropica*, *13*, 283–285.

Politi, N., Hunter, M. Jr., & Rivera, L. (2009). Nest selection by cavity-nesting birds in subtropical montane forests of the Andes: Implications for sustainable forest management. *Biotropica*, *41*, 354–360.

Politi, N., Hunter, M. Jr., & Rivera, L. (2010). Availability of cavities for avian cavity nester in selectively logged subtropical montane forest of the Andes. *Forest Ecology and Management*, *260*, 893–906.

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge, England: Cambridge University Press.

Renton, K., & Brightsmith, D. J. (2009). Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru. *Journal of Field Ornithology*, *80*, 1–8.

Renton, K., & Salinas-Melgoza, A. (1999). Nesting behavior of the Lilac-crowned Parrot. *Wilson Bulletin*, *111*, 488–493.

Renton, K., Salinas-Melgoza, A., De Labra-Hernández, M. A., & de la Parra-Martínez, S. M. (2015). Resource requirements of parrots: Nest site selectivity and dietary plasticity of Psittaciformes. *Journal of Ornithology*, *156*, S73–S90. doi:10.1007/s10336-015-1255-9.

Rivera, L., Politi, N., & Bucher, E. H. (2012). Nesting habitat of the Tucuman Parrot *Amazona tucumana* in an old-growth cloud-forest of Argentina. *Bird Conservation International*, *22*, 398–410.

Robinet, O., & Salas, M. (1999). Reproductive biology of the endangered Ouvea Parakeet *Eunymphicus cornutus uvaeensis*. *Ibis*, *141*, 660–669.

Rodríguez Castillo, A. M., & Eberhard, J. R. (2006). Reproductive behavior of the Yellow-crowned Parrot (*Amazona ochrocephala*) in western Panama. *Wilson Journal of Ornithology*, *118*, 225–236.

Rzedowski, J. (2006). *Vegetación de México* [Vegetation of Mexico]. Mexico City, Mexico: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Retrieved from http://www.biodiversidad.gob.mx/publicaciones/librosDig/pdf/VegetacionMx_Cont.pdf

Saunders, D. A., Mawson, P. R., & 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. *Biological Conservation*, *177*, 185–193.

Saunders, D. A., Smith, G. T., & Rowley, I. (1982). The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. *Australian Wildlife Research*, *9*, 541–556.

Snyder, N. F. R., Wiley, J. W., & Kepler, C. B. (1987). *The parrots of Luquillo: Natural history and conservation of the Puerto Rican Parrot*. Los Angeles, CA: Western Foundation of Vertebrate Zoology.

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.

Symes, T. A., & Perrin, M. R. (2004). Breeding biology of the Greyheaded Parrot (*Poicephalus fuscicollis suahelicus*) in the wild. *Emu*, *104*, 45–57.

Torres Colín, R. (2004). Tipos de vegetación [Vegetation types]. In A. J. García-Mendoza, M. J., Ordoñez, & M. Briones-Salas (Eds.). *Biodiversidad de Oaxaca* [Biodiversity of Oaxaca] (pp. 105–117). Mexico City, Mexico: Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-Mexico.

Trejo, I. (2004). Clima [Climate]. In A. J. García-Mendoza, M. J., Ordoñez, & M. Briones-Salas (Eds.). *Biodiversidad de Oaxaca* [Biodiversity of Oaxaca] (pp. 67–85). Mexico City, Mexico: Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-Mexico.

Vázquez, L. D., & Renton, K. (2015). High density of tree-cavities and snags in tropical dry forest of western Mexico raises questions for a latitudinal gradient. *PLoS ONE*, *10*, e0116745. doi:10.1371/journal.pone.0116745.

Walker, J. S., Cahill, A. J., & Marsden, S. J. (2005). Factors influencing nest-site occupancy and low reproductive output in the critically endangered Yellow-crested Cockatoo *Cacatua sulphurea* on Sumba, Indonesia. *Bird Conservation International*, *15*, 347–359.

Wenner, T. J., Russello, M. A., & Wright, T. F. (2012). Cryptic species in a Neotropical parrot: genetic variation within the *Amazona farinosa* species complex and its conservation implications. *Conservation Genetics*, *13*, 1427–1432.

Wiebe, K. L. (2001). Microclimate of tree cavity nests: Is it important for reproductive success in Northern Flickers? *Auk*, *118*, 412–421.

Wilcove, D. S. (1985). Nest predation in forest tracts and the decline of migratory songbirds. *Ecology*, *66*, 1211–1214.

Zar, J. H. (1999). *Biostatistical analysis* 4th ed. Upper Saddle River, NJ: Prentice Hall Inc.