

Effect of forest logging on food availability, suitable nesting habitat, nest density and spatial pattern of a Neotropical parrot

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ABSTRACT

Secondary cavity nesters, bird species that rely on the presence of existing cavities, are highly vulnerable to anthropogenic and stochastic processes that reduce the availability of cavity bearing trees. The most common logging practice in Neotropical forests is selective logging, where a few valuable tree species are logged, primarily old, large trees that are the most prone to develop cavities and produce larger amounts of fruits and seeds. Tucuman Amazon, *Amazona tucumana*, is a threatened parrot that relies on the tree-cavities and food provided by large, old trees. Our objective was to evaluate how logging affects 1) stand and nest plot forest structure, 2) nesting site selection, 3) food availability, 4) density of suitable cavities, 5) nest density, and 6) nest spatial pattern of Tucuman Amazon by comparing a mature undisturbed forest in a National Park (NP) vs a logged forest (LF). We determined the availability of suitable cavities and food resources consumed by Tucuman Amazon, and we compared nest density and spatial pattern of nests between NP vs LF. The Index of food availability for all tree species consumed by Tucuman Amazon and for *P. parlatoresi* were significantly higher in NP than in LF ($34.5 \pm 13.3 \text{ m ha}^{-1}$ vs. $3.5 \pm 1.0 \text{ m ha}^{-1}$ and $5.6 \pm 2.3 \text{ m ha}^{-1}$ vs. $1.2 \pm 1.0 \text{ m ha}^{-1}$, respectively). Density of suitable cavities for nesting in the NP was significantly higher than in the LF: $4.6 \text{ cavities ha}^{-1}$ [C.I. 95 %: $3.07 - 7.04 \text{ cavities ha}^{-1}$] vs. $1.1 \text{ cavities ha}^{-1}$ [C.I. 95 %: $0.73 - 1.66 \text{ cavities ha}^{-1}$], respectively. Mean density of Tucuman Amazon nests was significantly higher in the NP than in LF (0.25 ± 0.04 vs. $0.06 \pm 0.04 \text{ nest ha}^{-1}$, respectively). Food availability is an important factor that affects Tucuman Amazon populations and when food is not limiting, the availability of suitable cavities and territorial behavior could play a role in regulating nest density. When evaluating the limiting factors for secondary cavity-nesting species of conservation concern it is important to evaluate the interplay of a set of potential limiting factors to propose sound forest management recommendations.

1. Introduction

Unsustainable use of resources puts unprecedented pressure on natural environments, threatening species' populations and changing natural habitats (Newbold et al., 2016; Venter et al., 2016). At a global scale, at least 400 million hectares of tropical and subtropical forests worldwide (53%) are under timber management (Blaser et al., 2011; Martin et al., 2015). Logged tropical forests are now more widespread than intact primary forests across most of the tropics (Laurance et al., 2014). Within this context, effective conservation and management of threatened species for maintaining or increasing their population

numbers in managed landscapes requires understanding which factors or specific habitat elements limit breeding density or productivity (Catry et al., 2013; Martin and Fuller, 2015). Selective logging, in which a few valuable tree species are logged, is the most common practice in Neotropical forests (Fimbel et al., 2001; FAO, 2020). Selective logging removes old large trees, the very individuals most prone to develop cavities (Cornelius, 2008; Politi et al., 2009; Cockle et al., 2010) and those that produce the largest amount of fruit and seeds that are used as food source by animals (Burivalova et al., 2015; Rivera et al., 2019).

Secondary cavity nesters, those bird species that rely on the presence of existing cavities generated by other species (woodpeckers) or natural

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processes (wood decay by fungi), are highly vulnerable to anthropogenic and stochastic processes that reduce the availability of cavity bearing trees (Newton, 1994; Cornelius et al., 2008; Politi et al., 2009; Cockle et al., 2010). Many studies conducted in mature or unmanaged forest suggest that breeding populations of cavity-nesting birds are not limited by availability of nest sites (Brightsmith, 2005; Wesolowski, 2007; Zheng et al., 2009; Wiebe, 2011; Rivera et al., 2012; Altamirano, 2014; Ibarra et al., 2020). However, other studies suggest that for some cavity nesting birds, even in cavity-rich forests, the most important limiting factor is availability of suitable cavities for nesting (cavities with specific characteristics or quality) rather than overall cavity abundance (Cockle et al., 2010; Aitken and Martin, 2012; Robles et al., 2012; de la Parra-Martínez et al., 2015). Unoccupied cavities in cavity-rich forests may not always indicate a surplus of nest-sites for cavity-nesting birds, since these unoccupied cavities may be of low quality, completely unsuitable or unavailable within the territory of a competitor (Newton, 1998). In some secondary cavity-nesting bird species, nesting pairs can limit the use of clustered cavities (i.e., a high concentration of suitable cavities in forest patches) by defending an area around the nest from other pairs influencing spacing of conspecific and nest density (Wiley, 1985; Salinas-Melgoza et al., 2009). When suitable nest sites are not the limiting factor for secondary cavity nesters, populations can be limited by food availability (Newton, 2003; Catry et al., 2013; Martin and Fuller, 2015; Stojanovic et al., 2016). For example, availability of food may determine the carrying capacity of breeding pair density when nest sites are in ample supply (Brawn and Balda, 1988; Webb et al., 2017). Food shortage can also have an effect on spacing behavior producing a regular dispersion pattern within the area occupied (Newton, 2002, 1992).

Parrot species are mainly secondary cavity nesters that nests in large living trees of the forest canopy (Marsden and Jones, 1997; Renton and Salinas-Melgoza, 1999). In many forest settings these large trees are also the most valuable for logging (Fimbel et al., 2001; Stojanovic et al., 2014; Lindenmayer and Laurance, 2017; Politi and Rivera, 2019). Logging has affected many populations of parrot species in different continents (Martin et al., 2014; Olah et al., 2016; Berkunsky et al., 2017; Webb et al., 2019). After agriculture and pet trade, logging affected 105 (55%) of the populations of Neotropical parrots (Berkunsky et al., 2017). Some parrot species strongly select nest cavities for particular morphological traits (Stojanovic et al., 2012; de la Parra-Martínez et al., 2015). This behavior makes them especially sensitive to selective logging (Monterrubio-Rico et al., 2009) by limiting their breeding density in some areas (Beissinger and Bucher, 1992; Newton, 1994). Forest dependent parrot species are also likely to be threatened by lack of sufficient food availability (Olah et al., 2016).

Tucuman Amazon *Amazona tucumana* is an endemic, threatened, secondary cavity nesting and forest dependent parrot species. Tucuman Amazon breeds in tree cavities and relies on seeds of *Podocarpus parlatorei* trees for feeding its nestlings during the breeding season (Pidgeon et al., 2015; Rivera et al., 2019). The species is categorized as globally Vulnerable (IUCN, 2021) and occurs only in Andean montane forests of northwestern Argentina and southern Bolivia, known as Southern Yungas (Fjeldså and Krabbe, 1990). Tucuman Amazon breeds in the cloud forest of the Southern Yungas (1500–2200 m a.s.l.) between December and February (Rivera et al., 2014). The Southern Yungas harbors 20 economically valuable tree species, and has been under extensive selective unsustainable logging (Politi et al., 2010; Politi and Rivera, 2019). Due to its specialized requirements for nesting and feeding relying on large trees, Tucuman Amazon can be used to evaluate simultaneously the effects of selective logging over suitable tree cavity and food resource availability for their influence on nest density. Previous studies that evaluated limiting factors on populations of Neotropical parrots analyzed them separately; either tree cavities or food resources (see Renton et al., 2015 for a detailed accounting on nesting and diet studies on parrots).

In this work our objectives were to evaluate how logging affects 1) stand and nest plot forest structure, 2) nesting site selection, 3) food

availability, 4) density of suitable cavities, 5) nest density, and 6) nest spatial pattern of Tucuman Amazon. Logging has noticeable effects on forest stand structure so we expect to find lower values for forest structure variables in logged than unlogged stands. Tucuman Amazon is a habitat specialized species so we expect a pattern of selection of trees bearing-cavities and nest-cavity characteristics that will be consistent in both type of forests. We also expect that logging will decrease the density of suitable cavities and the availability of food for Tucuman Amazon since there will be decrease in the density of large trees. Changes in availability of suitable cavities and food resources due to logging will influence nest density so we expect a lower density in logged than in unlogged stands. Nest spatial pattern can be influenced by nesting pair territorial behavior so we expect that the pattern hold despite the influence of logging on nest density. If the pattern of simultaneous active nests is dispersed and the pattern of all nest-bearing trees is aggregated we can infer an influence of behavior on the spatial pattern.

2. Material and methods

2.1. Study area

The Southern Yungas in northwestern Argentina is the southernmost neotropical forest that supports a semi-evergreen subtropical montane cloud forest (Cabrera, 1976). The cloud forest where Tucuman Amazon reproduces (Rivera, 2011) is dominated by *Podocarpus parlatorei*, *Alnus acuminata* and trees of the Myrtaceae family. This study was conducted in the central sector of the Southern Yungas; i.e., the Sierras Subandinas Centrales or Sistema de Santa Bárbara – a mountain range ~100 km long, between the Cordillera Oriental to the west and the Chaco plain to the east (Cabrera, 1976). The local climate has a marked dry season from May to October and a rainy season from November to April. Annual rainfall is 800–1500 mm and mean annual temperature is 11.7 °C (Mendoza, 2005). Within the central sector of the Southern Yungas, we focused on two areas at an elevation between 1450 and 2100 m above sea level: (1) El Rey National Park (hereafter NP) and, (2) a Logged Forest (hereafter LF). The NP (24° 43S, 64° 38W), is located in Salta Province, was established in 1948, and covers an area of 44,000 ha. We chose the NP as our reference site since it includes some of the last undisturbed mature cloud forest of the Southern Yungas (Rivera et al., 2012). The study area in NP was 45 ha of cloud forest with a richness of 12 tree species, accessible only by walking 12 km. The LF (24° 05S, 64° 26W) is a privately owned property of 1,000 ha. The study area in LF was 170 ha of cloud forest with a richness of 14 tree species, selectively logged during the second half of the 20th century, accessible by horse-riding or walking 8 km. The LF was under typical forest practices of the region; i.e., a polycyclic reentry, with each stand logged at least every 20–30 years (del Castillo et al., 2005). The logging process begins by removing valuable timber and progressively shifting toward less valuable species (del Castillo et al., 2005). Logging operations in the LF did not have a Forest Management Plan to guide forest practices, so decisions about logging were made *in situ* by people with no technical training in silviculture. In cloud forests, loggers select primarily three tree species (*Cedrela lilloi*, *Podocarpus parlatorei* and *Juglans australis*) and legal minimum cut diameters are 40 cm DBH (Politi et al., 2021).

2.2. Data collection

2.2.1. Stand and nest plot forest structure

To characterize the reproductive habitat of Tucuman Amazon, we randomly placed 20 circular plots of 0.05 ha (12 m radius) at LF and 20 circular plots of 0.05 ha at NP. Plots were at least 150 m apart. Within each plot, we identified, counted, and measured the height and the diameter at breast height (DBH) of all trees > 10 cm DBH. To characterize habitat of Tucuman Amazon that surrounded nest-trees, we established 0.05 ha circular plots with the nest-trees as center, measuring the same variables as in random plots, with the exception of

tree height.

2.2.2. Nesting sites selection

We carried out daily nest searches during Tucuman Amazon's reproductive season, which is from December to February, between the years 2004 and 2009 in LF and between the years 2005 and 2009 in NP. We found nests by following males to the nest area and locating the cavity when the female left the nest to be fed by the male (Rivera et al., 2014). For most nests (those < 15 m above the ground) we confirmed an active status by using a mini-camera system attached to an extendable pole, known as a tree-peeper (Richardson et al., 1999). Nests > 15 m above the ground were visually inspected using climbing equipment to reach the nest. After each nest was no longer occupied we measured nest-cavity characteristics, and recorded: 1) height from the ground to the cavity entrance; 2) size of cavity entrance (height and width); 3) internal diameter at the cavity floor; 4) internal cavity depth from cavity entrance to the floor; 5) trunk or branch diameter at cavity entrance; 6) tree diameter at the cavity floor; 7) tree diameter at breast height (DBH); 8) tree height; 9) tree species; 10) cavity origin (excavated or decayed); 11) cavity location (tree trunk or primary branch); 12) tree condition (alive or dead); and 13) tree coordinate (latitude and longitude).

2.2.3. Food availability

We determined diet of Tucuman Amazon by direct observation of feeding activity in both areas from the year 2005 to 2009 (Rivera, 2011; Rivera et al., 2019). On each of the two study sites, we established 10 6x100-m phenology plots to determine resource availability (Chapman et al., 1994; Renton, 2001). Within each plot, we marked and identified tree species of > 10 cm DBH. We monitored all marked trees monthly from December to February from the year 2006 to 2009 in NP and from the year 2005 to 2009 in LF. Using binoculars we recorded presence of flowers and/or fruits or seeds to determine variation in resource availability (Renton, 2001; Rivera et al., 2019).

2.2.4. Density of suitable cavities

To assess availability of suitable cavities for Tucuman Amazon, we conducted cavity sampling during the non-breeding season (April–August 2007 and 2008) when many trees are leafless. We used distance sampling methodology to estimate the density of suitable cavities due to their low density and dispersed distribution. Distance sampling allowed us to cover a large area and model cavity detectability (Politi, 2008). In each site we performed 20 variable-width, random location, 300-m long transects that were at least 150 m apart and non-overlapping. We measured the perpendicular distance from the central line of the transect to each detected cavity. We inspected each potential usable cavity with the tree-peeper and measured the same characteristics as for used nests (see above). We only considered a cavity to be suitable if it had a hollow chamber surrounded by sound, not collapsing, wood, could be accessed by an entrance hole, and had a floor to support an incubation chamber and a roof to provide overhead protection. Suitable cavities had a minimum diameter entrance of 5 cm, an internal diameter of at least 15 cm (minimum cavity dimensions suggested for *Amazona* species of similar body size to Tucuman Amazon; Snyder et al., 1987; Enkerlin-Hoeflich, 1995), a minimum cavity height from the ground of 2 m, cavity depth from 0 to 200 cm, and a tree DBH of 0.30 m (minimum dimensions observed for Tucuman Amazon in the two first years of the study). By measuring the characteristics of cavities we avoided bias associated with under- or overestimating suitable cavity availability as suggested in other studies (Cockle et al., 2010; Stojanovic et al., 2012).

2.3. Data analysis

2.3.1. Stand and nest plot forest structure

We used Mann-Whitney *U* test for paired variables to compare between average DBH, tree basal area, density of all trees > 10 cm DBH,

density of tree species used as nesting or food resources > 40 cm DBH at random plots and at nest-tree plots in NP vs. LF, and between random plots and nest-tree plots within NP and within LF. We conducted data analyses in Infostat (Di Rienzo et al., 2012). We reported values as mean \pm standard deviation.

2.3.2. Nesting site selection

We fitted a MANOVA that allows more than one observed variable to be analyzed at once, to compare traits of nest-bearing trees and nest-cavities between LF and NP (Dytham, 2011). We used Generalized Linear Models to explore the importance of tree species, characteristics of the nest-bearing tree (DBH and tree height), and nest-cavity (nest height, internal diameter, nest depth, entrance width and entrance height) in the selection of nest sites by Tucuman Amazon. We included in the models those tree species with 10 or more nests or suitable cavities. We used binomial models with use/non-use as the response variable and fitted separated models for LF and NP. We maintained separated the two sites because we were interested in understanding the variables selected by Tucuman Amazon when the site underwent logging and its implications for forest management. We tested for correlations of paired variables and discarded one of them in case they were highly correlated (correlation coefficient > 0.70). We retained all variables in NP and only discarded DBH that was highly correlated with tree height in LF. These analyses were performed in R version 4.0.1 (R Development Core Team, 2020).

2.3.3. Food availability

We considered DBH of trees as an index of fruit or flower production following Chapman et al. (1992) who determined that for tropical forests DBH is a consistent exact estimator that shows low levels of variation between observers. To obtain an index of total food availability for each month of the reproductive season (December to February) in the study sites, we summed DBH of trees with food resources present (seeds or fruits) in 1 ha, (Renton, 2001) in each month (Rivera et al., 2019). To calculate the index of total food availability we only included those species known to provide food resources consumed by Tucuman Amazon (Rivera, 2011). Additionally, we estimated a monthly index of *Podocarpus parlatorei* availability for the reproductive season, because this tree species' seeds are a key food resource for Tucuman Amazon during the breeding season (Pidgeon et al., 2015; Rivera et al., 2019). This monthly index is obtained by summing the DBH of all the *Podocarpus parlatorei* trees with fruits each month. We obtained the mean index of *Podocarpus parlatorei* availability by averaging the monthly index for the breeding seasons 2006–2009. We compared between NP and LF the mean index of total food availability, as well as the mean index of *Podocarpus parlatorei* availability. All values are expressed as mean \pm standard deviation (SD) unless otherwise specified. We set the significance level of statistical tests at $P < 0.05$.

2.3.4. Suitable cavity density

We used distance sampling (Buckland et al., 2001; Thomas et al., 2006) to estimate suitable cavity density using detection probabilities that we estimated from distance-to-cavity data. We first built box plots of perpendicular distances to identify outliers visually. Then we discarded outliers from the data set after thoroughly evaluating the data to ensure that they were extreme values, since no fixed width was established (Buckland et al., 2001). We then constructed histograms to evaluate concentration of records and made grouping of the data in distance bands when necessary. We fitted detection functions using models combining density function (Uniform, Half-normal, and Hazard-rate) with cosines, simple, and hermit-polynomials expansions. We selected functions that fitted the data well and had the lowest Akaike's Information Criterion (Burnham and Anderson, 2002). We assessed the adequacy of the selected model using a Kolmogorov–Smirnov test (Buckland et al., 2001).

2.3.5. Nest density

We determined the average nest density by calculating the mean number of nests found in 45 ha in NP during four breeding seasons and in 170 ha in LF during five breeding seasons.

2.3.6. Spatial pattern of nests

We used the Spatial Analyst tool of ArcGIS to determine distances among all simultaneously active nests and among all the nests used in any breeding season, using the locations of all trees used as nest-sites over the entire study. We compared distances to determine whether the spacing pattern of breeding pairs differed from the distribution of all nest-trees used in any year. Each nest-tree location was considered only once for the analysis regardless of how many times the tree was reused as a nest-site. To evaluate the influence of conspecifics on the spacing of parrot nests, we used a paired Wilcoxon test to compare the distance from an active nest to the nearest active nest vs. the distance from an active nest to the nearest unoccupied nest-tree for each parrot nest active in the 2008–2009 breeding season for NP and in the 2006–2009 for LF. We restricted this analysis to the 2008–2009 and 2006–2009 datasets, because these had the most complete record of potential nest-trees. Finally, we used distance values among all nests to assess if the spatial pattern of nest-bearing trees and active nests within and among years, was aggregated, random or dispersed with the Average Nearest Neighbor Distance tool from ArcGIS (Mitchell, 2005; Salinas-Melgoza et al., 2009).

3. Results

3.1. Stand and nest plot forest structure

We found significantly larger tree height, DBH, basal area, and density of tree > 40 cm DBH used as nesting or food resource in NP than in LF (Table 1). At each study site, nesting habitat at nest plots was similar to stand scale nesting habitat in random plots, with no difference in tree density, basal area, or DBH (Table 1). When we compared nest plots between sites, we found significant larger basal area and DBH in NP compared to LF (Table 1).

3.2. Nesting site selection

We found and characterized 43 nests of Tucuman Amazon in LF and 37 in NP. Tucuman Amazon uses mainly living trees (94%) for nesting in both sites. Nest cavities origins were mainly (91–95%) from decay process in both sites and were located mainly (43%) in primary branches in NP and (70%) in tree trunk in LF. More than >80% of nests of Tucuman Amazon were located in *Podocarpus parlatorei* (30.2%), *Alnus*

Table 1

Structural variables of the forest in nest plots of Tucuman Amazon and random plots in El Rey National Park (NP) and in Logged forest (LF), in Northwestern Argentina. Values are mean \pm S.D. Different letters show significant differences calculated from U Mann-Whitney test (W), at $\alpha = 0.05$. Lower case letters compare measures within study sites (nest vs. random plots), while upper case letters compare measures between study sites.

	NP		LF	
	Nest plots	Random plots	Nest plots	Random plots
Tree height (m)	–	16 \pm 6 ^A	–	12 \pm 3 ^B
DBH (cm)	34 \pm 8 ^{aA}	31 \pm 9 ^{aA}	27 \pm 9 ^{aB}	23 \pm 6 ^{aB}
Tree density (trees/ha)	353 \pm 104 ^{aA}	406 \pm 136 ^{aA}	436 \pm 213 ^{aA}	486 \pm 192 ^{aA}
Density of tree species used as nesting or food resource (>40 cm DBH trees/ha)	92 \pm 36 ^{aA}	89 \pm 38 ^{aA}	68 \pm 32 ^{aB}	54 \pm 38 ^{aB}
Basal area (m ² /ha)	50 \pm 18 ^{aA}	45 \pm 21 ^{aA}	31 \pm 11 ^{aB}	26 \pm 10 ^{aB}

acuminata (27.9 %) and *Ilex argentina* (23.3 %) in LF while in NP the main tree species that represented >80% of the nests were *Blepharocalyx salicifolius* (59.5 %), *Juglans australis* (13.5 %), and *Podocarpus parlatorei* (8.1 %). Nest-bearing trees and nest-cavity characteristics were different between NP and LF ($F = 10.73$, $p = 0.001$). Cavity entrance width, internal diameter at nest entrance, and internal diameter at nest chamber showed no difference between nest-cavities from NP vs LF (Table 2). The best-supported model to explain selection of nest sites for NP was an additive model that included tree species, nest height, and internal diameter (Supplementary Table 1). The best-supported model (Supplementary Table 2) for LF was an additive model that included nest height and nest depth.

3.3. Food availability

Tree species that had available food for Tucuman Amazon in the reproductive habitat both in NP and LF were *Podocarpus parlatorei*, *Blepharocalyx salicifolius*, *Myrcianthes pseudomato*, *Cedrela angustifolia* and *Ocotea porphyria*.

Monthly mean food availability for the breeding season was higher in NP than in LF (34.5 ± 13.3 m ha⁻¹ vs. 3.5 ± 1.0 m ha⁻¹; $W = 45$, $P < 0.01$) (Fig. 1). Monthly mean availability of *P. parlatorei* seeds for the breeding season was higher in NP than in LF (5.6 ± 2.3 m ha⁻¹ vs. 1.2 ± 1.0 m ha⁻¹; $W = 122$, $P < 0.01$).

When we explored the relationship between Tucuman Amazon nest density and availability of *P. parlatorei* for the different reproductive seasons in both sites a similar pattern of variation was observed (Fig. 2).

3.4. Suitable cavities density

Density of suitable cavities for nesting for Tucuman Amazon was significantly greater in NP than in LF (4.6 cavities ha⁻¹ [95%: C.I. 3.07 – 7.04 cavities ha⁻¹] vs. 1.1 cavities ha⁻¹ [95%: C.I. 0.73 – 1.66 cavities ha⁻¹], respectively).

3.5. Nest density

Mean density of nests of Tucuman Amazon was significantly greater in NP than in LF (0.25 ± 0.04 vs. 0.06 ± 0.04 nest ha⁻¹ respectively; $W = 30$, f.d. = 3, $P < 0.01$).

Table 2

Comparison (MANOVA test) of Tucuman Amazon (*Amazona tucumana*) nest-bearing trees and nest-cavities characteristics between unlogged (NP) and logged (LF) forest in the Southern Yungas of northwestern Argentina. Values are shown as mean \pm SD and in parenthesis the variable range.

Variable	NP	LF	F-value	P-value
DBH (cm)	90 \pm 27 (41–175)	66 \pm 24 (33–140)	16.78	0.001
Tree height (m)	23.5 \pm 4.9 (11–32)	15.3 \pm 5.3 (7–30)	52.73	0.001
Cavity height (m)	14.4 \pm 3.9 (8.3–23.8)	8.5 \pm 3.8 (2.29–20.0)	44.88	0.001
Cavity depth (cm)	38 \pm 38 (0–200)	66 \pm 39 (0–155)	10.92	0.001
Cavity entrance height (cm)	24 \pm 13 (7–67)	41 \pm 23 (6–100)	19.94	0.001
Cavity entrance width (cm)	13 \pm 4 (5–26)	16 \pm 8 (6–33)	3.14	0.08
Trunk diameter at cavity entrance (cm)	59 \pm 21 (25–150)	48 \pm 15 (27–111)	6.45	0.01
Trunk diameter at nest chamber (cm)	55 \pm 20 (29–150)	46 \pm 11 (25–78)	6.31	0.01
Internal diameter at nest entrance (cm)	30 \pm 9 (13–53)	27 \pm 10 (14–55)	1.74	0.19
Internal diameter at nest chamber (cm)	27 \pm 7 (13–40)	30 \pm 11 (10–65)	1.76	0.18

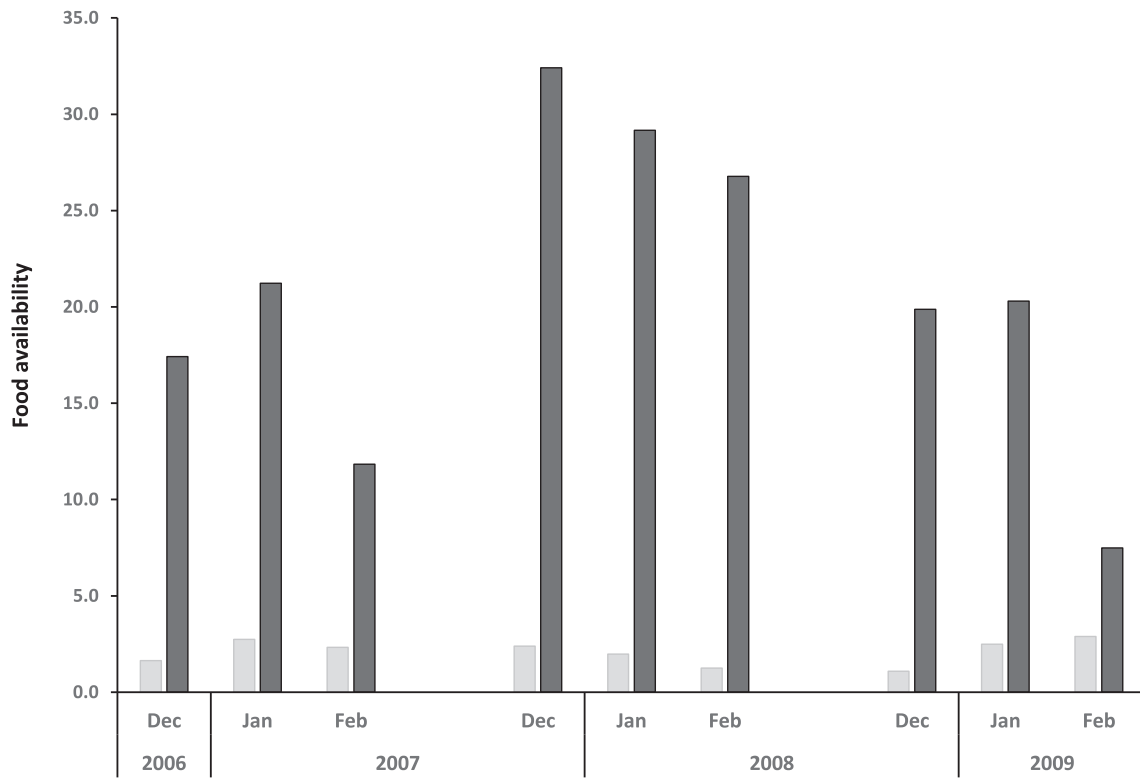


Fig. 1. Total food availability expressed as summation of DBH of tree species consumed by Tucuman Amazon in the cloud forest of NP (dark gray bars) and LF (light gray bars) during three breeding seasons (December to February) i.e. the period during which the vast majority of parrots complete activities from egg laying through young fledging and leaving nests.

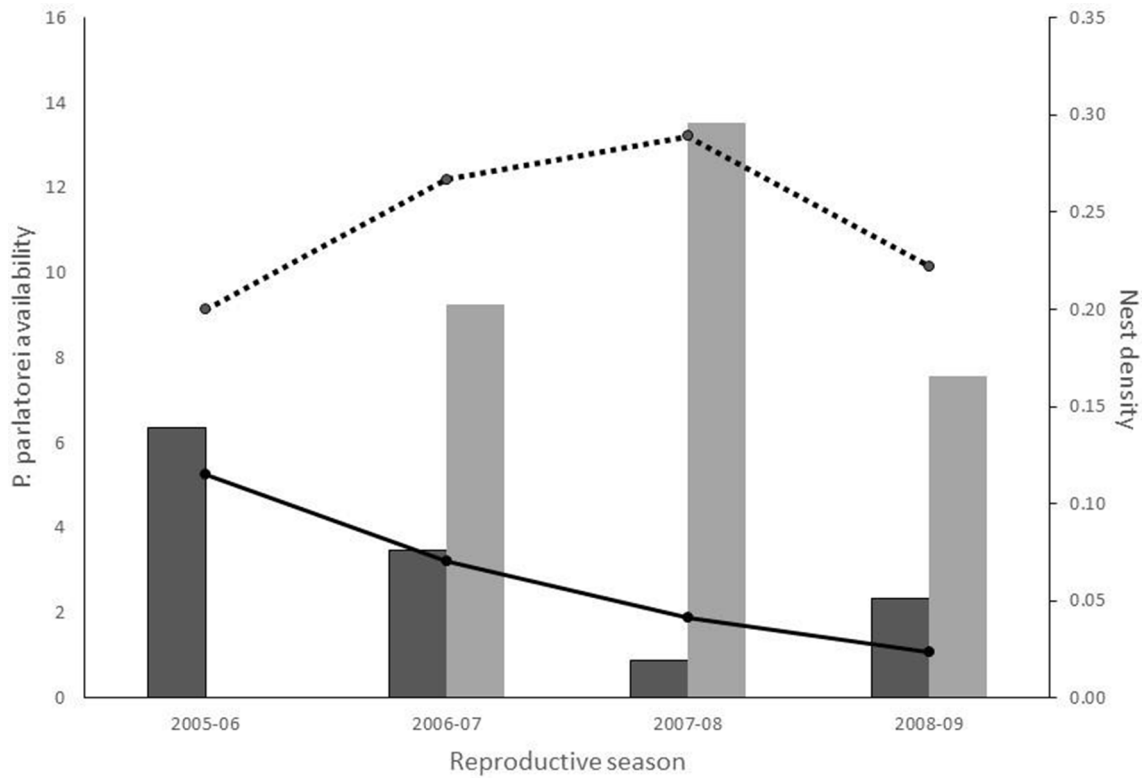


Fig. 2. Index of availability of *P. parlatorei* (DBH summation) for LF (black bars) and NP (gray bars). Dotted line represents nest density of Tucuman Amazon in NP and continuous line represents nest density in LF.

3.6. Spatial pattern of nests

In NP and LF, the mean distance from active nests to the nearest active nest was significantly greater than mean distance between nearest nests used in any reproductive seasons (potential nests) (Table 3). When we evaluated the influence of conspecifics on the location of active nests, the distance to the nearest active nest was significantly larger than the distance to the nearest nest-tree used in the previous reproductive seasons for NP and for LF (Table 3). We found that the spatial pattern for all nest-trees used in any year in both sites was aggregated (Supplementary Table 3). However, when we considered separately active nests by each reproductive season the pattern change to dispersed in LF and to dispersed or random in NP (Supplementary Table 3).

4. Discussion

We found that conventional selective logging in the Southern Yungas of Argentina affected nesting site selection, food availability, density of suitable cavities and nests, and the nest spatial pattern of Tucuman Amazon.

4.1. Stand and nest plot forest structure

Tucuman Amazon nesting habitat in LF shows a different structure compared to NP. In LF, valuable timber tree species such as *Cedrela lilloi* and *Juglans australis* are represented by few large individuals in poor health conditions or by trees of small DBH at high density as *Podocarpus parlatorei*. Decreases in basal area, DBH, and density of large trees (>40 m BH) are reported consistently in other studies on effects of selective logging (Pinazo and Gasparri, 2003; Politi et al., 2009; de la Parra-Martínez et al., 2015; Politi and Rivera, 2019). Although nest plots in NP are structurally different from those in LF, nest plots are similar to stand plots selected at random in NP. The same pattern was observed in LF, probably indicating that nest-site selection occurs at nest-bearing tree or cavity-nest scale (e.g., micro-site).

4.2. Nesting site selection

Selection of nesting sites showed some differences between NP and LF. In NP tree species, cavity height, and internal diameter were important features influencing selection of nest sites for Tucuman Amazon. *Blepharocalyx salicifolius* the tree species with the 60 % of nests in NP is a large canopy tree with cavities high from the ground and with ample nest chambers. In LF cavity height and cavity depth were the most important variables influencing the selection of nesting sites. The importance of cavity height in the selection of nest sites as found in NP and LF can be explained by its role in protection against predators for

Table 3

Distance from active nest to nearest active nest in the same reproductive season (A-A), from active nest to the nearest nest used in any reproductive season (A-U), and from active nest to the nearest nest used in previous reproductive season (A-PU) for Tucuman Amazon in NP and LF. (Mean \pm S.D.)

Year	A-A (m)	A-U (m)	A-PU (m)	Statistical Test and p-value
NP				
2005–09	144.1 \pm 152.8	66.5 \pm 52.7		W = 520; P < 0.001
2008–09	138.1 \pm 165.3		53.5 \pm 19.5	Z = 2.29; P < 0.02
LF				
2004–09	261.1 \pm 167.4	109.9 \pm 87.3		W = 1283; <0.001
2006–09	351.9 \pm 227.9		124.0 \pm 79.8	Z = 3.3; p < 0.001

Z Wilcoxon test for paired samples; W Mann-Whitney test.

nests higher from the ground (Marsden and Jones, 1997; Saab et al., 2004; de la Parra-Martínez et al., 2015). In a review of nesting requirement of parrots, Renton et al. (2015) found that parrots use nest cavities in large trees, high above the ground, with large and deep nest chambers, and entrance diameters related to body size of the species. In LF trees of *Ilex argentina* and *Alnus acuminata* supply most of the nest sites for Tucuman Amazon since both species are prone to develop cavities, even at small size, for example *Ilex argentina* of 33 cm of DBH had an active nest of Tucuman Amazon. Nests of *Ilex argentina* were at a lower height from the ground because these are small trees, but their cavities were very deep. A deeper incubation chamber can provide the same advantage than high cavities (Snyder et al., 1987; Gibbons et al., 2002), making harder the access to the nest by the majority of birds and mammals predators (de la Parra-Martínez et al., 2015). There could be a trade-off for Tucuman Amazon between selecting higher and shallower vs. lower and deeper nest cavities as reported for Military Macaw in Mexico (de la Parra-Martínez et al., 2015).

4.3. Food availability

In LF the lower availability of food for Tucuman Amazon is explained by a smaller density of big trees remaining in the stands, especially of those species that are also valuable for timber as *Podocarpus parlatorei*, *Cedrela lilloi*, and *Juglans australis*. Selective logging of forests removes a small number of tree species in a polycyclic scheme, but can remove key tree species used as food source by animals (Johns, 1988; Burivalova et al., 2015; Rivera et al., 2019). As the intensity of logging increases, food availability decreases with a larger impact on animal populations (Skorupa, 1986).

4.4. Suitable cavities density

Higher availability of suitable cavities for Tucuman Amazon in NP than in LF is probably explained by a higher density of large trees of the tree species used for nesting. We recorded 87 trees ha⁻¹ larger than 40 cm DBH of the tree species used for nesting by Tucuman Amazon in NP against 60 trees ha⁻¹ in LF. Selective logging in Neotropical forests extracts valuable tree species as soon they reach a commercial size at 30–40 cm DBH resulting in low availability of suitable cavities for nesting birds (Fimbel et al., 2001; Cornelius et al., 2008; Monterrubio-Rico et al., 2009; Politi et al., 2010; Cockle et al., 2010). In NP there is a surplus of suitable tree cavities for Tucuman Amazon with 16 suitable cavities every active nest suggesting that cavity availability is not a limiting factor in this mature forest. For Tucuman Amazon the density of suitable cavities for nesting is higher than nest density either in LF or in NP suggesting that reproductive pairs probably are not limited only by the availability of suitable cavities.

4.5. Nest density and nests spatial distribution

Higher availability of suitable nesting cavities in NP could explain a higher nest density of Tucuman Amazon. At the same time, a higher density of suitable cavities and active nests in NP could explain the spatial closeness of the nests compared to LF. In NP active nests in each breeding season are located at a shorter distance among them than in LF. However, the dispersed distribution pattern of active nests in each breeding season in NP and the excess of suitable cavities not used in relation to occupied cavities suggest that some type of territorial behavior by the nesting parrot pairs can be limiting the density of active nests. This is supported by the larger distance among neighbor active nests in each year compared to the distance among active nests to neighbor nest-cavities used in any year (144.1 \pm 152.8 vs. 66.5 \pm 52.7 m). In LF we found the same pattern suggesting that territorial behavior holds limiting the use of closer cavities by reproductive pairs. As was reported for *A. finschi* (Salinas-Melgoza et al., 2009), *A. vittata* (Wiley, 1985), and *Probosciger aterrimus* (Murphy et al., 2003) it seems that each

parrot breeding pair tries to hold a territory around the nest tree with a high density of suitable cavities.

Besides cavity availability and territorial behavior there would be other factors limiting nest density of Tucuman Amazon. In LF we found a mean nest density of 0.06 nest ha⁻¹, or 1 nest 16 ha⁻¹, or a mean of 11 nests year⁻¹ for the entire study site. In the 2005–06 parrot reproductive season, we recorded the highest density of 23 nests in LF, with some of the nests having uncommon characteristics for suitable cavities, e.g. cavities open above and exposed to rain or cavities with rotten walls consisting in exposed platforms, that could have been classified as poor quality cavities. However, 70% of the 23 nests were successful in producing at least one fledgling (Rivera, 2011). Concomitantly, in the 2005–06 parrot reproductive season we recorded a higher availability of *Podocarpus parlatorei* fruits and seeds. The highest food availability for Tucuman Amazon recorded in the 2005–06 reproductive season could explain the highest density of nesting pairs in LF and suggest that the availability of suitable cavities only is limiting parrot nesting density when food is not limiting (Newton, 1994). In the remaining parrot reproductive seasons nest density was close to 10 nests for LF. The large variation in nest density of Tucuman Amazon in LF (CV = 56.07) among reproductive seasons could be explained by the variation in food availability. Newton (2002) suggested that differences in bird densities between habitats of distinct qualities can be attributed to food availability, with a tendency among bird species to nest at higher densities in areas where food is more abundant. Additionally, in poor quality habitat bird population numbers can show a large variation among years and hardly reach the level at which territorial behavior limit bird density (Newton, 2002). A similar pattern was observed in NP but in a different breeding season since the availability of *Podocarpus parlatorei* fruits and seeds was higher in 2007–08. Despite some variation in annual nest density that reflected *P. parlatorei* food availability among years, this variation was small (CV = 16.06), and the distance among active nests in every year was similar (Rivera et al., 2012) probably representing a minimum distance between active nests in NP.

Although LF represents a lower quality habitat for Tucuman Amazon the species can thrive in this area. However, the high variation and low stability in reproductive pair density of the species in LF can influence its population size and total productivity in the long term.

5. Conclusions

Despite changes in forest structure from selective logging in the Southern Yungas resulting in a lower quality habitat for Tucuman Amazon the species can remain in logged forests as long as some components and characteristics of the forest keeps. Considering that logging has been carried out with no consideration to minimize ecological or biodiversity impacts we should consider the situation in LF as a minimum threshold from which most of the forest management can improve with some guidelines. For specialized species such as Tucuman Amazon that requires cavity-trees for nesting and key tree species for feeding during the nesting period it is essential to consider availability of both cavity and food resources for evaluating limiting factors and habitat quality. For example, the retention of at least 12 trees ha⁻¹ > 60 DBH of *P. parlatorei* and 25 trees ha⁻¹ > 50 DBH of *B. salicifolius* to ensure the production of enough food and provision of cavities for nesting could be necessary to sustain nest densities of Tucuman Amazon as in NP (Rivera et al., 2019). For many tropical tree species, it has been shown that seed production increases with tree size (Chapman et al., 1992). Also is necessary to assure that enough young and recruited trees will grow to a large size in the future to develop cavities and provide food (Ball et al., 1999). Because the slow growth rate of *P. parlatorei* (0.3 cm/year, Carilla and Grau, 2011), individuals need at least 200 years to develop suitable cavities and 75 years to produce fruits; i.e., 23 cm of DBH (Rivera, 2011). Other tree species important for Tucuman Amazon that should be retained are *Juglans australis* and *Cedrela lilloi* because these tree species are selected for nesting or feeding by Tucuman Amazon and are valuable

to foresters for logging. Given the increasing social pressure to balance economic profits with the provision of ecosystem services (Hunter and Schmiegelow, 2011), it is possible to propose management guidelines that assure the conservation of biodiversity by minimizing impacts of selective logging (Gibbons and Lindenmayer, 1996; Abbott and Whitford, 2001). There is a potential to make the maintenance of Tucuman Amazon populations compatible with logging if management guidelines are followed and applied to ensure an adequate supply of food and nesting sites.

CRedit authorship contribution statement

L. Rivera: Conceptualization, Investigation, Formal analysis, Writing – original draft, Writing – review & editing, Funding acquisition. **N. Politi:** Conceptualization, Investigation, Formal analysis, Writing – original draft, Writing – review & editing, Funding acquisition. **E.H. Bucher:** Conceptualization, Supervision, Writing – original draft, Writing – review & editing, Funding acquisition. **A. Pidgeon:** Conceptualization, Supervision, Formal analysis, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.120005>.

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