Nesting habitat of the Tucuman Parrot *Amazona tucumana* in an old-growth cloud-forest of Argentina

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Summary

Tucuman Parrot Amazona tucumana breeds in the cloud-forest of south-eastern Bolivia and north-western Argentina (or Southern Yungas forest). We studied the nesting requirements of the Tucuman Parrot and assessed cavity availability, reuse, and spatial pattern of nests in El Rey National Park - one of the last mature, undisturbed areas of the Southern Yungas forest. We recorded 44 nesting attempts in seven tree species, with most nests (95%) being located in live canopy trees > 60 cm DBH. Most parrot nest-cavities occurred in Blepharocalix salicifolius (60%) and cavities in this species were selected significantly more than expected based on availability. Nests were shallower and higher than nests of other Amazona species. For all years combined, mean nest density of Tucuman Parrot was 0.24 ± 0.04 nest ha⁻¹ and the distance to the nearest active nest was significantly greater than the distance between all trees used as nests. Nesting pairs of Tucuman Parrot were separated by 144.1 ± 152.8 m, while potential nest-trees were 66.0 ± 55.4 m apart. Density of suitable cavities for nesting was 4.6 cavities ha⁻¹. Approximately 16 suitable cavities were available for each breeding pair (0.24 breeding pair ha⁻¹ and four suitable cavities ha⁻¹) and 5% of the suitable cavities available were occupied, suggesting that suitable cavities are not a limiting resource. However, due to the territorial behaviour of breeding pairs, some of these cavities are unavailable to other breeding pairs. The spatial requirements of Tucuman Parrot for nesting could limit management actions intended to increase the density of nesting pairs.

Introduction

The Tucuman Parrot *Amazona tucumana* is a threatened species (Birdlife International 2008), with a small geographic range restricted to the narrow strip of montane forest on the eastern slopes of the Andes from south-eastern Bolivia to north-western Argentina, an area called the Southern Yungas (Fjeldså and Krabbe 1990). The species breeds in the cloud-forest (1,400–2,200 m asl) which is dominated by *Podocarpus parlatorei*, *Alnus acuminata*, and trees of the Myrtaceae family. Among Argentina's diverse forest ecosystems, the Southern Yungas forest is particularly rich, harbouring at least 20 economically valuable tree species and 50% of Argentina's avifauna (Brown *et al.* 1993, 2001). However, more than 30% of the Southern Yungas has already been transformed into agricultural land (Brown *et al.* 2002) and most remnant forests are highly degraded by inappropriate forest logging (Grau and Brown 2000, Pacheco and Brown 2006). In Bolivia, Southern Yungas is considered a threatened ecoregion because of forest fragmentation and conversion (Ibisch and Mérida 2003).

The significant forest reduction and degradation of the Southern Yungas have diminished the density of usable cavities which probably affects many cavity-nesting birds (Politi *et al.* 2010). Most psittacids are secondary cavity nesters, a group particularly sensitive to human activities,

because they depend on other species (e.g. woodpeckers) or factors (e.g. wood decay) for the generation of cavities (Land *et al.* 1989) and require large old trees and snags for nesting (Mawson and Long 1994). The scarcity of suitable cavities for nesting in forest under timber exploitation led to a sharp decline of populations of Thick-billed Parrot *Rhynchopsitta pachyrrhyncha* in Mexico (Lanning and Shiflett 1983, Monterrubio-Rico and Enkerlin Hoefflich 2004).

Most studies have determined the requirements of parrot species for nesting: cavity entrance width, internal diameter, depth, height above ground, orientation of openings, and tree diameter at breast height (DBH), and condition (Wiens 1989, Rowley 1990, Martuscelli 1995, Renton and Salinas Melgoza 1999, Fernandes Seixas and de Miranda Mourao 2002, Vaughan *et al.* 2003, Monterrubio Rico and Enkerlin Hoefflich 2004, Rodriguez Castillo and Eberhard 2006). Additional requirements have been defined at stand level (e.g. stands with numerous suitable cavities) (Salinas Melgoza *et al.* 2009). Finally, the spacing distance between nesting pairs has been reported to influence the occupation of nest-sites (Salinas Melgoza *et al.* 2009). However, few studies have determined nest-site selection, i.e. characteristics of available nest-sites compared with those used (Manly *et al.* 2002).

Information on habitat requirements allows predictions to be made on the ability of species to adapt to disturbed habitats (Saunders *et al.* 1982) and to develop effective strategies for conservation and management of threatened species (Renton 2000). It is necessary to conduct studies on mature or old-growth forests (*sensu* Hunter and White 1997) that set a reference for future comparisons against habitat modification. Moreover, most studies on parrot species have been conducted in the tropical lowlands and very few on parrot species of the montane forests of the Andes.

Prior to this study there were no specific studies on the reproductive ecology of Tucuman Parrot – there was one record of a nest, found in Chuquisaca, Bolivia, with a female incubating four eggs in January (Bond and Meyer de Schauensee 1943); a note that Tucuman Parrot nests in large trunks of *Alnus* or *Podocarpus* trees between January and March in forests located at an elevation of 2,600 m (Juniper and Parr 1998); and a comment that Tucuman Parrot places its nests at elevations between 900 and 2,100 m (Olrog pers. comm. 1986 in Low 2005). The objective of this study was to characterise the nesting habitat requirements of Tucuman Parrot in an old-growth forest and assess cavity availability, reuse, and spatial pattern of nests to set a reference for future comparisons and to discuss the conservation and management implications of our results.

Methods

Study area

We carried out the study in El Rey National Park (24°43′S, 64°38′W), Salta Province, Argentina. The park is located in the central sector of the Southern Yungas forests of north-western Argentina. The central sector is located on the eastern slopes of the sub-Andean mountains (Sistema de Santa Bárbara) and is more than 100 km in length. El Rey National Park has an elevation range between 700 and 2,300 m. The climate of the area is subtropical with a marked dry season (April–November) and rainy season (December–March). Rainfall ranges from 800 to 1,500 mm annually and mean annual temperatures are 12–20 °C (Mendoza 2005). El Rey National Park was created in 1948 with an area of 45,000 ha and contains a representative sample of one of the last mature undisturbed forests of the Southern Yungas (Grau and Brown 1998).

Nest search, inspection, and characteristics

We carried out fieldwork from December to March in 2005–2009. Nest searches were conducted daily during egg-laying and incubation periods (December to mid-January) covering an area of 45 ha in the cloud-forest. 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 (González Elizondo 1998). Nest-cavity

characteristics were determined by climbing (Perry 1978) and measuring cavity dimensions. We identified 44 active Tucuman Parrot nests and measured characteristics in 37 nest-cavities and nest-trees.

We recorded the following nest characteristics: 1) height from the ground to the cavity entrance; 2) size of cavity entrance (horizontal and vertical); 3) internal diameter at the cavity floor; 4) internal cavity depth from cavity entrance to the floor; 6) compass bearing of cavity entrance; 7) trunk or branch diameter at cavity entrance; 8) tree diameter at the cavity floor; 9) tree diameter at breast height (DBH); 10) tree height; 11) tree species; 12) cavity origin (excavated or decayed); 13) cavity location (tree trunk, primary branch, secondary branch or third branch); 14) tree status (alive or dead); and 15) tree location (latitude and longitude).

Availability of suitable cavities

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. We performed 20 variable-width, random direction, 300-m long transects that were at least 150 m apart. We measured the perpendicular distance from the central line of the transect to each detected cavity. We only considered a cavity to be suitable if it had a hollow chamber surrounded by sound wood (not collapsing wood), accessed by entrance holes with a floor to support an incubation chamber and a roof to provide overhead protection, 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 Parrot; 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 > 30 cm (minimum dimensions observed for Tucuman Parrot in another stand; Rivera 2011). Therefore, the minimum characteristics used to determine a suitable cavity were in the range of the cavities used for nesting. We used a tree-peeper (Richardson et al. 1999) to estimate or measure the following cavity and tree characteristics: 1) height from the ground to the cavity entrance using the graduated metric scale in the telescopic rod of the tree-peeper; 2) cavity entrance diameters (horizontal and vertical); 3) internal diameter at the cavity floor; 4) internal cavity depth from cavity entrance to the floor. Cavity entrance bearing was measured with a compass, tree DBH was measured with metric tape, and tree height with a hypsometer. Due to treepeeper limitations we only inspected suitable cavities below 15 m (Richardson et al. 1999).

Statistical analysis

Nest-cavity characteristics

We used Manly's selection index to compare use of cavities as nest-sites in different tree species with the availability of cavities in those tree species (Krebs 1999, Manly *et al.* 2002). We calculated a selection coefficient and the 95% confidence interval for the categorical nest-site variable (tree species). Coefficients greater than 1.0 indicated preference, while values less than 1.0 indicated avoidance (Krebs 1999, Manly *et al.* 2002, Aitken and Martin 2004). Selection coefficients were tested for significance using the log-likelihood ratio (G-test; Manly *et al.* 2002).

Frequencies of nest cavities in different categories (tree species, origin, and cavity location) were compared with a χ^2 test. For circular data such as orientation of the nest entrance, we calculated mean \pm deviation of the angular vector (μ) together with the confidence interval of 95% using the program Oriana (Kovach 2009). A Rayleigh test was used to compare the distribution of the orientations of nest entrance with a uniform distribution. We determined the number of cavities reused by Tucuman Parrot for nesting over several breeding season. We define reuse as those cases where the same cavity was used in more than one year (Berkunsky and Reboreda 2009) and a cavity was considered to be used if it contained eggs or chicks.

Suitable cavity availability

Cavity densities were analysed following line transect guidelines and modelled using the software Distance 5.0 (Buckland *et al.* 2001, Thomas *et al.* 2006). The model with the lowest Akaike's Information Criterion (AIC) was selected (Burnham and Anderson 2002). The adequacy of the selected model for the perpendicular distances was assessed using a Kolmogorov-Smirnov test (Buckland *et al.* 2001).

Nest density and spatial pattern

We determined the average nest density by calculating the mean of the number of nests found in 45 ha during the four breeding seasons. We used the Spatial Analyst tool of ArcGIS to determine distances to evaluate spacing among all simultaneously active nests and using the locations of all trees used as nest-sites over the four-year study (Salinas Melgoza et al. 2009). Each nest-tree location was considered only once for the analysis regardless of how many times the tree was reused as a nest-site. In addition, for each nest-tree used by parrots in any year we calculated the distance to the nearest neighbouring tree that had been used as a nest-site in any year. We compared the nearest neighbour distances for active nests among breeding seasons with a Kruskal-Wallis test. To determine whether the spacing of breeding pairs differed from the distribution of all nest-trees we compared distances among active breeding pairs with distances among nest-tree for all years combined, using a Mann Whitney U-test. Using a paired Wilcoxon test, we further evaluated the influence of conspecifics on the spacing of parrot nests to compare the distance to the nearest active nest vs. the distance to the nearest potential unoccupied nest-tree for each parrot nest active in the 2008–2009 breeding season. We restricted this analysis to the 2008–2009 datasets, which had the most complete record of potential nest-trees, to avoid overduplication of distance values between years (Salinas Melgoza et al. 2009). Distance values obtained previously among all nests were used to assess the spatial pattern of nest-bearing trees and active nests (Salinas Melgoza et al. 2009) with the Average Nearest Neighbor Distance tool from ArcGIS (Ebdon 1985, Mitchell 2005). All the values are expressed as mean \pm standard deviation (SD) unless otherwise specified. We set the significance level of statistical tests at P < 0.05.

Results

Characteristics of nest-cavities and trees

We recorded 44 Tucuman Parrot nesting attempts in 37 nest-trees, 30 during incubation and seven during brooding. Most Tucuman Parrot nests occurred in live trees (95%) of six species, and only 5% were in nest-cavities in snags. There was a significant difference in the frequency of tree species used for nesting ($\chi^2_3 = 27.6$, P < 0.001), with most nest-cavities in *Blephalocalyx salicifolius* (59.5%; 22 out of 37), followed by *Juglans australis* (13.5%; 5), *Podocarpus parlatorei* (8.5%; 3), *Cinnamomun porphyria* (5.4%; 2), *Cedrela lilloi* (5.4%; 2), and *Myrcianthes mato* (5.4%; 1), and 5.4% (2) of the nests were found in snags. Compared to the availability of cavities in different tree species, *B. salicifolius*, *J. australis*, and *C. lilloi* were used significantly more than expected ($G_6 = 91.6$, P < 0.01, Fig. 1). Most nests were found in decay-originated tree cavities (95%; n = 35), compared to nests excavated (5%; n = 2) ($\chi^2_1 = 21.5$, P < 0.001). Cavity location was predominantly in primary branches (43%, n = 16), followed by main trunk (32%, n = 12), secondary (16%, n = 6), and tertiary branches (8%, n = 3) ($\chi^2_3 = 8.9$, P < 0.03).

Most nests (92%) were found in trees with a DBH > 60 cm (Fig. 2). Average nest tree DBH was 89.9 ± 26.9 cm, cavities were located on average at 14.4 ± 3.9 m above the ground, had a horizontal entrance diameter of 13.3 ± 4.5 cm, and a depth of 38.2 ± 38.6 cm (Table 1). Orientation (bearing) of the nest entrances had a mean angular vector (μ) of $173.1 \pm 140.9^{\circ}$ (95% CI = $82.2-263.9^{\circ}$). The mean vector length is low, indicating there is small concentration of values near the mean (r = 0.05). Rayleigh test was not significant, suggesting that nest entrance

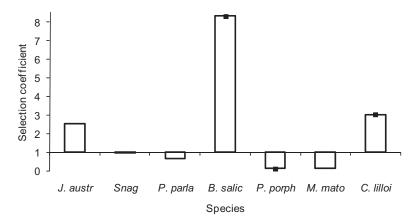


Figure 1. Selection of tree species for nesting by Tucuman Parrot in relation to availability in El Rey National Park, Salta Province, Argentina. The selection coefficient (± standard error) is the proportion of trees used versus available: values > 1 implies preference; < 1 implies avoidance (Manly et al. 2002). J. austr = Juglans australis, P. parla = Podocarpus parlatorei, B. salic = Blepharocalyx salicifolius, P. porph = Cinnamomun porphyria, M. mato = Myrcianthes mato, C. Lilloi = Cedrela lilloi. Number of nest-trees = 37.

orientations have a uniform distribution with no evidence of a selection (Z = 0.08, P = 0.98). Nests of Tucuman Parrot were found at an elevation range between 1,470 and 1,710 m asl.

Six of the 37 cavities (16 %) were reused. One nest-cavity was used in three breeding seasons and five were used twice. One nest-tree had two nest cavities used in separate years.

Density and spatial distribution of nests

Annual mean nest density in the study area was 0.24 ± 0.04 nests ha⁻¹ (n = 4). In two breeding seasons (2006–2007 and 2007–2008) the spatial pattern of active nests was dispersed (Z = 3.8,

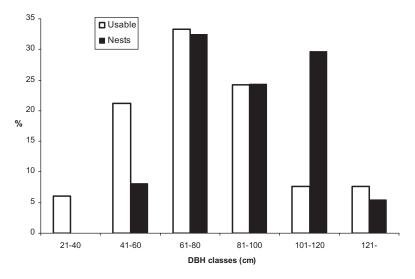


Figure 2. Percentage (%) of nests (black bars) and usable cavities (white bars) for Tucuman Parrot according to tree DBH classes (cm) in El Rey National Park between 2005 and 2009.

Table 1. Nest cavity and tree characteristics of Tucuman Parrot *Amazona tucumana* in El Rey National Park, Salta Province, Argentina. The range is shown in parentheses; SD: standard deviation, CV: coefficient of variation.

Variable	Mean ± SD	CV	
DBH (cm)	89.9 ± 26.9 (41–175)	29.9	
Horizontal diameter (cm)	$13.3 \pm 4.5 (5-26)$	33.8	
Vertical diameter (cm)	$23.7 \pm 13.4 (7.5-67)$	56.6	
Depth (cm)	$38.2 \pm 38.6 \text{ (o-200)}$	101.1	
Internal diameter (cm)	$29.9 \pm 9.7 (13-53)$	27.9	
Nest height (m)	$14.4 \pm 3.9 (8.3-23.8)$	27.6	
Tree height (m)	$23.5 \pm 4.9 (11-32)$	21.1	
Mean distance between active nests (m)	144.1 ± 152.8 (12–674)	106.0	

observed distance/expected distance = 1.6 and Z = 2.7, observed distance/expected distance = 1.4, respectively), random in 2005–2006 (Z = -0.3, observed distance/expected distance = 0.9), and intermediate between random and dispersed in 2008–2009 (Z = 1.8, observed distance/expected distance = 1.3). The spatial pattern of all nest trees used in the four breeding season was clustered (Z = 4.2, observed distance/expected distance = 0.6).

There was no significant difference in the nearest mean distance among active nests among breeding seasons (H=1.4, P=0.69). For all years combined, the distance to the nearest active nest was significantly greater than the distance between all trees used as nests (W=520, P<0.001, Table 4). Nesting pairs of Tucuman Parrot were separated by 144.1 \pm 152.8 m (range = 12–674 m), while potential nest trees were 66.0 ± 55.4 m apart (range = 12–252.4 m). Furthermore, for nests located in 2008–2009, the same pattern prevailed, a nesting pair being significantly farther from the nearest neighbouring pair (138.1 \pm 165.3) than from the nearest available nest tree (53.5 \pm 19.5; Z=2.29, P=0.02).

Availability of suitable cavities for nesting

The estimation with Distance of the density of available suitable cavities for nesting was 4.6 cavities ha^{-1} (95% CI = 3.1–7.0 cavities ha^{-1}), a coefficient of variation of 20% and an effective detection width of 9.1 m (95% CI = 7.5–11.1 m). The selected model had a Uniform function with Cosine expansion series.

Discussion

This study characterised the nesting habitat requirements and spatial pattern of Tucuman Parrot in a reference site and thereby set a baseline against which to compare nesting habitat in sites under different management. Tucuman Parrot suffers a high predation rate of eggs and nestlings (Rivera 2011), even more than some lowland *Amazona* species (Enkerlin-Hoeflich 1995, Koenig 2001, Rodríguez Castillo and Eberhard 2006, Sanz and Rodríguez Ferraro 2006); therefore we expected to find higher and deeper nest cavities (Nilsson 1984, Wilcove 1985, Marsden and Jones 1997, Snyder *et al.* 1987, Gibbons *et al.* 2002). However, nest cavities of Tucuman Parrot were higher, but shallower than nests of other *Amazona* species from the lowlands (Tables 1 and 2). This can probably be related to a lower rate of decomposition related to specific tree and sapwood characteristics that compartmentalise decaying wood or are very resistant to fungal decay (Shigo 1984) or to a lower temperature that retards decomposition rates (Politi *et al.* 2010). As expected, we found that nest cavities of Tucuman Parrot have a larger internal diameter than lowland parrots nests which can be an advantage to maximise nest space and thermal insulation (Joy 2000) in a high elevation breeding habitat where low temperatures are reached.

Table 2. Nest cavity and tree characteristics of *Amazona* species from the mainland and the Caribbean islands. Values are expressed as mean \pm SD; the range is shown in parentheses.

	A. autumnalis¹	A. oratrix ¹	A. viridigenalis¹	A. aestiva ²	A. pretrei ³	$A.\ brasiliens is ^4$	A. finschi ⁵	$A.\ ochrocephala^6$	A. vittata ⁷	A. guildingi ⁷	A. ventralis ⁷
DBH (cm)	73 ± 30.5	8o ± 45.7	96 ± 50.6	50.6 ± 9.6	46.4 ± 19.7	-	43 ± 11.4	-	95.7 ± 30.0	143.2 ± 72.7	80.0 ± 20.8
	(40-162)	(42-234)	(39-229)	(32-76)	(23.2-114.6)		(27.7-66.3)		(59-163)	(56-372)	(46-149)
Horizontal	11 ± 4.4	11 ± 3.5	10 ± 3.7	7.9 ± 2.3	12.6 ± 6.2	-	10.0 ± 2.3	15.6 ± 2.7	21.5 ± 9.9	31.8 ± 24.2	18.0 ± 17.4
diameter (cm)	(7-23)	(6-19)	(5-23)	(4-15)	(5-35.9)		(6.4-14)	(10.9-19.8)	(10-46)	(8-122)	(5-99)
Vertical	22 ± 12.4	20 ± 12.3	17 ± 11.2	16.2 ± 11.3	48.2 ± 51.4	-	21 ± 16	17.2 ± 2.8	59.1 ± 43.6	33.2 ± 23.7	23.7 ± 17.2
diameter (cm)	(9-55)	(10-59)	(8-49)	(6-79)	(8.5-278)		(7.5-71.6)	(12-22.5)	(15-140)	(13-127)	(8-99)
Depth (cm)	128 ± 82.9	140 ± 61.1	121 ± 108.4	149 ± 90	84.6 ± 71.7	75.2 ± 67.4	66.2 ± 51.7	99.2 ± 71.2	98.0 ± 36.9	140.7 ± 136.1	109.0 ± 50.1
	(23-350)	(51-260)	(40-454)	(30-450)	(6-358)	(5-420)	(24-260)	(34.8-445)	(61-170)	(36-635)	(25-290)
Internal	22 ± 4.8	27 ± 10.7	24 ± 11.9	22.7 ± 6.4	20.7 ± 8.7	25 ± 5.8	19.9 ± 6.8	-	33.0 ± 5.6	39.7 ± 14.9	34.0 ± 12.8
diameter (cm)	(14-37)	(14-52)	(13-71)	(14-57)	(12-70)	(18-40)	(10.5-35)		(25-41)	(25-76)	(13-71)
Nest height (m)	6.6 ± 2.0	5.6 ± 2.2	7.3 ± 2.4	5.8 ± 1.2	7.0 ± 3.7	5.7 ± 2.9	9.7 ± 1.7	12.4 ± 2.7	8.0 ± 3.2	17.5 ± 5.9	10.3 ± 4.9
	(3.8-11.3)	(2.8-11.5)	(3.8-135)	(2.9-10)	(1.4-25.3)	(1-12)	(7.4-14.7)	(9.2-16.5)	(3.2-16.8)	(6.1-30.2)	(2.1-20.7)
Tree height (m)	-	-	-	11.1 ± 2.3	13.2 ± 4.5	7.3 ± 4.2	-	19.2 ± 3.1	-	-	-
				(6-16)	(4.8-35)	(1-16)		(10.7-26.1)			

¹Enkerlin-Hoeflich 1995; ²Berkunsky and Reboreda 2009; ³Pauletti Prestes *et al.* 1997; ⁴Martuscelli 1995*; ⁵Renton and Salinas Melgoza 1999; ⁶Rodríguez Castillo and Eberhard 2006; ⁷Snyder *et al.* 1987*. *Indicates studies where means, SD, and range were not included therefore they were calculated.

Tucuman Parrot selects three tree species for 83% of nests. Many studies have shown that *Amazona* species concentrate nests on 1–3 tree species (Berkunsky and Reboreda 2009, Salinas Melgoza *et al.* 2009), however only a few studies compared tree species use with the availability of cavities in different tree species (Enkerlin-Hoeflich 1995, Rodríguez Castillo and Eberhard 2006). As with most *Amazona* (Pauletti Prestes *et al.* 1997, Salinas Melgoza *et al.* 2009, Berkunsky and Reboreda 2009), Tucuman Parrot sited a high number (95%) of nests in living trees. However, some parrot studies showed that dead trees were used equally or more frequently than living trees; this could be related to the fact that these studies were conducted in flooded forest habitat where a high number of dead trees occurs (Martuscelli 1995, Fernandes Seixas and de Miranda Mourao 2002). Although some cavity-nesting birds show a preference in the orientation of the cavity (Snyder *et al.* 1987), including some parrots (Guedes 1993, Pauletti Prestes *et al.* 1997), we were not able to detect a particular orientation of cavity entrance used more frequently by Tucuman Parrot.

Density and spatial distribution of nests

There are very few published data on nest densities for *Amazona*. We reported 0.24 nests ha⁻¹ (i.e. one nest every 4 ha) of Tucuman Parrot, a much higher value than that reported for Blue-fronted Amazon *A. aestiva* (0.005–0.0003 nests ha⁻¹ depending on habitat quality; Fernandes Seixas and de Miranda Mourao 2002), but similar to the density reported for *Amazona* species in Mexico (0.37 nests ha⁻¹; Enkerlin-Hoeflich 1995).

Active Tucuman Parrot nests have a dispersed distribution at a mesoscale of 45 ha of the study site. *Amazona* of the Caribbean islands tend to present an aggregated distribution of nests (Ridgely 1981, Snyder *et al.* 1987, Gnam 1990, Rojas Suarez 1991). However, these studies did not perform spatial analysis on the distribution of trees used as nests. Recently it has been suggested that behavioural spacing requirements of nesting parrots may limit breeding densities and restrict management strategies to increase numbers of nesting pairs within protected areas (Salinas Melgoza *et al.* 2009). A spatial pattern analysis has been carried out by Salinas Melgoza *et al.* (2009) who found that breeding pairs of Lilac-crowned Parrot *A. finschi* nest farther away than trees used as nests previously. We found a similar pattern for Tucuman Parrot since there were significantly shorter distances among nearest nest trees than distance among nearest breeding pairs in a breeding season suggesting that breeding pairs influence spacing of conspecifics.

The fact that we found a stable number of nests during the four breeding seasons for the fixed area under study, that the mean distance to the nearest breeding pairs was similar in every breeding season, and that the spatial pattern of active nests is mainly dispersed, suggests that spacing due to territorial behaviour could be limiting breeding pair density. This limitation may occur despite the availability of suitable cavities. We estimated that approximately 16 suitable cavities were available for each breeding pair (0.25 breeding pair ha⁻¹ and four suitable cavities ha⁻¹). The excess of available suitable cavities for each breeding pair is in agreement with the statement of Salinas Melgoza et al. (2009) that nesting pairs defend a large enough area around the nest to provide them with several cavities suitable for nesting. We did find two nests that were only 12 m apart, but one of them was successful and the other one failed, and although we do not have evidence of the cause of failure we cannot discount territorial behaviour and exclusion effects. The distance between nearest active nests for Tucuman Parrot (144 m) is lower than the distance reported for Lilaccrowned Parrot (952 m) (Salinas Melgoza et al. 2009). This shorter distance could be explained by the high number of suitable cavities available in El Rey National Park old-growth forest. However, due to several biases, we cannot discount an overestimation of the availability of suitable cavities for Tucuman Parrot. First, we recorded cavities in the non-breeding season and they could have been used in the breeding season by other species. Secondly, those cavities could have been located near a predator or had a high parasite load. Thirdly, if intraspecific territoriality holds, then many of those cavities would have been inside other territories, and therefore unavailable. Additionally, our study could have also underestimated suitable cavity availability, since only cavities higher than

2 m and below 15 m were considered. However, since < 10% of the cavities detected were above 15 m, this bias is probably low.

There are very few published studies on the availability of suitable cavities for *Amazona*. For Puerto Rican Amazon *A. vittata* there is a range of 0.2–0.9 suitable cavities ha⁻¹ depending on the definition of suitable cavity used in a range from optimum to minimal (Snyder *et al.* 1987). Enkerlin-Hoeflich (1995) found a density of 4.2 suitable cavities ha⁻¹ for three *Amazona* species in a dry forest from México, this value being almost equal to the 4.6 suitable cavities ha⁻¹ we obtained for our study site.

Tucuman Parrots occupied 5% of the suitable cavities available. Similar to the values found by Enkerlin-Hoeflich (1995) in which 6% of the cavities were used for parrots in dry forests in México, and by Brightsmith (2005) who reports an occupation of 5% of cavities in a mature tropical forest in the Peruvian Amazon. In all these forests the low percentage of occupancy could suggest that suitable cavities are plentiful (Newton 1994).

Nest reuse

A high variability (2–74 %) in the reuse of nests has been reported for 10 species of *Amazona* (Enkerlin-Hoeflich 1995, Renton and Salinas Melgoza 1999, Koenig 2001, Fernandes Seixas and de Miranda Mourao 2002, White *et al.* 2005, Rodríguez Castillo and Eberhard 2006, Berkunsky and Reboreda 2009). The percentage of reuse of cavity nests for Tucuman Parrot is similar to the value reported for Yellow-billed Amazon *A. collaria* inhabiting a tropical forest in Panama (Koenig 2001) and Yellow-cheeked Amazon *A. autumnalis* in a semi-deciduous forest in Mexico (Enkerlin-Hoeflich 1995). The relatively low percentage of reuse of nest cavities for Tucuman Parrot may show a strategy for avoiding predation, since predation is the main cause of nest loss for the species (Rivera 2011). Nests placed in new cavities have lower predation rates compared to nests in previously used cavities (Brightsmith 2005). The frequent shift of nesting sites to avoid predation is probably due to the high density of suitably cavities available for nesting in this mature forest.

Conservation implications

The probability of encountering a cavity increases with tree age (Newton 1994), therefore the surplus of suitable cavities found in this study for each breeding Tucuman Parrot pair in an old-growth forest is not surprising. In managed forests, the availability of suitable cavities for nesting might be lower (Newton 1994, Politi *et al.* 2010), and if Tucuman Parrots require a certain number of suitable cavities in their home range, it is expected that the species will be particularly vulnerable to the loss of nesting habitat through the impacts of selective logging or habitat modification (Monterrubio Rico *et al.* 2009). Considering that most of the Southern Yungas is under timber exploitation it is reasonable to expect that this might be the reason that Tucuman Parrot has not recovered (Rivera *et al.* 2010); i.e. large trees with cavities are probably lacking.

To ensure the conservation of Tucuman Parrot outside protected areas it is necessary that forest management guidelines promote the retention of large *B. salicifolius* trees, since this species was used more frequently than would be expected from its abundance. This might be possible because this species does not have a high timber value. However, this is probably more difficult with other tree species (such as *C. lilloi* and *J. australis*) that are selected for nesting by Tucuman Parrot but have high timber values. Finally, as suggested for Lilac-crowned Parrot (Salinas Melgoza *et al.* 2009), the nesting and spatial requirements of Tucuman Parrot could limit management actions intended to increase the density of nesting pairs. A mean distance among suitable cavities of at least 150 m could represent the minimum distance to consider in the spacing of active pairs to avoid exclusion by other pairs especially if nest box provision is necessary.

Acknowledgements

This study was supported by Loro Parque Fundación, Conservation Leadership Programme, Rufford Small Grants, WCS Research fellowships, Scott Neotropical Fund, Overbrook Fellowships for Career development, Idea Wild, CEBio Foundation, and YPF Foundation through a Doctoral fellowship to L.R. National Park Administration granted the research permit. We are very grateful to El Rey National Park personnel for their support during fieldwork. We thank Leónidas Lizarraga for his help in GIS analysis and the field assistants and students who collaborated in the study. The manuscript was substantially improved by comments of two anonymous reviewers, J. C. Reboreda, and P. Atkinson. L. R. carried out this work as a Doctoral Student at Córdoba University in Argentina.

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Received 4 September 2010; revision accepted 20 March 2011; Published online 4 January 2012