



# Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic Forest



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## ABSTRACT

Cavity-nesting vertebrates are an important component of biodiversity in tropical and subtropical forests, but their persistence will increasingly depend on remnant trees in logged forest and agricultural areas. To identify key habitat features for conservation, we examined the factors that influenced daily nest survival for a community of cavity-nesting birds along a gradient of human impact, from primary Atlantic Forest through logged forest to farms. We used logistic-exposure models to determine how characteristics of the habitat, nest tree, cavity, and timing influenced daily nest survival. Overall, predation and/or usurpation caused 92% of nest failures. Daily survival rates ranged 0.961–0.992 for five species of birds that could be studied best, giving probabilities of 0.19–0.62 of survival from laying to fledging. The top models predicting nest survival included cavity and tree characteristics but no habitat variables (canopy cover, forest condition, or distance to forest edge). Small birds (12–128 g) experienced higher nest survival in cavities with smaller entrance diameters, higher above the ground. Large birds (141–400 g) experienced higher nest survival in living trees than in dead trees. Birds experienced similar nest survival in primary forest, logged forest, and farms. Our results highlight the conservation value of cavity-bearing trees in anthropogenic habitats. A pressing policy issue for tropical and subtropical forests is to move beyond minimum diameter cutting limits and instead focus on retention of large old trees.

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## 1. Introduction

About 10% of all bird species, and many mammals, require tree cavities for reproduction (Newton, 1994). Populations of these cavity-nesters can be limited by the supply of suitable cavities, which usually occur in large old trees (Newton, 1994, 1998; Gibbons and Lindenmayer, 2002; Cockle et al., 2010, 2011a,b). Consequently, compared to other guilds, cavity-nesters can be disproportionately vulnerable to forest loss and degradation by logging (Monterrubio-Rico and Escalante-Pliego, 2006; Politi et al., 2012). Conservation efforts often focus on maintaining or restoring cavity trees in human-altered habitats, including logged forest and agricultural areas (Manning et al., 2004; Lindenmayer et al., 2006; Bednarz

et al., 2013). To decide which trees to target, managers and policy-makers must often rely on studies of nest-site selection (e.g. Lindenmayer et al., 1990; Gibbons et al., 2002; Cameron, 2006). Although such studies provide information about the nest-site features that animals choose, they cannot reveal how these features affect the fitness of individuals or the persistence of populations and communities.

Nest survival, a key component of avian fitness, influences population viability and community structure and can vary dramatically among nest sites (Martin, 1993; Beissinger et al., 2008; Robles and Martin, 2013). Cavity-nesting birds may be able to increase their reproductive output by using a cavity with features that protect young from predators and inclement weather (Lack, 1948; Wesolowski, 2002; Wesolowski and Rowiński, 2012). However, secondary cavity-nesters (which require but cannot produce a cavity) are constrained in nest placement to existing cavities (Newton, 1998). Moreover, cavity-nests can be difficult to conceal,

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and some predators remember cavity locations from year to year (Sonerud, 1989; Brightsmith, 2005; Mahon and Martin, 2006). By producing a new cavity, excavators (e.g. woodpeckers) may increase their chance of successfully fledging young, compared to secondary cavity-nesters (Li and Martin, 1991; Martin and Li, 1992; Deng and Gao, 2005), but even excavators are constrained to suitable substrates for excavation (Schepps et al., 1999). Also, both excavators and secondary cavity-nesters risk usurpation by intra- and inter-specific competitors (Lindell, 1996; Murphy et al., 2003; Deng and Gao, 2005; Fisher and Wiebe, 2006). In human-altered landscapes, a reduced number of cavities may allow predators to find nests more easily (Martin, 1988; Aitken and Martin, 2004). Although nest-site selection is generally assumed to be adaptive, birds may have difficulty assessing several simultaneous risks, especially in landscapes disturbed by humans, and cavity-nesters do not always select nest-site features that enhance their reproductive success (Díaz and Kitzberger, 2012; Tozer et al., 2012; Zhu et al., 2012).

Most cavity-nesting birds inhabit tropical or subtropical ecosystems subject to a variety of anthropogenic disturbances, but little is known about the habitat or other factors that influence their nest survival (Cornelius et al., 2008). There is some evidence that overall avian nest success declines toward the humid tropics (Ricklefs, 1969; Robinson et al., 2000; Remeš et al., 2012) but this may not be a general pattern (Oniki, 1979; Auer et al., 2007) and there is no evidence that it holds for cavity-nesters. Until recently, most studies introduced bias when studying the factors influencing nest fate, by making direct comparisons between failed and successful nests, without taking into account the length of time over which the nest was monitored, or the nest stage (i.e., incubation vs. nestling period; Schaffer, 2004). By examining the effects of nest-site features on daily survival rate of understory nests (not in cavities), several recent studies have shown lower survival in habitats degraded by humans (Rangel-Salazar et al., 2008; Young et al., 2008; Newmark and Stanley, 2011; Borges and Marini, 2010; but see Spanhove et al., 2014). Nest height and/or concealment also had a minor influence on nest survival for a few species (Rangel-Salazar et al., 2008; Ryder et al., 2008; Brawn et al., 2011; Newmark and Stanley, 2011). Few studies have examined the influence of nest-site characteristics on nest survival for cavity-nesting birds in tropical or subtropical forests (Brightsmith, 2005; Sanz, 2008; Britt et al., 2014; Olah et al., 2014). Only Britt et al. (2014) examined the influence of tree and cavity characteristics on daily survival rate, and none of the studies tested whether daily survival rate varied among habitats.

Many cavity-nesting birds, including globally threatened and near-threatened species, inhabit the subtropical Atlantic Forest of South America. The Atlantic Forest is a global biodiversity hotspot where forest cover has already been reduced to about 15% of its original extent and most remaining forest has been selectively logged (Myers et al., 2000; Ribeiro et al., 2009). In Argentina, selectively logged Atlantic Forest supported nine times fewer cavities and 17 times fewer nests of cavity-nesting birds compared to primary forest (Cockle et al., 2010). Nevertheless, cavity-nesting birds (including globally threatened species) did reproduce in logged forest, forest edges, and isolated trees on farms (Cockle et al., 2011b; Bonaparte, 2014). In this system, cavity-level (but not tree-level) characteristics were important in nest-site selection by secondary cavity-nesting birds (Cockle et al., 2011b). The present study aims to assess the conservation value of cavity-bearing trees in Atlantic Forest habitat altered by humans, and to identify high-quality nest sites for protection or restoration. To this end, we studied how habitat, nest tree, and nest cavity characteristics influenced daily nest survival of cavity-nesting birds along a gradient of human impact in the Atlantic Forest of Argentina.

At the habitat level, we hypothesized that if selectively logged remnant forest and agricultural areas with scattered trees represent low quality habitat for forest birds, they might be sink habitats with lower daily survival rate than primary forest. At the level of the nest tree, we hypothesized that daily survival rate would increase with tree diameter, decrease with an increasing proportion of the crown touching other trees, and be higher for living trees than dead trees. Large living trees might provide better concealment of cavities and protection from adverse climatic conditions (extreme temperatures, wind and rain). Trees with a more connected canopy might be visited more often by predators that move through the canopy, such as brown capuchin monkeys (*Sapajus nigritus*). At the cavity-level, we hypothesized that daily survival rate would increase with decreasing entrance diameter, increasing height above ground, and increasing depth of cavities, because deep cavities with small entrances would exclude large predators and high cavities would be more difficult for terrestrial predators to reach. Finally, because nest survival often varies with nest stage and time-of-year (Murphy et al., 2003; Renton and Salinas-Melgoza, 2004; Kozma and Kroll, 2010; Brawn et al., 2011), we predicted that nest survival might vary across the nesting period (e.g. with higher daily survival rate during the incubation than the nestling period) and breeding season.

## 2. Methods

### 2.1. Study area

We studied cavity-nesting birds in the Atlantic Forest, Misiones province, northeastern Argentina. Parts of the Atlantic Forest are located south of the Tropic of Capricorn, including all of Misiones; however, floristics, physiognomy and fauna unite these southern forests with the northern Atlantic Forests and we therefore include them under the broader category of tropical moist forests (Negrelle, 2002; Oliveira-Filho and Fontes, 2000).

Our study area was a mosaic landscape of primary and logged forest, parks, and small farms from San Pedro (26°38'S, 54°07'W) to Parque Provincial (PP) Cruce Caballero (26°31'S, 53°59'W) and Tobuna (26°27'S, 53°54'W), San Pedro department, and PP Caá Yará (26°52'S, 54°14'W), Guaraní department. The vegetation is classified as semi-deciduous Atlantic mixed forest with laurels (*Nectandra* and *Ocotea* spp.), guatambú (*Balfourodendron riedelianum*), and Paraná pine (*Araucaria angustifolia*; Cabrera, 1976). Elevation is 520–700 m asl and annual rainfall 1200–2400 mm distributed evenly throughout the year.

### 2.2. Field methods

We monitored cavity-nests of forest birds found over eight breeding seasons (August–January 2006–2007 and 2007–2008; September–December 2008; October–December 2009 and 2010; September–December 2011 and 2012; August–December 2013). We searched for nests from public trails in parks, roads, and open farmland (2006–2013); from within primary and logged forest where we cut temporary trails to find nests (2006–2013); on randomly placed 1-ha plots in primary and logged forest (2006–2009); and along a grid of transects (total 27 km) spaced every 500 m in primary and logged forest (2011–2013). Search effort was greater in primary forest than in other habitats, but nests were easier to find in the more open farm areas. We stopped frequently to observe the behavior of adult birds and look for evidence of recent wear around cavity entrances, and occasionally asked farmers and park rangers to show us nesting trees they knew of. When we saw adult birds repeatedly visit the same tree, fly out of a tree suddenly,

disappear from view for long periods, cling to a cavity entrance, perch near a cavity, enter a cavity or exit a cavity, we used a 1.5–5 cm diameter video camera to inspect the inside of the cavity. We inserted the cameras into the cavities using a 15 m telescoping pole, or climbed the tree using a rope (if it had a sturdy fork) or 10-m ladder. These cavities were considered active nests if they contained eggs and/or chicks. Inaccessible cavities were observed from the ground for several periods of at least 2 h, and were considered active if adult behavior indicated incubation or nestling-provisioning. We included inaccessible nests in our general description of nest sites, but not in our analysis of nest survival. Once used, cavities were checked every year for new nests. We were interested in nests of forest bird species, so we excluded nests of farmland species (i.e., house wren *Troglodytes aedon*, campo flicker *Colaptes campestris*, American kestrel *Falco sparverius*, and chopi blackbird *Gnorimopsar chopi*).

For accessible nests, we attempted to observe contents every 2–6 days, with visits most frequent around the expected hatching dates. We assumed hatching failure or abandonment if a cavity contained eggs well beyond the expected hatching date. We interpreted that the nest was depredated or usurped if all eggs or nestlings disappeared, or if we found their remains in or around the nest cavity. We interpreted that an adult was killed on the nest if we found (1) a dead adult in or below the cavity, or (2) many adult feathers in a cavity that recently contained eggs or unfeathered nestlings. We assumed that a nest was successful (i.e., at least one chick fledged) if fledging was observed directly, or if at least one well-feathered nestling was observed in the cavity near the expected fledging date and no subsequent evidence indicated predation.

In studying daily nest survival, the basic unit of observation is the exposure period. An exposure period is the interval between two subsequent visits to a nest, on the first of which the nest is determined to be active, and on the second of which the nest is determined either to be active or to have failed. Because of logistic constraints, and because models of daily survival rate only included visits when we could be sure of nest contents (i.e., no adult bird covering eggs or nestlings), our actual exposure periods ranged 1–43 days (mean  $\pm$  SE:  $4.8 \pm 0.2$  days).

We classified each exposure period into one of three nest stages based on the nest contents (or expected contents, if contents were gone): (1) eggs, (2) hatching (one or more eggs hatched during the exposure period), or (3) nestling. Hatching occurs over an extended period for many of the species we studied (e.g. >6 days is common for some parrots) and we considered that the risk of nest predation could change over the course of hatching and nestling development. Exposure periods were classified as “hatching stage” if (1) the nest contained both nestlings and eggs that eventually hatched, or (2) the exposure period included the expected hatch date but the contents were gone. However, they were classified as “nestling stage” if the nest contained nestlings and eggs that failed to hatch.

At each nesting cavity we measured variables expected to affect nest survival at the scale of habitat, tree and cavity. At the habitat scale, we assigned the nest to primary forest or human-altered habitat based on observed current land cover and history reported by Bertolini (1999, 2000), park rangers and local inhabitants. We estimated canopy cover in a 30 m radius around the nest tree. If the nest was in a forest, we used Google Earth to measure the distance to the nearest open area > 5 ha and assigned it a positive value. If the nest was in an open area, we measured the distance to the nearest forest patch > 5 ha and assigned it a negative value. At the tree scale, we measured diameter at breast height (DBH) using a diameter tape, estimated the proportion of the crown touching other trees, and determined whether the tree was dead or alive. In measuring cavity depth we aimed to reflect the distance

a predator would have to enter or reach, to access the nest contents. Thus we took the maximum depth of the cavity, whether this was horizontal or vertical (from the lowest entrance, if the cavity had more than one entrance). In measuring entrance diameter, we aimed to reflect the maximum size of predator (or body part of a predator) able to enter the cavity. Thus, we measured the minimum distance across the widest part of the entrance. For a circular entrance, this was the diameter of the circle. For a long vertical slit, it was the horizontal distance across the widest part of the slit (not the vertical length of the slit). For a pear-shaped entrance, it was the distance across the widest part of the entrance. If the cavity had more than one entrance, we used the measurement of the largest entrance. Cavity height was measured using a 50-m measuring tape from the forest floor to the lower lip of the lowest cavity entrance. Where we could not climb to the cavities but could access them with the pole-mounted camera (cavities 8–15 m high in trees without a sturdy fork for climbing), we estimated the diameter of the cavity entrance and horizontal depth of the cavity by comparing the cavity to a ruler on the camera. In these cases we measured cavity height using the telescoping pole and we estimated the vertical depth of the cavity using the camera image.

### 2.3. Statistical analysis

All statistical analyses were performed in R version 3.0.3 (R Core Team, 2014). To study daily nest survival we constructed generalized linear mixed models using the glmer command in the lme4 package, with a logistic-exposure link function (Schaffer, 2004) and combinations of fixed effects related to habitat, tree, cavity, or timing (Table 1). For this analysis we had to exclude nests that had missing values for any of the independent variables (e.g. cavities destroyed or occupied by bees before they could be measured). Because an exploratory analysis suggested interactions between adult body mass and cavity characteristics (but no effect of taxonomic group: toucan, woodpecker, parrot, raptor, trogon, or passerine), we performed the analyses separately for small (12–128 g) and large (141–400 g) birds. Body mass was taken for each species from Dunning (2008), labels on museum specimens, and our own unpublished data from mist net captures (preference given to the latter if available). All models included three random effects: (1) bird species, to control for effects of bird species on nest survival, (2) cavity ID, to control for multiple observations at the same cavity, and (3) year, to control for interannual variation in nest survival. When there was more than one model with  $\Delta AICc < 2$ , we used model averaging to determine averaged parameter estimates, then divided these estimates by their standard error to test for significance. To reduce the risk of type II error, we considered slope parameters significant at  $\alpha = 0.1$ .

For species with at least 15 nests and 100 exposure days, we examined species-specific survival rates by constructing constant-only logistic-exposure models with no fixed effects and only cavity ID and year as random effects.

We calculated daily survival rates following Schaffer (2004), as

$$DSR = \frac{e^{b_0 + b_1 x_1 + b_2 x_2}}{1 + e^{b_0 + b_1 x_1 + b_2 x_2}}$$

where DSR is the daily survival rate,  $b_0$  is the intercept parameter,  $b_1$  and  $b_2$  are the slope parameters, and  $x_1$  and  $x_2$  are the values of the predictor variables. We determined the length of the nesting period (from laying to fledging) for each species from published literature and our own unpublished observations. We estimated the proportion of nests surviving the entire nesting period by multiplying daily survival rate for each day of the nesting period (i.e.,  $DSR^{\text{nesting\_period}}$ ).

**Table 1**  
Mixed-effects logistic-exposure models used to predict nest survival of cavity-nesting birds in the Atlantic Forest, with number of parameters ( $k$ ), number of observations ( $N$ ), difference in value of Akaike Information Criterion (corrected for small sample size) between each model and the top model ( $\Delta\text{AICc}$ ) and Akaike weight ( $w_i$ ). All models included bird species, cavity ID, and year as random effects.

Model	Fixed effects	$k$	Small birds			Large birds		
			$N$	$\Delta\text{AICc}$	$w_i$	$N$	$\Delta\text{AIC}$	$w_i$
Constant	–	4	641	3.6	0.12	274	1.0	0.33
Habitat	Habitat (primary forest/human-altered), distance to edge, % canopy cover	7	641	9.4	0.01	274	5.7	0.03
Tree	DBH, tree (live/dead), % crown touching other trees	7	641	3.5	0.13	274	0.0	0.55
Cavity	Height, diameter, depth	7	641	0.0	0.73	274	4.6	0.06
Timing	Nest stage (egg/hatching/nestling), julian date	7	641	8.7	0.01	274	5.5	0.04
Global	Habitat (primary forest/human-altered), distance to edge, % canopy cover, DBH, tree (live/dead), % canopy touching other trees, height, diameter, depth, nest stage, julian date	16	641	12.8	0.00	274	15.4	0.00

### 3. Results

We found 300 nests of 35 species of cavity-nesting forest birds in 175 cavities. Cavities used by small birds were  $6.8 \pm 0.3$  cm (mean  $\pm$  SE) in entrance diameter (range: 2.0–24 cm,  $N = 162$ ),  $53 \pm 3.5$  cm deep (range: 10–312 cm,  $N = 148$ ), and  $12.4 \pm 0.5$  m above ground (range: 1.5–32 m,  $N = 188$ ). They occurred in trees  $71 \pm 2.4$  cm in DBH (range: 13–180 cm,  $N = 190$ ), with  $34 \pm 2.5\%$  of the crown perimeter within 1 m of other trees or vegetation (range: 0–100,  $N = 185$ ), in primary forest ( $N = 136$ ) and human-altered habitats (logged forest and pastures;  $N = 55$ ).

Cavities used by large birds were  $10.2 \pm 0.7$  cm in entrance diameter (range: 4.3–49 cm,  $N = 102$ ),  $71 \pm 6.0$  cm deep (range: 17–346 cm,  $N = 94$ ), and  $14.0 \pm 0.5$  m above ground (range: 4.0–27 m,  $N = 109$ ). They occurred in trees  $71 \pm 2.6$  cm in DBH (range:

21–180 cm,  $N = 108$ ), with  $24 \pm 1.9\%$  of the crown perimeter within 1 m of other trees or vegetation (range: 0–80%,  $N = 105$ ), in primary forest ( $N = 74$ ) and human-altered habitats (logged forest and pastures;  $N = 35$ ).

#### 3.1. Nest survival rates

We monitored 157 nests of 27 species of cavity-nesting birds in 98 cavities to examine nest survival in relation to habitat condition, tree characteristics, cavity characteristics, and timing (Table 2). For small birds, the Cavity model received the most support from the data (Table 1). Cavity diameter had a slope significantly different from zero and cavity height was marginally significant (Table 3). Probability of surviving increased with decreasing cavity diameter and increasing height above ground

**Table 2**  
Sample size (number of nests, visits, and exposure days), by species of bird, for logistic-exposure models predicting nest survival from habitat, tree, cavity and timing characteristics.<sup>a</sup> Exposure days are the days between finding the nest and checking it for the last time; here values have been summed over all nests for each species. Body mass is given in parentheses. Mass is taken from Dunning (2008), labels on museum specimens, and our own unpublished data from mist net captures. For most analyses, species were combined into groups based on body mass. Length of nesting period is given when known.

Species	Length of nesting period (days)	$N$ nests	$N$ visits	$N$ exposure days
<i>Small birds (12–128 g)</i>				
Ferruginous pygmy-owl <i>Glaucidium brasilianum</i> (65 g)	57	8	54	339
Surucua trogon <i>Trogon surrucura</i> (73 g)	41	15	130	356
Ochre-collared piculet <i>Picumnus temminckii</i> (12 g)	43	1	20	42
Yellow-fronted woodpecker <i>Melanerpes flavifrons</i> (57 g)		1	2	29
White-spotted woodpecker <i>Veniliornis spilogaster</i> (40 g)		1	2	19
Green-barred woodpecker <i>Colaptes melanochloros</i> (127 g)	42	13	62	223
Helmeted woodpecker <i>Dryocopus galeatus</i> (128 g)	45	2	29	83
Pileated parrot <i>Pionopsitta pileata</i> (109 g)		2	5	80
Maroon-bellied parakeet <i>Pyrrhura frontalis</i> (80 g)	72	24	133	810
Short-tailed anthrush <i>Chamaeza campanisona</i> (98 g)	46	6	36	109
Olivaceous woodcreeper <i>Sittasomus griseicapillus</i> (13 g)		2	14	21
Planalto woodcreeper <i>Dendrocolaptes platyrostris</i> (65 g)	37	8	20	111
White-throated woodcreeper <i>Xiphocolaptes albicollis</i> (113 g)	43	8	62	165
Black-billed scythebill <i>Campylorhamphus falcularius</i> (42 g)		1	1	7
Scalloped woodcreeper <i>Lepidocolaptes falcinellus</i> (29 g)	39	2	41	66
Sharp-billed treehunter <i>Heliobletus contaminatus</i> (14 g)		1	15	35
Buff-browed foliage-gleaner <i>Syndactyla rufosuperciliata</i> (25 g)	44	1	12	28
Streaked flycatcher <i>Myiodynastes maculatus</i> (44 g)	39	1	2	35
Swainson's flycatcher <i>Myiarchus swainsoni</i> (27 g)		1	1	10
Total (median)	(43)	98	641	2568
<i>Large birds (141–400 g)</i>				
Red-breasted toucan <i>Ramphastos dicolorus</i> (400 g)	59	19	96	629
Chestnut-eared aracari <i>Pteroglossus castanotis</i> (260 g)	60	2	9	88
Lineated woodpecker <i>Dryocopus lineatus</i> (210 g)	38	9	52	165
Robust woodpecker <i>Campyphilus robustus</i> (270 g)		2	4	41
Barred forest-falcon <i>Micrastur ruficollis</i> (141 g)	74	1	5	64
Scaly-headed parrot <i>Pionus maximiliani</i> (293 g)	75	17	92	603
Vinaceous-breasted parrot <i>Amazona vinacea</i> (382 g)	90	5	8	157
White-eyed parakeet <i>Psittacara leucophthalmus</i> (159 g)	77	4	8	36
Total (median)	(74)	59	274	1783

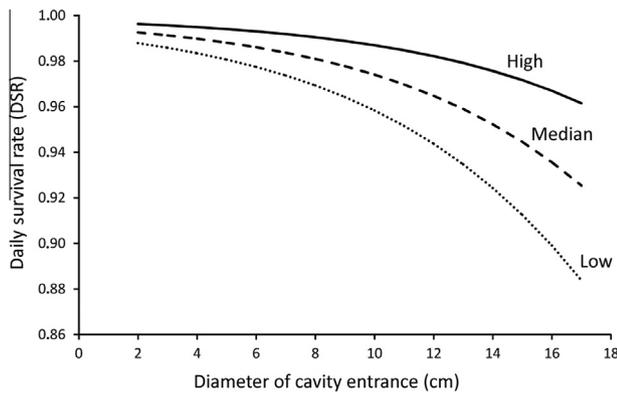
<sup>a</sup> A total of 157 nests were used to estimate nest survival. Of the total 300 nests we found, 57 could not be measured for one or more independent variables, and 86 were not monitored, either because they already contained well-feathered nestlings when found, or because we needed to leave the study area.

(Fig. 1 and Table 3). Overall, for the set of cavities that were used by small birds, assuming median depth (40 cm), the probability of surviving the entire median nesting period (43 days) ranged 0.06 (for a cavity 15 cm in diameter, 7 m high) to 0.78 (cavity 2 cm in diameter, 13 m high), with a survival probability of 0.55 in a cavity

**Table 3**

Parameter estimates for the top logistic-exposure models predicting nest survival for small (12–128 g) and large (141–400 g) cavity-nesting birds in the Atlantic Forest. The models included bird species, cavity ID and year as random effects. Parameters with  $|Z| > 1.96$  have 95% confidence intervals that do not overlap 0. Parameters in bold are significant at  $\alpha = 0.1$ .

Parameter	<i>b</i>	SE	Z	<i>P</i>
<i>Small birds: cavity model</i>				
Intercept	4.32	0.645	6.69	<0.001
<b>Height of cavity above ground</b>	<b>0.070</b>	<b>0.042</b>	<b>1.67</b>	<b>0.095</b>
<b>Entrance diameter of cavity</b>	<b>-0.16</b>	<b>0.060</b>	<b>-2.63</b>	<b>0.009</b>
Depth of cavity	0.0065	0.0061	1.06	0.288
<i>Large birds: tree model</i>				
Intercept	4.34	0.735	5.92	<0.001
DBH	-0.023	0.014	-1.59	0.111
<b>Tree condition (living)</b>	<b>1.63</b>	<b>0.647</b>	<b>2.52</b>	<b>0.012</b>
Percent of crown touching other trees	0.0021	0.012	0.18	0.859



**Fig. 1.** Daily survival rate (DSR) predicted by the top logistic-exposure model (Cavity model) vs. cavity entrance diameter for cavities high above the ground (19 m; solid line), median height above ground (9.2 m; thick broken line) and low to the ground (2 m; finely-dotted line), for small (12–128 g) cavity-nesting birds in the Atlantic Forest of Argentina. Cavity depth is held constant at its median (40 cm).

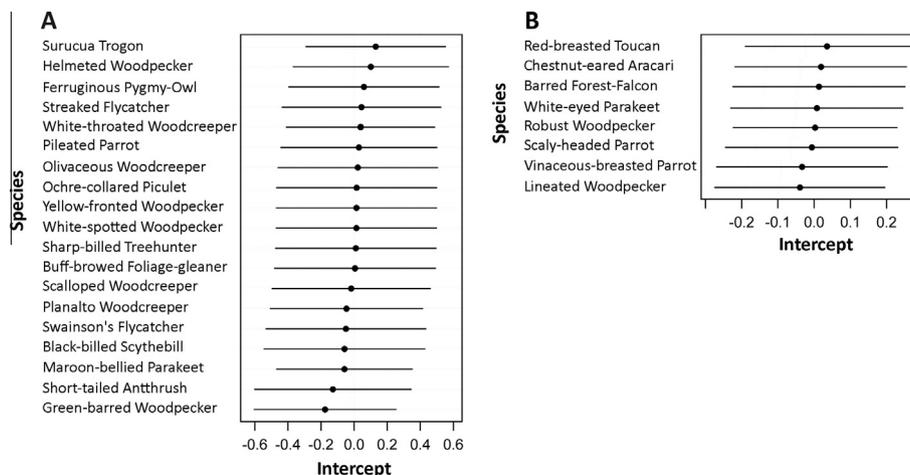
of median height (9.2 m) and entrance diameter (6 cm). Random effects suggested that surucua trogon (*Trogon surrucura*) and ferruginous pygmy-owl (*Glaucidium brasilianum*) had particularly high nest survival, whereas green-barred woodpecker (*Colaptes melanochloros*), short-tailed antthrush (*Chamaeza campanisona*) and planalto woodcreeper (*Dendrocolaptes platyrostris*) had particularly low nest survival, although 95% prediction intervals overlapped for all species (Fig. 2A).

For large birds, the Tree model received most support from the data, but the Constant model also received support (Table 1). After model averaging, only tree condition was a significant predictor of nest survival for large birds ( $Z = 2.52, P = 0.012$ ). We thus used the Tree model to calculate daily survival rate for large birds, holding at their medians DBH (median = 57) and the percent of crown touching other trees (median = 20). Daily survival rate was 0.991 for nests in living trees, and 0.981 for nests in dead trees, which translates to probabilities of 0.52 (living tree) and 0.24 (dead tree) of surviving the median nesting period for these species (74 days). Random effects suggest that red-breasted toucan (*Ramphastos dicolorus*) and chestnut-eared aracari (*Pteroglossus castanotis*) had particularly high nest survival, and lined woodpecker (*Dryocopus lineatus*) and vinaceous-breasted parrot (*Amazona vinacea*) had particularly low nest survival, although as with the smaller birds 95% prediction intervals overlapped for all species (Fig. 2B).

For the five species with at least 15 nests monitored, daily nest survival ranged from 0.961 to 0.992, resulting in a probability of 0.19 to 0.62 (mean 0.43) of surviving the entire nesting period (Table 4).

3.2. Nest fate

We considered 64 nests to be successful and confirmed that 63 nests failed. Clutch size and number of fledglings were determined for 29 of 64 successful nests, 21 of which (72%) experienced partial loss of eggs and chicks. Causes of complete nest failure included predation and/or usurpation ( $N = 58$ ); abandonment, flooding or failure to hatch ( $N = 4$ ); and mechanical damage when the nest tree fell ( $N = 1$ ). The cavity was destroyed at only two of the depredated nests (surucua trogon and scaly-headed parrot *Pionus maximiliani*), and the entrance was enlarged slightly at one nest (surucua trogon). We found evidence that adults had been killed inside the cavity at three nests (scaly-headed parrot, white-throated woodcreeper *Xiphocolaptes albicollis* and scalloped woodcreeper *Lepidocolaptes falcinellus*; Bodrati and Cockle, 2011).



**Fig. 2.** Random effects of species in top logistic-exposure models predicting nest survival for (A) small (12–128 g; Cavity model) and (B) large (141–400 g; Tree model) cavity-nesting birds of the Atlantic Forest. A positive random effect indicates a tendency to higher than average nest survival, whereas a negative effect indicates a tendency to lower than average nest survival. Error bars represent 95% prediction intervals.

**Table 4**  
Estimated nest survival for five cavity-nesting species from the Atlantic Forest (species for which we monitored 15 or more nests) using intercept-only models. Some sample sizes are larger than those in Table 2 because here we included nests for which we could not take cavity measurements. DSR = estimated daily survival rate; SCN = secondary cavity-nester.

Species	Mode of cavity acquisition	N nests	N observations	N exposure days	DSR (95% CI)	Length of nesting period (days)	Probability of surviving entire nesting period
Red-breasted toucan	SCN	19	96	629	0.992 (0.970–0.998)	59	0.62
Surucua trogon	Excavator	16	137	365	0.987 (0.956–0.996)	41	0.60
Maroon-bellied parakeet	SCN	24	133	810	0.987 (0.976–0.993)	72	0.38
Scaly-headed parrot	SCN	18	94	626	0.987 (0.973–0.993)	75	0.36
Green-barred woodpecker	Excavator	15	65	250	0.961 (0.899–0.986)	42	0.19

## 4. Discussion

### 4.1. Conservation value of human-altered habitat

For Atlantic Forest birds using tree cavities, we found no evidence that daily nest survival was influenced by canopy cover, forest condition, or distance to forest edge. Our result that cavity-nesting birds did not experience lower reproductive success when nesting in anthropogenic habitats, contrasts with most studies of non-cavity nesters from tropical and subtropical forests (Rangel-Salazar et al., 2008; Young et al., 2008; Newmark and Stanley, 2011; Borges and Marini, 2010). Cavity-nesters may be buffered against differences in predator abundance among habitats because cavities physically restrict access to nests. In contrast, shrub- and ground-nesters do not physically restrict predator access and rely primarily on concealment, which may be compromised in anthropogenic habitat (Rangel-Salazar et al., 2008). Although logging and conversion to farmland strongly reduce the supply of cavities in the Atlantic Forest (Cockle et al., 2010; Bonaparte, 2014), our results suggest that the few remaining cavities provide high quality nesting sites for forest birds. It is important to note that cavity-nesting species from the same community may differ in their response to anthropogenic habitat change (Deng and Gao, 2005; Saab et al., 2011), and some Atlantic Forest species are certainly less common in human-altered habitats. However, for cavity-nesters as a guild, our results support the conclusions of Manning et al. (2004, 2006) that remnant cavity-bearing trees and forest patches within agricultural areas can have high conservation value.

### 4.2. Nest-site characteristics and nest survival

Small birds (12–128 g) in our study experienced higher nest survival in cavities with smaller entrance diameters, higher above the ground, and large birds (141–400 g) in cavities in living trees. The vast majority of nest failures were attributed to predation or usurpation (however, in most cases we could not rule out the possibility that the nests were abandoned and then scavenged). Although only anecdotal information is available, birds (e.g. toucans and wood-creepers) and mammals (including possums *Didelphis* spp. and monkeys) appear to be responsible for most nest predations in the Atlantic Forest (Duca and Marini, 2004; Martinez et al., 2008; Fraga, 2011; pers. observ.), whereas snakes are important nest predators in many other Neotropical forests (Skutch, 1985; Robinson et al., 2005; Berkunsky et al., 2011). Our observation of higher nest survival of small birds in narrow-diameter cavities (e.g. <4 cm) is likely related to their ability to exclude larger mammalian and avian predators. We found no relationship between entrance diameter and nest survival for larger birds (141–400 g), probably because entrances wide enough to permit the passage of birds  $\geq$  141 g were also wide enough for most predators.

Several other studies have also found cavity and tree characteristics to be much more important than habitat in predicting nest survival of cavity-nesting birds (Mahon and Martin, 2006; Zhu et al., 2012; but see Kozma and Kroll, 2010). Similar to our results, other studies have found nest survival to be greater in higher cavities (Nilsson, 1984; Rendell and Robertson, 1989; Li and Martin, 1991; Mahon and Martin, 2006; Sanz, 2008) with smaller entrance diameter (Wesołowski and Rowiński, 2004, 2012; Zhu et al., 2012) and in living wood (Wesołowski, 2002). In contrast, daily nest survival of cavity-nesting scarlet macaws (*Ara macao*) in Central America was best predicted by canopy connectivity (Britt et al., 2014). Nest survival in a small sample of midstory cavity-nesters, in primary tropical rainforest of Peru, was not associated with height above ground, entrance diameter, or horizontal cavity depth, and only appeared to be affected by the age of the cavity (Brightsmith, 2005).

We found that most characteristics of habitat, trees, and cavities had little impact on daily nest survival. The diversity of predators and nest-site competitors, and temporal fluctuations in their local densities, may limit the ability of birds to select a nest site that can reduce the overall risk of nest failure. Studies in temperate forests have shown that cavity-nesting birds face trade-offs in nest-site selection between sites vulnerable to predation and those vulnerable to usurpation (Nilsson, 1984; Fisher and Wiebe, 2006). Likewise, in the Atlantic Forest and other tropical and subtropical forests, a high nest may be less vulnerable to terrestrial mammals such as cats (Felidae), but more vulnerable to toucans which usurp tree cavities in addition to preying on eggs and nestlings.

In addition to the role of nest site selection, nesting success may be strongly related to parental behaviors. Our result that daily survival rate did not differ between egg- and nestling- stages suggests that, in our study area, overall risk of predation is not related to olfactory cues (from nestling feces) or parental activity at the nest. We found no evidence that excavators have higher nesting success than non-excavators, in contrast to studies from temperate areas (Martin and Li, 1992; Deng and Gao, 2005; Paclík et al., 2009). Nor was there an obvious relationship between body mass and nest survival (contra Li and Martin, 1991). Rather, the species with highest predicted daily survival rate seemed to be the most aggressive nest defenders. They included an owl and two toucan species that prey on adult birds and their nests. The adults of species with high daily survival rates were almost always inside the cavity when we arrived (at least until nestlings were feathered), and often refused to leave during nest inspections. The high daily survival rate of surucua trogon is remarkable because trogons excavated their cavities in very decayed trees (or occasionally in termitaria), a characteristic associated with increased predation risk in other species of birds (Christman and Dhondt, 1997; Wesołowski, 2002; Tozer et al., 2012). Surucua trogons often attacked the camera and researchers (pers. observ.). Assuming they also display such aggression toward potential nest

predators, adult behavior may partially compensate a weak substrate. In contrast, the species with low nest survival, lined woodpecker, green-barred woodpecker, and vinaceous-breasted parrot were passive around their nests, nearly always flushing before researchers arrived. Behavioral plasticity within species or individuals could also compensate differences in predation pressure among habitats (Rangel-Salazar et al., 2008).

Future studies should examine the trade-offs among traits and behaviors that cavity-nesting birds may employ to optimize their reproductive success in tropical and subtropical forests. Individuals and species vary considerably in traits such as nest-site selection, cavity excavation (vs. reuse), clutch size, nest attentiveness, aggression, feeding rate, and removal of nestling feces, all of which are likely to influence reproductive output. Video monitoring, including nocturnal footage, would allow researchers to quantify many of these traits and to examine how predator-specific nest predation rates vary with human impact to Neotropical forests.

#### 4.3. Management recommendations

Managers will usually be unable to assess the suitability of tree cavities from the ground, and should aim to conserve several large trees (>60 cm DBH) per hectare as potential cavity-bearing trees (Cockle et al., 2010, 2011b). Living trees that have already been used for nesting are especially important, as they remain standing for many years and are often reused, providing high-quality, multi-annual nest sites for most species of cavity-nesters (Cockle et al., 2011a; Bonaparte, 2014; this study). Current policies in most tropical and subtropical forests, including the Atlantic Forest of Argentina, rely on minimum diameter cutting limits that allow harvesting of all trees larger than a certain DBH (e.g. >55 cm diameter for many species in the Atlantic Forest; Province of Misiones Forest Law XVI; Putz et al., 2001; Sist et al., 2003; Zimmerman and Kormos, 2012). Such policies are insufficient to ensure long-term sustainability of the logging industry, and encourage people to cut the large old trees that are most suitable for cavity-nesting vertebrates (Putz et al., 2001; Cockle et al., 2010, 2011b; Politi et al., 2010). Large old trees support not only cavity-nesters but also a great diversity of other organisms, yet they are disproportionately threatened in human-altered landscapes and are declining globally (Lindenmayer et al., 2012, 2014). A pressing policy issue for tropical and subtropical forests is to move beyond minimum diameter cutting limits, to focus on the retention and recruitment of large old trees.

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