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RESEARCH ARTICLE

Nest niche overlap among the endangered Vinaceous-breasted Parrot (*Amazona vinacea*) and sympatric cavity-using birds, mammals, and social insects in the subtropical Atlantic Forest, Argentina

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ABSTRACT

Many forest bird species require tree cavities for nesting, and share this resource with a diverse community of animals. When cavities are limited, niche overlap can result in interspecific competition, with negative consequences for threatened populations. Vinaceous-breasted Parrots (*Amazona vinacea*) are endangered cavity nesters endemic to the subtropical Atlantic Forest, where cavities are scarce. We examined nest niche overlap among Vinaceous-breasted Parrots and 9 potential competitors (birds and mammals >140 g, and social insects) in Argentina, considering (1) timing of breeding, (2) characteristics of cavities (depth, entrance diameter, height), trees (diameter at breast height [DBH], species, condition), and habitat (surrounding land use, distance to edge), and (3) interspecific cavity reuse. During 10 breeding seasons we studied nests and roosts, measured their characteristics, and monitored cavities to detect reuse. We used multinomial logistic regression to determine whether the 6 most abundant taxa differed in nest and roost site characteristics. Timing of breeding overlapped for all bird species except the White-eyed Parakeet (*Psittacara leucophthalmus*). No combination of cavity, tree, and habitat characteristics predicted the taxa that utilized cavities. Moreover, 8 of the 10 taxa reused cavities interspecifically. The high level of overlap in realized nest niche, combined with previous evidence that cavities could limit bird density in our study area, suggest the possibility of interspecific competition for cavities among multiple taxa. Although models did not perform well at classifying cavities by taxon, some characteristics of cavities, trees, and habitat were selected more by Vinaceous-breasted Parrots than by other taxa, and we recommend targeting conservation efforts toward cavities and trees with these characteristics (7–40 cm entrance diameter, >10 m high, DBH >55 cm). We found 62% of Vinaceous-breasted Parrot nests on farms (vs. $\leq 50\%$ for other taxa), highlighting the importance of working with local farmers to conserve cavities in anthropogenic habitats as well as in protected areas.

Keywords: Argentina, *Amazona vinacea*, cavity-using fauna, nest site, niche overlap, secondary cavity-nesters, subtropical forest, tree cavities

Solapamiento de nicho de nidificación entre *Amazona vinacea* y aves, mamíferos e insectos sociales simpátricos que nidifican en cavidades en la Selva Atlántica, Argentina

RESUMEN

Muchas especies de aves en bosques requieren de cavidades para nidificar, y comparten este recurso con una diversa comunidad de animales. Cuando las cavidades son limitantes, el solapamiento del nicho de nidificación puede resultar en competencia interespecífica, con consecuencias negativas para poblaciones amenazadas. *Amazona vinacea* es una especie amenazada que nidifica en cavidades, endémica de la Selva Atlántica, donde las cavidades son escasas. Buscamos determinar si existe solapamiento de nicho entre *Amazona vinacea* y 9 potenciales competidores (aves y mamíferos >140 g e insectos sociales), en Argentina, considerando (1) época reproductiva, (2) atributos de las cavidades (profundidad, diámetro de la entrada, altura, origen), árboles (diámetro a la altura del pecho DAP, especie, condición vivo/muerto) y hábitat (distancia a borde, tipo de ambiente), y (3) reutilización interespecífica. Buscamos y monitoreamos nidos de aves en 10 temporadas reproductivas; medimos características del sitio de nidificación; e inspeccionamos las cavidades en busca de reutilización interespecífica. Usamos regresión logística multinomial para determinar si los taxa diferían en características de sitio de nidificación/dormidero. Todas las especies de aves, excepto *Psittacara leucophthalmus*, solaparon su principal época reproductiva. Ninguna combinación de características de cavidad, árbol y hábitat predijo correctamente el taxon que utilizó las cavidades. Incluso, 8 de los 10 taxa reutilizaron cavidades interespecíficamente. El alto solapamiento de nicho realizado, sumado a la evidencia de que las cavidades limitan la densidad de nidos en nuestro sitio de estudio, sugiere la posibilidad de competencia interespecífica entre múltipes taxa. Aunque los modelos no clasificaron bien las cavidades según taxa, algunas características de cavidades, árboles y hábitat fueron seleccionadas más por *Amazona vinacea* que por otro taxa, y recomendamos dirigir esfuerzos de conservación hacia cavidades y árboles con esas características (>10 m de altura, 7–40 cm de diámetro de entrada, en árboles con DAP >55 cm). Nuestro resultado de 62% de nidos de *Amazona vinacea* en chacras (vs. ≤50% para otros taxa) resalta la importancia de trabajar con pobladores rurales para conservar cavidades en hábitats antropogénicos como en áreas protegidas.

Palabras clave: Argentina, *Amazona vinacea*, fauna que utiliza cavidades, sitio de nificiación, solapamiento de nicho, usuarios secundarios de cavidades, bosque subtropical, cavidades en árboles

INTRODUCTION

Many species of bird, mammal, and insect require tree cavities for roosting or nesting; however, most of these animals cannot excavate their own cavities and instead rely on existing cavities created by avian excavators or wood decay (e.g., Newton 1994, Gibbons and Lindenmayer 2002, Monterrubio-Rico and Escalante-Pliego 2006, Cockle et al. 2011a, Ruggera et al. 2016). Populations of these secondary cavity-using animals (nonexcavators) can hence be limited by the resource of high-quality cavities (within which they can reproduce successfully), particularly when humans reduce the number of large trees through forest harvesting (Newton 1994, Lõhmus and Remm 2005, Cockle et al. 2010, Aitken and Martin 2012, Robles et al. 2012). To conserve these communities, it is critical to understand how species-specific nest- and roost-site requirements influence nest-site limitation and interspecific competition.

Nesting and roosting requirements can be considered dimensions of a species' niche (Holt 1987), whereby the fundamental niche includes the entire range of conditions under which the species is able to persist, and the realized niche is the portion of the fundamental niche actually occupied by the species in the presence of other interacting species (competitors, facilitators, etc.; Hutchinson 1957). If 2 or more sympatric species overlap in their fundamental niche relative to a limiting resource, competition for this resource could lead to displacement of their realized niches (niche partitioning), one of the mechanisms that permits species to coexist in the long term (Hutchinson 1957, MacArthur 1958). Niche partitioning has been invoked to explain the existence of diverse communities of cavity-using animals, which may avoid interspecific competition for a limited supply of nest sites by breeding at different times of year or in different types of cavities, trees, or habitats (Nilsson 1984, Ingold 1989, Lindenmayer et al. 1991, Aitken and Martin 2008, Vierling et al. 2009, Robles et al. 2012, Steward et al. 2013). However, the stabilizing effects of niche differences on coexistence are likely to conflict with environmental pressures that favor similar niches under similar conditions (Leibold and McPeek 2006). Birds with similar diets, for example, are likely to experience a tradeoff between breeding synchronously at times of peak food availability and avoiding interspecific competition for nest sites by breeding at other times (e.g., Steward et al. 2013). Also, in many communities, especially those recently influenced by humans, competition for nest sites can be an important driver of population declines of threatened species (Brazill-Boast et al. 2010, 2011, Edworthy 2015, Menchetti et al. 2016).

An understanding of the nest niche is important for identifying threats and conservation priorities for cavity-nesting birds, especially in highly diverse communities with a scarcity of suitable nesting cavities. In tropical and subtropical forests, in particular, the few available studies suggest that cavity-nesting communities are characterized by (1) high species diversity, (2) a reliance on (probably slow-forming) decay-produced cavities in large trees, and (3) limited availability of nesting sites, especially for large birds in disturbed habitats (Heinsohn et al. 2003, Marsden and Pilgrim 2003, Cockle et al. 2010, 2012, Politi et al. 2012, Warakai et al. 2013). There is some evidence of nest niche differences among cavity-nesting birds in tropical and subtropical forests, but there is also evidence of nest usurpation and competition for nest sites involving a wide variety of taxa, including mammals, lizards, snakes, and social insects (Poonswad 1995, Arendt 2000, Vega Rivera et al. 2003, Datta and Rawat 2004, Martinez and Prestes 2008, Renton and Brightsmith 2009). Given the high diversity of tropical and subtropical forests, combined with habitat loss and logging of large trees, studies of nest niche are important to evaluate the potential for nest-site competition, identify potential competitors, and tailor nest-site conservation and restoration to target species.

The subtropical Atlantic Forest of Paraguay, Argentina, and southeastern Brazil is a rapidly disappearing biodiversity hotspot, where loss of nest sites may be an important threat to several globally red-listed secondary cavity-nesting birds (Prestes et al. 1997, Cockle et al. 2007, Waugh 2009, Schunck et al. 2011). In Argentina, Cockle et al. (2010) found 4.5 suitable nesting cavities ha^{-1} in primary Atlantic Forest, compared with only 0.5 ha^{-1} in logged forest. Using a before-after-control-impact experiment, the authors showed that adding nest boxes led to increased nest density in both primary and logged forest, suggesting that the density of cavity-nesting birds may be limited by cavity supply in both of these habitats. One

Atlantic Forest endemic species likely to be threatened by scarcity of nest sites is the globally endangered, large-bodied (382 g) Vinaceous-breasted Parrot (*Amazona vinacea*). The Vinaceous-breasted Parrot shares its breeding range in Argentina with ~75 other cavity-nesting bird species, in addition to mammals and social insects that use cavities for nesting and/or roosting. To target conservation efforts, it is important to know the extent to which the Vinaceous-breasted Parrot shares its nest niche with other taxa, and to identify the cavity characteristics that will benefit this endangered species rather than its potential competitors.

The overall goals of our study were to determine the extent of nest niche overlap between the Vinaceous-breasted Parrot and its potential competitors, and to identify regions of nest niche singularity for the Vinaceous-breasted Parrot in the Atlantic Forest of Argentina. Because there is a well-established positive correlation between cavity entrance size and body size of birds and mammals (Saunders et al. 1982, Poonswad 1995, Datta and Rawat 2004, Martin et al. 2004, Renton et al. 2015), we included as potential competitors large-bodied (>140 g) secondary cavity-nesting birds and mammals, as well as social insects (bees and wasps). We assessed nest niche overlap by comparing, among taxa, (1) timing of breeding (birds only), (2) characteristics of cavities (depth, entrance diameter, height above ground), trees (diameter at breast height [DBH], species, condition [live or dead]), and habitat (distance to edge, surrounding land use), and (3) interspecific reutilization of cavities. Use of the same individual tree cavity by 2 animal species is considered to be an indication of overlap in at least some part of their fundamental and realized niches (sensu Van Balen et al. 1982).

METHODS

Study Area

We studied cavity nests in the area from Parque Provincial (PP) Caá Yarí (26.87°S, 54.23°W) to Santa Rosa (26.38°S, 53.88°W), including PP Araucaria and surrounds, PP Cruce Caballero and surrounds, and the farming area around Tobuna (Misiones province), Argentina. The area includes ~90% of the current population of Vinaceous-breasted Parrots in Argentina (Segovia and Cockle 2012). It is located in the Sierra Central, which divides the Paraná watershed (to the west) and the Uruguay watershed (to the east). Elevation is 500–700 m above sea level and annual precipitation is 1,200–2,400 mm, evenly distributed throughout the year. The natural vegetation is classified as mixed forest with laurel (Lauraceae), guatambú (*Balfourodendron riedalianum*), and Paraná pine (*Araucaria angustifolia*; Cabrera 1976). Most of the area is now occupied by small (5–50 ha) farms, which include annual crops, pastures, tree plantations, remnant forest in patches and corridors, and remnant native trees. There are also large extents of selectively logged forest (>1,000 ha) in parks and private lands, and a single remnant (400 ha) of primary forest (adjoining selectively logged forest) at PP Cruce Caballero, where we concentrated much of our search effort.

Field Methods

During 10 breeding seasons (September–December, 2006–2015) we searched for active nests of all cavity-nesting bird species in tree cavities in a range of habitats including primary forest, logged forest, and open farmland, within a total area of ~900 ha. We searched from public trails, a grid of transects spaced 500 m apart (total 27 km), temporary trails, and off-trail, stopping frequently to observe the behaviors of adult birds and to look for evidence of recent wear around cavity entrances. Search effort was ~6 observer-hr daily. We also occasionally asked farmers and park rangers to show us nesting trees. If we observed any indication that birds might be nesting, we used a 1.8-cm diameter video camera to inspect inside the cavity. To insert the camera, we used a 15-m telescoping pole, or climbed the tree using a rope (if it had a sturdy fork) or 10-m ladder. Cavities were considered to be active nests if they contained bird eggs and/or nestlings. Inaccessible cavities (above 15 m without a sturdy fork) were observed from the ground for several periods of at least 2 hr on different days, and were considered active if adult behavior indicated incubation or nestling provisioning.

Once used (by any cavity-nesting bird species, including primary excavators and species <140 g), cavities were rechecked periodically each year for new nests and roosts of birds >140 g (Vinaceous-breasted Parrot, Barn Owl [*Tyto alba*], Red-breasted Toucan [*Ramphastos dicolorus*], Saffron Toucanet [*Pteroglossus bailloni*], Chestnut-eared Aracari [*Pteroglossus castanotis*], Barred Forest-Falcon [*Micrastur ruficollis*], Scaly-headed Parrot [*Pionus maximiliani*], White-eyed Parakeet [*Psittacara leucophthalmus*]), mammals >140 g (opossums [*Didelphis* spp.]), or social insects (bees or wasps, Hymenoptera), until the cavity collapsed or logistic constraints prevented access. Cavities were considered to be used for roosting if we found a mammal or an owl resting inside the cavity during the day, or if a diurnal bird spent the night in an otherwise empty cavity. Cavities were considered to contain nests of bees or wasps if we observed these insects entering and exiting and (in most cases) could see their nest structure inside the cavity. Birds were identified to species when they entered or exited cavities; mammals (which remained inside cavities all day) were identified to genus using the video images; and insects were identified to order using binoculars. Although we were unable to search directly for cavities used by mammals and insects (because of logistical constraints), we included these animals in our dataset because they are hypothesized to compete with birds for nest sites (Kilham 1968, Martin et al. 2004, Goldingay 2009, Efstathion et al. 2015, Le Roux et al. 2016).

Timing of breeding. When a nest was confirmed as belonging to a secondary cavity-nesting bird >140 g, we observed it every 5.3 ± 0.2 days (mean ± SE), with visits most frequent around expected hatching dates, to determine the extent of overlap in timing of breeding among species of large-bodied, secondary cavity-nesting bird.

Cavity, tree, and habitat characteristics. For all studied taxa (birds and mammals >140 g and social insects), we recorded characteristics of each cavity, tree, and habitat after cavities were vacated. To access cavities for measuring we used single-rope climbing or a 10-m ladder. Cavity depth was measured from the entrance sill to the cavity bottom, entrance diameter was measured across the entrance (in the shortest direction, usually horizontal), and height was taken with a 50-m tape from the ground below the cavity to the lower sill of the cavity entrance. If the cavity had more than one entrance, we measured the entrance used by the animal.

If we could not climb to a cavity but could access it with the pole-mounted camera (cavities 9–15 m high in trees without a sturdy fork for climbing; 16% of accessible cavities), we estimated the diameter of the cavity entrance by comparing the entrance with a ruler on the rod supporting the camera. In these cases we used the telescoping pole to measure cavity height and the camera image to estimate cavity depth. To improve our depth estimates, we practiced estimating cavity depth from the camera image before measuring 18 accessible cavities. A plot of these estimates vs. their respective measurements revealed that, although there was error in our estimates ($|\text{estimate} - \text{measurement}|$: 11 ± 13 cm, $n = 18$ cavities), there was no systematic bias (estimate − measurement: mean ± SD = –2.0 ± 16.7).

For each cavity, we identified the tree species and measured the tree diameter at breast height (DBH) using a diameter tape. Trees were classified as either live or dead. The land use around each cavity was classified as forest (including both primary and logged forest) or farm. If the nest was in forest, we used Google Earth (Google, Mountain View, California, USA) to measure the distance to the nearest open area >5 ha and assigned this distance a positive value. If the nest was in an open area, we measured the distance to the nearest forest patch >5 ha and assigned this distance a negative value.

Cavity reuse. For all studied taxa (birds and mammals >140 g and social insects), we considered intraspecific reuse to have occurred for each cavity in which we found the same taxon nesting or roosting in at least 2 breeding seasons. We considered interspecific reuse to have occurred when 2 taxa used the same cavity in the same or different breeding seasons.

Statistical Analysis

To determine the extent of nest niche overlap among the studied taxa (birds and mammals >140 g and social insects), we compared characteristics of their cavities, trees, and habitats. Some individual cavities were used more than once by the same taxon (in different years), but we included each cavity only once for each taxon in our calculations. We included inaccessible nests (15% of all cavities) in our general description of used cavities, but not in our statistical analysis of niche overlap (see below).

To determine whether the taxa differed in cavity, tree, and habitat characteristics, we used an information-theoretic approach to compare 8 multinomial logistic regression models for the 6 taxa with at least 9 accessible cavities (see Results for details). Only accessible cavities were used in this analysis. Using the mlogit function (mlogit package) in R 3.2.4 (R Core Team 2016), we executed a series of multinomial logistic regression models to predict which taxon used each cavity. Multinomial logistic regression provides quantitatively similar results to multivariate discriminant analysis when the number of observations (n) is greater than 50, and was preferable for our data because it does not assume multivariate normality (Pohar et al. 2004). Multinomial logistic regression is similar to regular (binomial) logistic regression, but allows for 3 or more (vs. 2) possible outcomes; in our models, there were 6 possible outcomes (6 taxa that could have occupied the cavity). The Vinaceous-breasted Parrot was set as the reference taxon, with which the other taxa were compared.

Our 8 multinomial logistic regression models were: (1) the constant model (intercept only), (2) a cavity model (predictor variables: cavity depth, entrance diameter, and height), (3) a tree model (DBH and tree condition [live or dead]), (4) a habitat model (distance to edge), (5–7) each 2-way combination of cavity, tree, and habitat models (all predictor variables at each of the relevant scales), and (8) the global model (all variables). We employed Akaike's Information Criterion corrected for small sample size (AIC_c) to rank models, weighed the support for each model by calculating its Akaike weight (w_i), and then used model-averaging to calculate final averaged estimates (β), standard errors (SE), and odds ratios (OR) and their 90% confidence intervals (Burnham and Anderson 2002). We used 90% confidence intervals rather than 95% intervals to reduce the risk of type II error (failure to detect real differences in niches among taxa).

Each model's goodness-of-fit was assessed using the multinomial goodness-of-fit test proposed by Fagerland et al. (2008). This test involves sorting observations according to the complement of the estimated probability of the reference outcome, then forming g equal-sized groups of observations and calculating the Pearson's chi-square statistic from a $g \times c$ contingency table of observed and expected frequencies, where c is the number of possible outcomes for the response variable. In our case, $c = 6$ taxa and we used $g = 10$ following Fagerland et al. (2008) and Fagerland and Hosmer (2012). Under the null hypothesis (good model fit), the test statistic (C_g) is chi-square and has $(g - 2)(c - 1)$ degrees of freedom.

RESULTS

In 78 cavities, we found a total of 153 nests and 16 roosts of 8 bird species >140 g, 1 mammal genus >140 g, and 1 insect order. Specifically, we found 21 nests of Vinaceous-breasted Parrot in 14 cavities, 1 nest and 1 roost of Barn Owl in 2 cavities, 39 nests and 1 roost of Red-breasted Toucan in 21 cavities, 4 nests of Saffron Toucanet in 4 cavities, 6 nests and 1 roost of Chestnut-eared Aracari in 4 cavities, 3 nests of Barred Forest-Falcon in 1 cavity, 34 nests of Scaly-headed Parrot in 26 cavities, 25 nests of White-eyed Parakeet in 13 cavities, 13 roosts of opossums in 13 cavities, and 20 nests of social bees and wasps in 14 cavities.

Timing of Breeding

We began to find nests of the Vinaceous-breasted Parrot, Barred Forest-Falcon, and Scaly-headed Parrot in September, with the greatest number of active nests in October and November, and few active nests in December (Figures 1A, 1F, and 1G). Nests of the Red-breasted Toucan, Saffron Toucanet, and Chestnut-eared Aracari were found beginning in October, and the highest numbers of active nests of these 3 species were recorded in November (Figures 1C, 1D, and 1E). In contrast, White-eyed Parakeets began laying in late November or December, after most individuals of the other bird species had finished nesting (Figure 1H).

Cavity, Tree, and Habitat Characteristics

The characteristics of cavities and trees used by Vinaceous-breasted Parrots varied widely, overlapping with those of most of the other studied taxa (birds and mammals >140 g and social insects; Tables 1 and 2, Figure 2). All of the cavities used by Vinaceous-breasted Parrots overlapped in depth, entrance diameter, and height with cavities used by one or more other taxa. The characteristics of cavities, trees, and habitats also overlapped greatly among taxa other than Vinaceous-breasted Parrot (Tables 1 and 2, Figure 2). The nests of all taxa were found primarily in live trees of native species (Table 2, Figure 2). However, 62% of the nest trees used by Vinaceous-breasted Parrots were on farms, vs. $\leq$50% for all other taxa except Barn Owls (Table 2).

The multinomial logistic regression models included 85 nests or roosts of 6 taxa (9 of Vinaceous-breasted Parrot, 18 of Red-breasted Toucan, 23 of Scaly-headed Parrot, 13 of White-eyed Parakeet, 13 of opossum, and 9 of bees or wasps). The global model was an improvement over the constant (intercept-only) model (likelihood ratio test: $\chi^2 = 49.84$, $P = 0.01$); however, it assigned only 38% of cavities to the correct taxon (56% for Vinaceous-breasted Parrot, 22% for Red-breasted Toucan, 52% for Scaly-headed Parrot, 46% for White-eyed Parakeet, 38% for opossum, and 0% for bees or wasps; Table 3). The habitat model ($w_i = 0.62$) received the most support, but the constant (null) model was closely competitive (within 2 AIC_c of the habitat model; Table 3).

Model-averaging revealed significant predictors of cavity use by Vinaceous-breasted Parrots vs. each of the other 6 taxa at the cavity, tree, and/or habitat scales (Table 4). At the cavity scale, the odds of a cavity being used by White-eyed Parakeets (vs. Vinaceous-breasted Parrots) doubled for each 35 cm ($1.02^{35} \approx 2$) increase in cavity depth (Table 4). There was, however, considerable overlap in depth between the cavities used by Vinaceous-breasted Parrots and White-eyed Parakeets: 92% of cavities used by White-eyed Parakeets were within the range of depth used by Vinaceous-breasted Parrots. Smaller entrance diameter was also a significant predictor of cavity use by White-eyed Parakeets and Red-breasted Toucans vs. Vinaceous-breasted Parrots (Table 4). For each 1 cm decrease in entrance diameter, the odds that a cavity would be used by White-eyed Parakeets increased by a factor of 1.7 ($0.59^{-1} \approx 1.7$), and the odds that it would be used by Red-breasted Toucans increased by a factor of 1.2 ($0.83^{-1} \approx 1.2$; Table 4). Nevertheless, 23% of cavities used by White-eyed Parakeets and 56% of cavities used by Red-breasted Toucans had entrance diameters larger than 7.0 cm, which overlapped with the size range used by Vinaceous-breasted Parrots (Table 1, Figure 2B). Also, each 2 m decrease in cavity height approximately doubled the odds of use by Red-breasted Toucans, Scaly-headed Parrots, White-eyed Parakeets, and opossums (Table 4). Again, however, there was considerable overlap in cavity height between cavities used by all of these taxa and those used by Vinaceous-breasted Parrots, as 71% of cavities used by Red-breasted Toucans, 73% of cavities used by Scaly-headed Parrots, 69% of cavities used by White-eyed Parakeets, and 62% of cavities used by opossums were above 10.6 m, the lowest height of cavities used by Vinaceous-breasted Parrots (Table 1, Figure 2C).

At the tree scale, there was a tendency for Vinaceous-breasted Parrots to use larger trees than Red-breasted Toucans, Scaly-headed Parrots, opossums, and bees or wasps. For each 10 cm decrease in DBH, the odds of the cavity being used by Red-breasted Toucans, Scaly-headed Parrots, opossums, or bees or wasps (vs. Vinaceous-

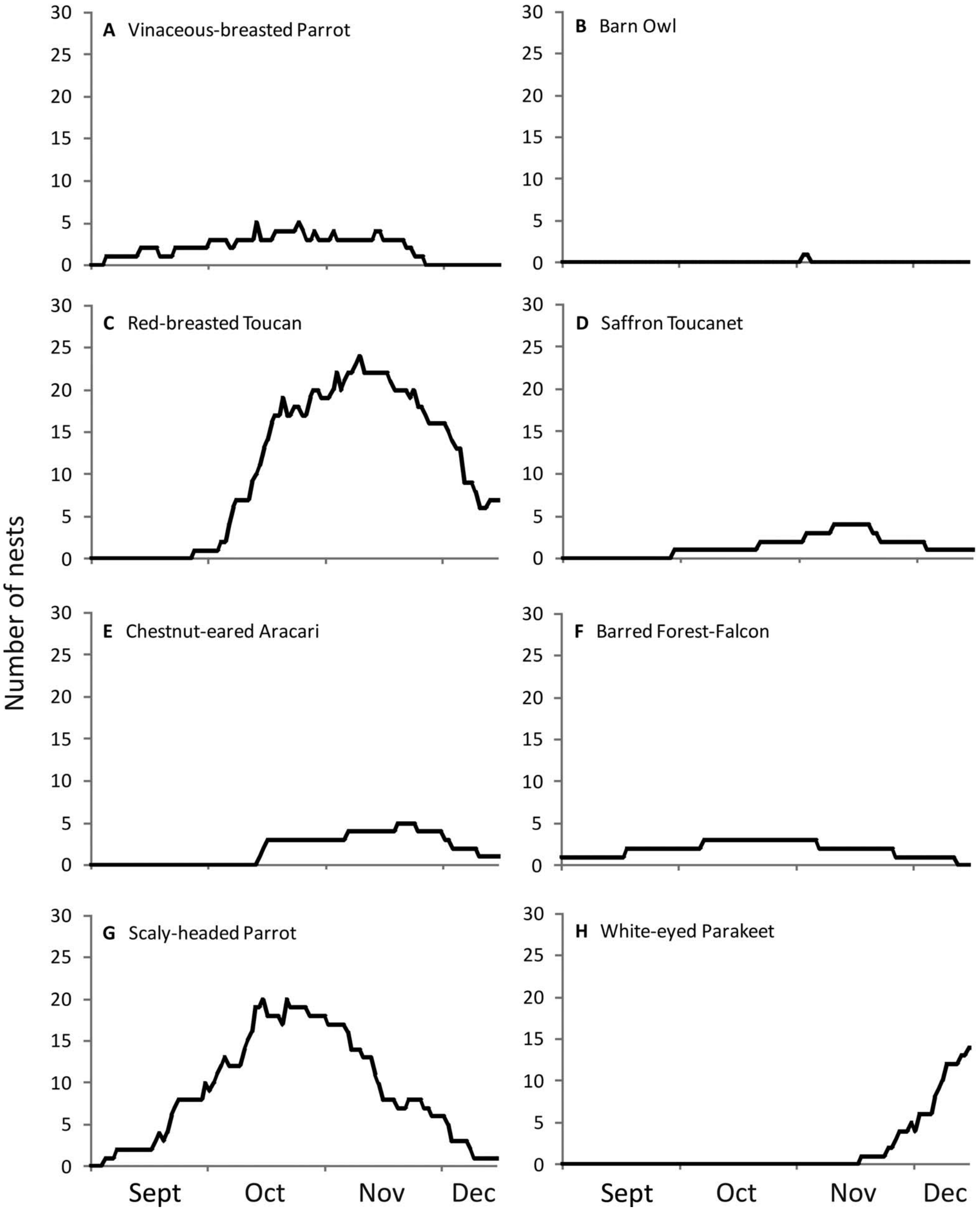

FIGURE 1. Number of active nests of 8 cavity-nesting bird species over the main breeding season in the Atlantic Forest of Argentina, 2006–2015. (**A**) Vinaceous-breasted Parrot ($n = 15$ nests), (**B**) Barn Owl ($n = 1$), (**C**) Red-breasted Toucan ($n = 40$), (**D**) Saffron Toucanet ($n = 3$), (**E**) Chestnut-eared Aracari ($n = 6$), (**F**) Barred Forest-Falcon ($n = 3$), (**G**) Scaly-headed Parrot ($n = 33$), and (**H**) White-eyed Parakeet ($n = 21$).

breasted Parrots) increased by a factor of 1.7, 1.5, 2.1, and 1.5, respectively (Table 4). Nevertheless, 76% of cavities used by Red-breasted Toucans, 62% of those used by Scaly-headed Parrots, 38% of those used by opossums, and 86% of those used by bees or wasps were in trees ≥55 cm DBH, overlapping the DBH range used by Vinaceous-breasted Parrots. All cavities used by these taxa were in trees with DBH ≥21 cm (Figure 2D).

At the habitat scale, for each 200 m increase in distance to edge (i.e. trees 200 m farther inside the forest), the odds of the cavity being used by Red-breasted Toucans, Scaly-headed Parrots, White-eyed Parakeets, and opossums (vs. Vinaceous-breasted Parrots) increased by a factor of 1.8, 2.2, 2.2, and 1.5, respectively (Table 4).

Cavity Reuse

We observed intraspecific reuse of cavities by all taxa except the Barn Owl and Saffron Toucanet (Table 5). We observed intraspecific reuse of 28% of all cavities (31% for Vinaceous-breasted Parrot; Table 5; calculation includes

TABLE 1. Characteristics of cavities used by the Vinaceous-breasted Parrot and 9 sympatric taxa in the Atlantic Forest of Argentina, 2006–2015. An asterisk indicates a globally threatened or near-threatened species. Body mass is given in parentheses after the taxon. For sexually dimorphic species, we provide the mass of the larger sex (female, F). Depth and entrance diameter could only be measured for accessible cavities, so the sample sizes (*n*; number of cavities) for these characteristics are sometimes slightly lower than those for cavity height.

	Cavity depth (cm)			Entrance diameter (cm)			Cavity height (m)		
Taxon (mass)	Mean ± SE	Range	*n*	Mean ± SE	Range	*n*	Mean ± SE	Range	*n*
Vinaceous-breasted Parrot * (382 g) [a]	89.6 ± 27.4	1.0–270.0	9	13.9 ± 3.0	7.0–34.7	9	17.7 ± 1.2	10.6–24.0	13
Barn Owl (F: 374 g) [b]	72.5 ± 37.5	35.0–110.0	2	34.5 ± 6.27	20.0–49.0	2	10.6 ± 3.1	7.5–13.8	2
Red-breasted Toucan (331 g) [c]	69.7 ± 12.4	28.0–270.0	18	7.9 ± 2.1	5.0–15.0	18	13.7 ± 1.1	4.0–22.0	21
Saffron Toucanet* (146 g) [c]	49.0 ± 14.7	20.0–68.0	3	5.5 ± 5.1	4.3–7.4	3	17.8 ± 4.0	7.0–24.0	4
Chestnut-eared Aracari (244 g) [c]	52.0 ± 2.1	49.0–56.0	3	5.8 ± 5.1	4.5–7.5	3	19.5 ± 3.1	11.9–27.0	4
Barred Forest-Falcon (F: 196 g) [c]	75.0	—	1	12.0	—	1	13.7	—	1
Scaly-headed Parrot (244 g) [d]	58.9 ± 5.7	18.0–110.0	23	9.5 ± 1.9	5.2–20.0	23	13.5 ± 0.9	5.9–22.0	26
White-eyed Parakeet (160 g) [d]	83.1 ± 22.8	36.0–346.0	13	6.2 ± 2.5	4.5–9.0	13	12.6 ± 1.3	5.6–21.4	13
Opossum (850–972 g) [e, f]	60.6 ± 11.2	1.0–158.2	13	9.7 ± 2.5	4.0–34.7	13	11.4 ± 1.0	3.8–17.6	13
Bees or wasps	72.2 ± 26.5	11.9–270.0	9	11.8 ± 3.0	4.3–49.0	9	15.2 ± 1.6	7.2–23.6	14

[a] Mean mass of 4 wild specimens at Museu de História Natural Capão da Imbuia, Brazil: MHN 6707, MHN 6242, MHN 6241, and MHN 5544.
[b] Salvador (2014).
[c] Dunning (1993).
[d] Schuck-Paim et al. (2008).
[e] de Almeida et al. (2008).
[f] Forero-Medina and Vieira (2009).

cavities found in the last year of the study). One cavity was used by Vinaceous-breasted Parrots in at least 4 consecutive years.

We observed interspecific reuse of 32% of all cavities, and 46% of the cavities used by Vinaceous-breasted Parrots. Vinaceous-breasted Parrot cavities were reused by Barn Owls, Red-breasted Toucans, opossums, and bees or wasps (Table 5). Cavities of nearly all bird species were reused by opossums and/or bees or wasps (Table 5).

DISCUSSION

In the globally threatened Atlantic Forest of Argentina, the supply of suitable tree cavities has been shown to limit the breeding density of at least some bird species (Cockle et al. 2010). The present study, in the same forest, confirms that several sympatric large-bodied birds, mammals, and social insects (1) use cavities simultaneously, (2) overlap in their nest- and roost-site characteristics, and (3) reuse cavities interspecifically. In particular, globally endangered Vinaceous-breasted Parrots overlap in breeding season and nest-site characteristics with Barn Owls, Red-breasted Toucans, Barred Forest-Falcons, Scaly-headed Parrots, opossums, and bees or wasps. The combination of a limited resource and overlap in realized niches suggests the potential for interspecific competition (Colwell and Futuyma 1971).

In our study area, none of the cavity-using taxa could be predicted accurately from models that included cavity, tree, and habitat characteristics. In contrast, similar approaches in North America, Australia, and India have revealed considerable niche partitioning within communities of cavity-nesting birds, marsupials, and hornbills, respectively (Li and Martin 1991, Lindenmayer et al. 1991, Datta and Rawat 2004). Additionally, we found that cavities were just as likely to have been reused by different taxa (32%) as by the same taxon (28%), again suggesting niche overlap among taxa, but contrasting with the results of studies conducted in temperate forests in Poland, Canada, and Mongolia, where cavities used by secondary cavity-nesters were much more likely to have been reused by the same species than by different species (Wesołowski 1989, Aitken et al. 2002, Bai and Mühlenberg 2008). Our results are consistent with several other studies that have found high levels of niche overlap within cavity-nesting communities, showing that 2 or more co-occurring taxa can exploit the same types of cavity resources at the same time (Van Balen et al. 1982, Enkerlin-Hoeflich 1995, Guerrero Ayuso and Arambiza Segundo 2004, Sarà et al. 2005). Processes other than interspecific competition are likely to be important drivers of nest-site selection, limiting multiple species to a similar realized niche. For example, whereas species' fundamental niches might include cavities at any height above ground, low nests suffer high predation rates in the Atlantic Forest, and birds benefit from selecting high cavities in greater proportion to their availability (Cockle et al. 2011b, 2015). Although niche partitioning can be an important mechanism for species

TABLE 2. Characteristics of the trees and habitats of the cavities used by the Vinaceous-breasted Parrot and 9 sympatric taxa in the Atlantic Forest of Argentina, 2006–2015. Tree species codes: a =*Apuleia leiocarpa*, b = *Araucaria angustifolia*, c = *Cabralea canjerana*, d = *Nectandra lanceolata*, e = *Ocotea pulchella*, f = *Parapiptadenia rigida*, g = *Prunus myrtifolia*, h = *Ruprechtia laxiflora*, i = *Ateleia glazioviana*, j = *Cedrela fissilis*, k = *Chrysophyllum marginatum*, l = *Enterolobium contortisiliquum*, m = *Melia azedarach* (exotic), n = *Ocotea lancifolia*, o = *Aspidosperma australe*, p = *Diatenopteryx sorbifolia*, q = *Myrocarpus frondosus*, r = *Alchornea triplinervia*, s = *Peltophorum dubium*, t = *Syagrus romanzoffiana*.

	Tree DBH (cm)			% in living tree [*n*]	Tree species [no. cavities]	Distance to edge (m) [a]			% on farms [*n*]
Taxon	Mean ± SE	Range	*n*			Mean ± SE	Range	*n*	
Vinaceous-breasted Parrot	94 ± 10	55–180	13	69 [13]	a [2], b [4], c [1], d [2], e [1], f [1], g [1], h [1]	249 ± 109	−197 to 1120	13	62 [13]
Barn Owl	103.6 ± 0.4	103–104	2	50 [2]	h [2]	−167 ± 185	−352 to 18	2	100 [2]
Red-breasted Toucan	66 ± 4	23–95	21	76 [21]	a [2], c [1], e [1], f [1], i [1], j [6], k [3], l [1], m [1], n [1]	545 ± 113	−73 to 1612	21	33 [21]
Saffron Toucanet	83 ± 18	44–132	4	100 [4]	a [3], o [1]	982 ± 158	550 to 1298	4	0 [4]
Chestnut-eared Aracari	96 ± 24	51–163	4	100 [4]	a [3], i [1]	407 ± 519	2 to 1097	4	50 [4]
Barred Forest-Falcon	83	—	1	100 [1]	a [1]	1529	—	1	0 [1]
Scaly-headed Parrot	66 ± 5	21–121	26	85 [26]	a [3], b [1], c [2], d [1], e [1], f [2], g [2], j [3], k [1], n [1], p [1], r [2], s [1], t [1]	608 ± 79	−121 to 1233	26	15 [26]
White-eyed Parakeet	76 ± 6	48–115	13	92 [13]	a [4], b [1], c [3], j [2], k [1], p [1], q [1]	659 ± 114	23 to 1506	13	8 [13]
Opossum	59 ± 6	30–110	13	92 [13]	a [2], c [2], d [1], g [2], i [1], n [1], r [2]	423 ± 68	2 to 841	13	15 [13]
Bees or wasps	71 ± 5	32–104	14	93 [14]	a [1], b [1], c [2], f [2], g [1], h [1], j [4], k [1]	416 ± 123	−352 to 1199	14	36 [14]

[a] Distance-to-edge values are positive for trees inside forest, and negative for isolated trees in cleared areas.

coexistence, other mechanisms (e.g., frequency-dependent predation and source–sink dynamics) can operate simultaneously to maintain biodiversity in the same communities, and the coexistence of species that share a niche does not necessarily contradict niche theory (Chesson 2000, Leibold and McPeek 2006).

Although our models could not predict which taxa used cavities based on cavity, tree, and habitat characteristics, we did find evidence of nest niche differences between some pairs of species. The near-threatened Saffron Toucanet, the Chestnut-eared Aracari, and the White-eyed Parakeet were the smallest birds that we considered (146–244 g), and they almost always used cavities $<$7 cm in entrance diameter, cavities that are probably inaccessible to the larger Vinaceous-breasted Parrot (382 g). This positive relationship between bird body size and cavity entrance size is consistent with the results of other studies at both local and global scales (Martin et al. 2004, Renton et al. 2015). Nevertheless, Scaly-headed Parrots, which also average 244 g, often used cavities $>$7 cm in entrance diameter, overlapping the Vinaceous-breasted Parrot's nest niche (Figure 2).

White-eyed Parakeets nested at a different time of year from nearly all of the other birds studied in the Atlantic Forest, laying their first eggs around the time that Vinaceous-breasted Parrots and other species were fledging (Cockle and Bodrati 2009, Bodrati and Cockle 2011, Bodrati et al. 2012, 2014, 2015, this study; Figure 1). The

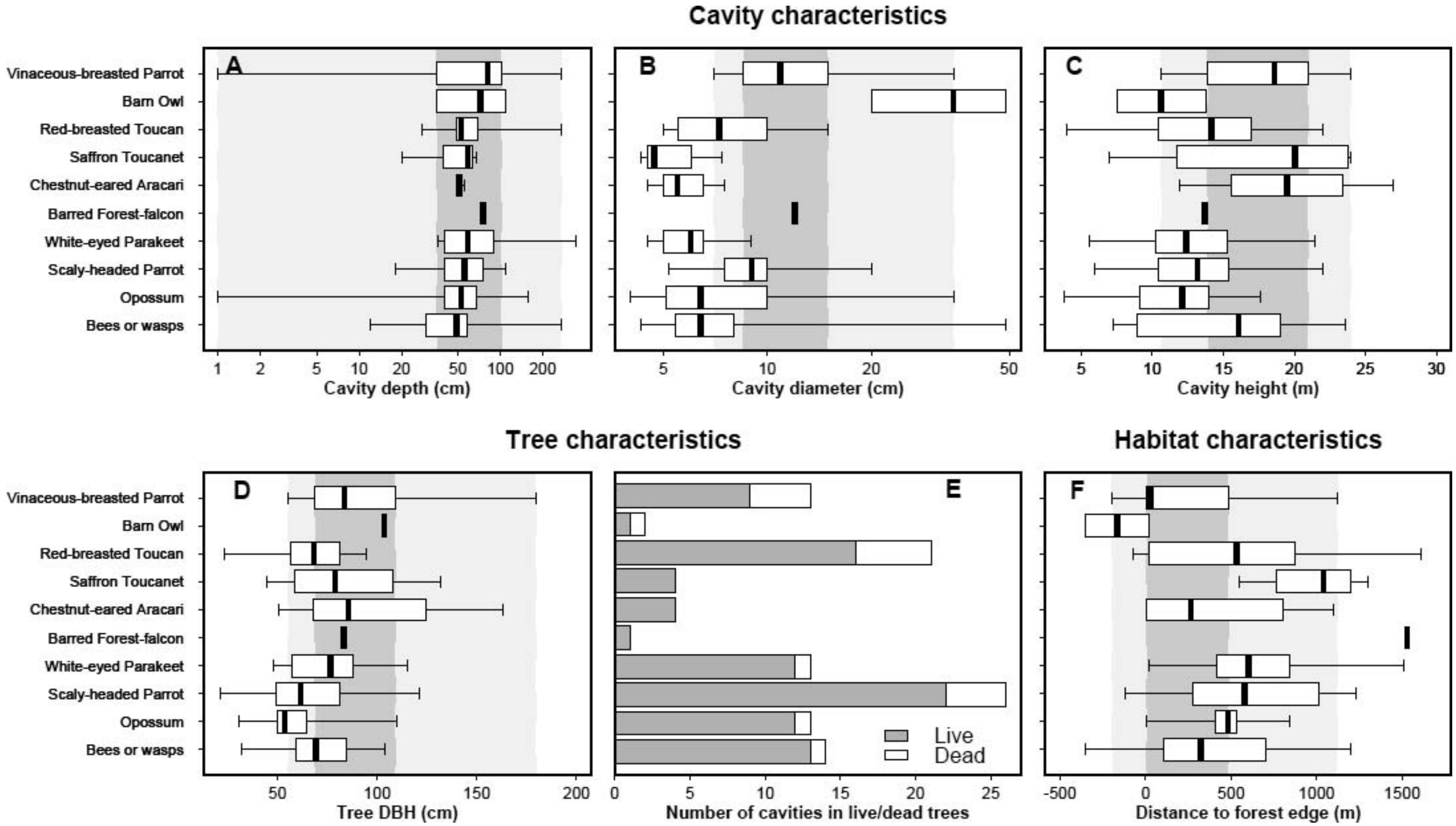

FIGURE 2. Characteristics of cavities, trees, and habitat used by the Vinaceous-breasted Parrot and 9 sympatric cavity-using taxa in the Atlantic Forest of Argentina, 2006–2015. Box plots show the median (thick vertical line), 1st and 3rd quartiles (box edges), and range (whiskers) of measurements. Range and interquartile range for the Vinaceous-breasted Parrot are highlighted in light and dark gray shading, respectively. Cavity depth and diameter are shown on a logarithmic scale to improve clarity. Distance-to-edge values are positive for trees inside forest, and negative for trees in the open. Sample sizes are given in Tables 1 and 2.

TABLE 3. Multinomial logistic regression models at 3 scales, predicting whether cavities were used by Vinaceous-breasted Parrots (reference taxon), Red-breasted Toucans, Scaly-headed Parrots, White-eyed Parakeets, opossums, or bees or wasps in the Atlantic Forest of Argentina, 2006–2015. Predictor variables included nest-site characteristics at the scale of the cavity (depth, entrance diameter, and height), the tree (DBH and tree condition [live or dead]), and the habitat (distance to edge). Sample size was 85 nests. For each model, we indicate the number of parameters (*K*), difference in value of Akaike's Information Criterion corrected for small sample size between each model and the top model (ΔAIC_c), Akaike weight (w_i), goodness-of-fit statistic (C_{10}) and associated probability (*P*; large *P*-values indicate good model fit), McFadden's R^2, and the percentage of observations that the model classified correctly.

Model	K	ΔAIC_c	w_i	C_{10}	P	R^2	% correctly classified
Habitat [a]	10	0.0	0.62	46.9	0.21	0.04	32
Constant [b]	5	1.3	0.32	—	—	—	27
Habitat + cavity	25	6.8	0.02	26.7	0.95	0.13	31
Cavity	20	7.1	0.02	39.5	0.49	0.09	28
Habitat + tree	20	8.0	0.01	37.4	0.59	0.09	26
Tree	15	9.2	0.01	32.4	0.80	0.04	27
Tree + cavity	30	17.2	0.00	45.1	0.27	0.13	35
Habitat + tree + cavity [c]	35	17.5	0.00	32.6	0.79	0.17	38

[a] AIC_c value of the best model = 303.3.
[b] Null model.
[c] Global model.

limited data on the breeding phenology of parrots suggests that, as in other birds, reproduction often coincides with a peak in food availability (Poulin et al. 1992, Young 1994, Hau et al. 2008, Díaz et al. 2012, Renton et al. 2015). If White-eyed Parakeets exploit different food resources than the other cavity-nesting birds in our study area, their late breeding could be explained by different phenology of their food source (Brightsmith 2005). The diet of White-eyed Parakeets appears to be broad, including seeds, fruits, and flowers of many plant species, similar to the diet of Vinaceous-breasted Parrots (Collar 1997, Di Giacomo 2005, Cockle et al. 2007, Gilardi and Toft 2012, Lee et al. 2014, A. Bodrati personal communication). These food items appear to be relatively stable year-round in our study area, and indeed several food plants (such as *Ficus* spp. and *Syagrus romanzoffiana*) exhibit asynchronous flowering within species (Agostini et al. 2010); nevertheless, it is possible that White-eyed Parakeets time their breeding to coincide with a specific food source, similarly to some other Neotropical parrots (Botero-Delgadillo et al. 2010, Botero-Delgadillo and Páez 2011). Another (nonexclusive) hypothesis is that breeding at a different time could be a strategy to avoid competition for scarce suitable cavities (Ingold 1989, Brightsmith 2005, Steward et al. 2013). In support of this hypothesis, we have recorded White-eyed Parakeets laying eggs in cavities recently vacated by other bird species (9 of 35 nests; K. L. Cockle and E. B. Bonaparte personal observations). Studies of the White-eyed Parakeet's diet and phenology throughout its large range would help to determine whether food and/or cavity availability may be driving the late breeding of this species in the Atlantic Forest.

Our study has several caveats that should be considered when interpreting our results. The first is the coarser scale of our data on cavities used by opossums and bees or wasps compared with birds. We grouped the former taxa because we could not usually identify individuals to species; however, the species within these groupings could differ in their nest- and roost-site preferences. Furthermore, cavities used by these animals were only recorded if they were also used by at least one species of bird (including smaller birds and cavity excavator species excluded from the present study). Thus, we may have underestimated the range of nest- and roost-site characteristics of cavities that could be used by these animals, and overestimated their niche overlap. For example, whereas Vinaceous-breasted Parrots and other birds consistently select high cavities (Cockle et al. 2011b, 2015, this study), at least some species of bees and wasps occupy cavities near ground level, which were not measured in the present study (K. L. Cockle personal observation). A second caveat is that natural nests are difficult to find in the Atlantic Forest, so, despite searching during 10 breeding seasons, we found relatively few nests per taxon compared with studies in temperate forests (e.g., Martin et al. 2004). For some taxa, such as the Barn Owl and Barred Forest-Falcon, we found only 1 or 2 cavities, so that we almost certainly underestimated the breadth of their nest niche. A third caveat is that we did not take into account the success or failure of nests, and may have overestimated the breadth of cavity characteristics that permit successful nesting by each taxon. However, whether or not its nest is successful, an animal occupying a given cavity still excludes other animals from that cavity, temporarily reducing the availability of the cavity resource. Despite the above limitations, our results demonstrate that Vinaceous-breasted Parrots overlap in their timing of breeding and in many nest-site characteristics with many other bird

TABLE 4. Model-averaged parameter estimates (*b*), standard errors (SE), odds ratios, and their 90% confidence intervals, from 7 multinomial logistic regression models predicting whether cavities were used by Vinaceous-breasted Parrots (reference taxon), Red-breasted Toucans, Scaly-headed Parrots, White-eyed Parakeets, opossums, or bees or wasps, in the Atlantic Forest, Argentina, 2006–2015. Model-averaged intercept estimates were: Red-breasted Toucan, 0.23 ± 0.44; Scaly-headed Parrot, 0.15 ± 0.44; White-eyed Parakeet, –0.31 ± 0.54; opossum, 0.11 ± 0.47; bees or wasps, –0.05 ± 0.48. For the reference taxon, all parameter estimates are 0 and odds = 1. Parameters in bold font have odds ratios with 90% confidence intervals that do not overlap 1. Odds ratios above 1 indicate a positive relationship between the predictor variable and the probability of use by the respective taxon (vs. Vinaceous-breasted Parrot). Odds ratios below 1 indicate a negative relationship between the predictor variable and the probability of use by the respective taxon (vs. Vinaceous-breasted Parrot). Odds ratios between any 2 taxa may be calculated by dividing the odds ratios provided here for each taxon.

Parameter	*b* ± SE	Odds ratio	Odds ratio CI
Red-breasted Toucan			
Cavity depth	0.009 ± 0.008	1.010	0.997–1.020
Entrance diameter	**-0.187 ± 0.098**	**0.829**	**0.706–0.974**
Cavity height	**-0.284 ± 0.140**	**0.753**	**0.599–0.946**
DBH	**-0.046 ± 0.022**	**0.955**	**0.920–0.991**
Tree condition (live)	0.820 ± 1.510	2.270	0.191–27.027
Distance to edge	**0.003 ± 0.001**	**1.003**	**1.000–1.005**
Scaly-headed Parrot			
Cavity depth	0.001 ± 0.009	1.000	0.987–1.015
Entrance diameter	-0.064 ± 0.058	0.938	0.853–1.031
Cavity height	**-0.264 ± 0.135**	**0.768**	**0.615–0.959**
DBH	**-0.045 ± 0.021**	**0.956**	**0.923–0.990**
Tree condition (live)	1.072 ± 1.503	2.922	0.248–34.360
Distance to edge	**0.003 ± 0.001**	**1.003**	**1.001–1.005**
White-eyed Parakeet			
Cavity depth	**0.018 ± 0.010**	**1.018**	**1.002–1.035**
Entrance diameter	**-0.526 ± 0.194**	**0.591**	**0.430–0.813**
Cavity height	**-0.357 ± 0.151**	**0.699**	**0.546–0.896**
DBH	-0.028 ± 0.022	0.973	0.938–1.009
Tree condition (live)	1.410 ± 1.772	4.078	0.223–74.602
Distance to edge	**0.004 ± 0.001**	**1.004**	**1.001–1.006**
Opossum			
Cavity depth	0.003 ± 0.010	1.003	0.988–1.02
Entrance diameter	-0.072 ± 0.063	0.930	0.840–1.031
Cavity height	**-0.353 ± 0.147**	**0.702**	**0.552–0.893**
DBH	**-0.076 ± 0.027**	**0.926**	**0.886–0.969**
Tree condition (live)	2.941 ± 1.807	18.930	0.978–366.491
Distance to edge	**0.002 ± 0.001**	**1.002**	**1.000–1.005**
Bees or Wasps			
Cavity depth	0.003 ± 0.009	1.003	0.999–1.018
Entrance diameter	-0.042 ± 0.058	0.959	0.872–1.054
Cavity height	-0.234 ± 0.151	0.791	0.617–1.015
DBH	**-0.042 ± 0.025**	**0.959**	**0.920–0.999**
Tree condition (live)	1.553 ± 1.792	4.725	0.250–89.325
Distance to edge	0.001 ± 0.001	1.001	0.999–1.004

species, opossums, and social insects in the Atlantic Forest, and use some of the same individual cavities.

To test whether 2 species compete for a given resource it is necessary to modify the abundance of 1 species (and/or the resource) experimentally, and then measure the effect on demographic parameters of the other species, such as its abundance, breeding density, or reproductive output (Pulliam 2000, Dhondt 2012). With so many native species potentially competing for nest sites in the Atlantic Forest, and the high level of threat facing this ecosystem, there is limited scope for such an experiment. However, management efforts to conserve wild birds, particularly *Amazona* species, sometimes involve manipulating either cavity supply (by providing nest boxes or modifying tree cavities) or the abundance of potential competitors (e.g., by culling exotic bees; White et al. 2005, Waugh 2009, Kilpp et al. 2014, Efstathion et al. 2015). With some thought to experimental design (e.g., Lõhmus and Remm 2005, Sarà et al. 2005), researchers could harness such programs to measure species' fundamental nest niches (by creating an oversupply of cavities) and test hypotheses about interspecific competition, even in diverse and threatened habitats such as the Atlantic Forest. Such experiments, accompanied by studies of nest niches in natural tree

TABLE 5. Cavity reuse among 10 cavity-using taxa in the Atlantic Forest of Argentina, 2006–2015. Values indicate the number of cavities that were used more than once by the same taxon (intraspecific reuse), or by each pair of taxa (interspecific reuse, $n =$ total number of cavities used by each taxon). Empty cells indicate no reutilization for that pair of taxa. Dashes (—) indicate redundant cells.

	Vinaceous-breasted Parrot	Barn Owl	Red-breasted Toucan	Saffron Toucanet	Chestnut-eared Aracari	Barred Forest-Falcon	Scaly-headed Parrot	White-eyed Parakeet	Opossum	Bees or wasps	*n*
Vinaceous-breasted Parrot	4	1	2						2	2	13
Barn Owl	—									1	2
Red-breasted Toucan	—	—	7		1		6	4	2	6	21
Saffron Toucanet	—	—	—							1	4
Chestnut-eared Aracari	—	—	—	—	2				1		4
Barred Forest-Falcon	—	—	—	—	—	1					1
Scaly-headed Parrot	—	—	—	—	—	—	6	—	3	3	26
White-eyed Parakeet	—	—	—	—	—	—	2	6	2	2	13
Opossum	—	—	—	—	—	—	—	—	1	1	13
Bees or wasps	—	—	—	—	—	—	—	—	—	3	14

cavities, could produce management tools to reduce interspecific competition for nest sites, favoring threatened species (e.g., Snyder et al. 1987, Efstathion et al. 2015).

Of particular concern for conservation of the Vinaceous-breasted Parrot is that its nest niche overlapped with the niches of 3 taxa known to be nest predators and/or usurpers (Red-breasted Toucan, opossums, and bees or wasps), a result that may explain the low rates of nest survival that have been recorded for Vinaceous-breasted Parrots (Jablonski et al. 2013, Cockle et al. 2015, 2016). Although the Vinaceous-breasted Parrot overlapped in nest niche with many other taxa and we found no region of complete nest niche singularity, some types of cavities were selected more by these parrots than by their potential competitors. Cavities and trees with these characteristics should be targeted for conservation: high (>10 m), large cavities (7–40 cm diameter), in large-diameter trees (>55 cm). At the habitat level, Vinaceous-breasted Parrots selected cavities on or near farmland in higher proportion than the other taxa; however, such nest sites may expose them to an increased risk of poaching (Segovia and Cockle 2012). We recommend conserving and recruiting cavity trees for Vinaceous-breasted Parrots both on farms and in forests. Our results that 62% of Vinaceous-breasted Parrot cavities were found on farms, and 31% were reused by Vinaceous-breasted Parrots over the course of the study, highlight the importance of working with local farmers toward long-term protection of the trees in which they have observed these parrots nesting.

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Ethics statement: We followed the Ornithological Council's *Guidelines to the Use of Wild Birds in Research*.

Author contributions: K.L.C. conceived the initial idea, and both authors contributed to funding, study design, data collection, statistical analyses, and writing and editing the paper.

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