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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.

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; Wesołowski, 2002; Wesołowski 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 Yarí (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,