Forest Ecology and Management 384 (2017) 200–207

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Persistence and loss of tree cavities used by birds in the subtropical Atlantic Forest

Kristina L. Cockle [a,b,c,*], Kathy Martin [b,d], Alejandro Bodrati [c]

[a] Instituto de Bio y Geociencias del NOA (IBIGEO-CONICET-UNSa), Av. 9 de Julio 14, Rosario de Lerma, Salta 4405, Argentina
[b] Centre for Applied Conservation Research, Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada
[c] Proyecto Selva de Pino Paraná, Vélez Sarsfield y San Jurjo S/N, San Pedro, Misiones 3352, Argentina
[d] Environment and Climate Change Canada, 5421 Robertson Road, RR1, Delta, BC V4K 3N2, Canada

ARTICLE INFO

Article history:
Received 30 July 2016
Received in revised form 20 October 2016
Accepted 24 October 2016

Keywords:
Atlantic Forest
Hole-nesting bird
Nest site
Tree hollow
Wood density
Woodpecker

ABSTRACT

An important goal for the conservation of tropical forest biodiversity is to maintain adequate supplies of tree cavities to support diverse communities of cavity-nesting and roosting vertebrates over the long term, especially in human-modified landscapes. The conservation and replacement of nesting cavities depend critically on cavity persistence, which is predicted to decline with increasing anthropogenic impact to the habitat, and to vary according to characteristics of trees and excavators. We used Cox proportional-hazards models to study the factors influencing persistence of 277 cavities used by 43 species of nesting birds in 38 species of trees, across a gradient of human impact in the subtropical Atlantic Forest of Argentina, 2004–2016. Median cavity persistence was 6 years, with 79% of cavity losses caused by the collapse of either the whole tree or the section of the tree holding the cavity. Contrary to predictions, cavity persistence did not vary across habitats (primary forest, degraded forest, farm) or excavator types (true woodpecker vs. weak excavator). Persistence was highest (median > 10 years) for non-excavated cavities in live trunks of healthy trees, and increased with tree size and species-specific wood density. Thus, although logging and conversion to farmland remove most cavities, the cavities that remain in these human-modified habitats provide high quality, multi-annual nest sites for forest birds. Preserving and restoring these cavities should be a priority for conservation of forest vertebrates. The positive effect of species-specific wood density on cavity persistence suggests a trade-off in rates of cavity turnover, whereby cavities are produced early but lost quickly in fast-growing (low wood density) pioneer tree species, and produced late but persist much longer in slow-growing (high wood density) climax species.

1. Introduction

An important long-term goal for the conservation of forest biodiversity is to maintain adequate supplies of tree cavities to shelter nesting and roosting vertebrates, especially in human-modified landscapes (Lindenmayer et al., 2006; Politi et al., 2012). Most cavity-nesting vertebrates are non-excavators (secondary cavity-nesters) that cannot produce their own cavities, and instead rely on avian excavators and natural decay processes to produce this critical resource (Newton, 1994; Martin and Eadie, 1999; Martin et al., 2004). As a result, populations of non-excavators may frequently be limited by cavity supply, especially in human-altered landscapes (Newton, 1994; Cockle et al., 2010). To ensure a sufficient supply of nest sites in logged or cleared areas, conservation policies for cavity-nesting vertebrates often include retention of legacy trees. To be effective, such efforts require information about the persistence times of tree cavities under a range of ecological and environmental conditions.

In temperate forests, tree cavities can persist more than 30 years, during which time they can be used by a diverse sequence of vertebrates (Aitken et al., 2002; Wesołowski, 2012). Cavities in temperate forests are typically destroyed by tree fall, breakage, decay of cavity walls, occlusion (growing over), or vertebrate damage (Wesołowski, 2011, 2012; Edworthy et al., 2012). However, persistence of tree cavities varies geographically and according to characteristics of the habitat, trees and cavities, with longer persistence in closed forest and large living trees (Sedgwick and Knopf, 1992; Lindenmayer and Wood, 2010; Cockle et al.,

* Corresponding author at: Instituto de Bio y Geociencias del NOA (IBIGEO-CONICET), Av. 9 de Julio 14, Rosario de Lerma, Salta 4405, Argentina.
E-mail addresses: kristinacockle@gmail.com (K.L. Cockle), kathy.martin@canada.ca (K. Martin), alebodrati@gmail.com (A. Bodrati).

http://dx.doi.org/10.1016/j.foreco.2016.10.052
0378-1127/

2011a; Wesołowski, 2011, 2012; Edworthy et al., 2012; Lindenmayer et al., 2012; Edworthy and Martin, 2013).

Within geographic locations, cavity persistence can vary among tree species (Nielsen et al., 2007). Wesołowski (2012) observed a threefold difference in cavity persistence among tree species at a single site in Poland, and proposed that this variation could be related to species-specific wood hardness. Although not studied specifically for cavity-bearing trees, high wood density appears to convey resistance to both decay and breakage (Chambers et al., 2000; Chave et al., 2009). Decay resistance (durability) also results from secondary chemical compounds in the heartwood, which allow trees of some species to stand >1000 years before collapsing (Scheffer and Cowling, 1966; Loehle, 1987; Hennon et al., 2002; Kurokawa et al., 2003; Oliveira et al., 2005). At a given location, then, we can predict cavity persistence to increase with species-specific wood density and durability.

Cavity persistence has also been linked to excavator species (Wesołowski, 2011; Edworthy et al., 2012). True woodpeckers (Picinae) have morphological adaptations that allow them to excavate cavities into hard wood (Burt, 1930; Spring, 1965; Kirby, 1980; Lorenz et al., 2015). Lacking these adaptations, other species, including piculets (Picumninae), trogons (Trogonidae), and tits (Paridae), must excavate in softer wood, often in advanced stages of decay (Skutch, 1959; Collias, 1964; Christman and Dhondt, 1997; Steward and Pierce, 2011; Manegold and Töpfer, 2013), which can lead to more rapid collapse of their cavities (Edworthy et al., 2012).

Although most cavity-nesting vertebrates inhabit the tropics and subtropics, little is known about the persistence of tree cavities at these latitudes, where warm conditions favourable for decay organisms may lead to high rates of cavity loss. In the subtropical humid Atlantic Forest of Argentina, 77 species of birds (16 excavators and 61 non-excavators) use tree cavities for nesting (Cockle et al., 2011a, KLC unpubl. data). The Atlantic Forest once covered much of south-eastern Brazil, eastern Paraguay, and north-eastern Argentina, but >85% has been replaced by ranching, agriculture and urbanization, and the region is considered one of the top global priorities for biodiversity conservation (Myers et al., 2000). Previous work showed that persistence was higher for non-excavated cavities than for bird-excavated cavities in the Atlantic Forest (Cockle et al., 2011a). Other factors likely to influence cavity persistence, such as stand context, or characteristics of trees and excavators, have not been studied, to our knowledge, in any tropical or subtropical forest.

Building on work presented in Cockle et al. (2011a), the present study aimed to determine how characteristics of stands, trees, and cavities influenced the persistence of cavities used by birds, and thus their long-term availability to cavity-dependent birds and other vertebrates in the Atlantic Forest. At the stand level, we hypothesized that the removal of neighbouring trees increases the risk of wind throw (Ferreira and Laurance, 1997; Scott and Mitchell, 2005; Mascarúa López et al., 2006), leading to lower persistence of cavities in selectively-logged or cleared areas. At the tree level, we hypothesized that trees would be more stable if they were healthy and larger in diameter, with high-density, durable (decay-resistant) wood. We predicted that cavity persistence would decrease with increasing decay stage, and increase with tree diameter, wood specific gravity (density) and wood durability. At the cavity-level, we hypothesized that high, dead limbs would be unstable. We therefore predicted a negative relationship between cavity persistence and cavity height, higher persistence in living than dead substrates, and higher persistence in tree trunks than in limbs. Additionally, we predicted persistence to be higher for true woodpeckers (Picinae) compared to weak excavators (*Trogon* and *Picumnus* spp.). Finally, we compare our results to cavity persistence studies from temperate forests of Australia, Europe and North America.

2. Methods

2.1. Study area

We studied tree cavities used by nesting birds in the Atlantic Forest, Misiones province, north-eastern Argentina. Parts of the Atlantic Forest, including Misiones, are located south of the Tropic of Capricorn. 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 (unlogged) 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 (Misiones, Argentina). 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 a.s.l. Annual rainfall is 1900 mm distributed evenly throughout the year.

2.2. Field methods

We studied cavities used for nesting by birds in primary forest, logged forest, and farms, from 2004 to 2016. We found about 90% of nests by observing the behaviour of adult birds (about 6 observer-hours daily from September to December, 2006–2015), from permanent and temporary trails, off-trail, and a grid of transects spaced every 500 m (total 27 km). A few additional nesting trees were shown to us by rangers, farmers, and colleagues, some of whom were studying radio-tagged woodpeckers (2004–2015). When we detected bird activity at a cavity, we inserted a 1.8-cm diameter video camera to confirm nest contents. Cameras were mounted either on the tip of a horizontal rod at the top of a 15-m telescoping pole, or at the end of a 2-m hose which we carried to the cavity via ladder (10 m) or single-rope tree-climbing (any height, if the tree had a sturdy fork). Cavities were included in our study if they contained eggs and/or chicks. About 20% of nest cavities were not accessible using the pole, ladder, or tree climbing. They were observed from the ground for several periods of at least 2 h each, and were included in the study only if bird behaviour indicated the presence of eggs or nestlings. Once used, cavities were revisited every subsequent year until September 2016 to determine their persistence. A cavity was considered "lost" if (1) the tree or cavity-bearing limb had fallen to the ground, (2) the cavity had deteriorated so that it no longer had walls and a bottom, or (3) bark closed off the cavity entrance.

At each nest tree we measured variables expected to affect cavity persistence at the stand, tree and cavity scales. At the stand scale, we assigned the nest to one of three habitat types: primary forest, degraded forest, or farm. To be included in the "primary forest" category, cavities had to be >10 m from vehicle roads or cleared areas, in forest with no history of timber harvesting (Bertolini, 1999, 2000). Cavities were included in the "farm" category if they were in isolated trees within cultivated land or pastures (these trees were 23–474 m from forest edge). All other cavities were included in the "degraded forest" category (i.e., the forest had been selectively harvested for timber, the forest had been cleared and grown back, or the tree was within 10 m of