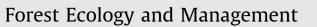
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## Responses to experimental reduction and increase of cavities by a secondary cavity-nesting bird community in cavity-rich Pyrenean oak forests

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#### ABSTRACT

Cavity shortage limits secondary cavity-nesting birds (SCN) assemblages in intensively-managed forests with few cavities, but whether cavity availability limits SCN in cavity-rich forests remains unclear. To address this issue, we used a replicated before-after-control-impact design in which the availability of cavities was experimentally reduced and increased in cavity-rich Quercus pyrenaica forests. Cavity-blocking and nest-box addition led to reduction by 66% and increase by 185%, respectively, of nest densities of blue (Cyanistes caeruleus) and great (Parus major) tits. Analysis of cavity characteristics suggests that tits occupied less suitable cavities in blocking plots compared to control and nest-box addition plots after treatments, further indicating that the availability of suitable nest-sites may limit tit populations. No effect of cavity manipulation was found for short-toed treecreepers (Certhia brachydactyla) and Eurasian nuthatches (Sitta europaea), which defend larger territories than tits and whose numbers may be more influenced by territoriality than by nest-sites. Alternatively, high plasticity in nest-site use of treecreepers may enable them to cope with reductions in cavity availability and increased interspecific competition. Spotless starlings (Sturnus unicolor) were little affected by cavity manipulation. Often foraging on pastures, starlings may be more limited through reduced foraging opportunities in this forested landscape than by nest-sites. In addition, starlings may exclude other species from their preferred cavities to cope with reductions in numbers of suitable cavities. Community responses to the variation in cavity abundance in cavity-rich Pyrenean oak forests may therefore vary considerably among species, depending on their plasticity in nest-site use, behavioral dominance, foraging conditions or social structure. Thus, management actions aimed to increase cavity abundance and suitability for SCN communities in cavity-rich forests should consider inter-specific interactions and species-specific characteristics of the targeted species.

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#### 1. Introduction

Secondary cavity-nesting birds (SCN), which cannot create their own breeding cavities, occupy either cavities excavated by woodpeckers or created by decay processes (e.g. Martin et al., 2004; Strubbe and Matthysen, 2009; Robles et al., 2011). Consequently, SCN populations and communities have been shown to be strongly affected by cavity abundance, particularly in managed forests that hold low numbers of suitable cavities for breeding (Caine and Marion, 1991; Newton, 1994; Sánchez et al., 2007; Cockle et al., 2010; Robles et al., 2011). However, despite extensive research on the ecology of SCN, it remains unclear whether cavity availability limits SCN assemblages in cavity-rich forests (Wiebe, 2011),

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where SCN comprise a major component of avian communities (Newton, 1994). In addition, the species-specific responses of SCN to changes in cavity availability are poorly known (Wiebe, 2011) and probably more complex than a priori expected (e.g. Eadie et al., 1998; Aitken and Martin, 2008; Blanc and Walters, 2008). This is particularly relevant because SCN species often differ in nest-site use, population densities, social structure or foraging strategies, which can influence the response of individual SCN species to cavity shortage. Consequently, there is not a clear picture on which species can be most limited by cavity shortage and, hence, how cavity abundance affects the relative abundances of SCN species, particularly in cavity-rich forests.

Two non-exclusive hypotheses may explain the response of individual species (and consequently, the response of the community) to the variation in the abundance of cavities (the critical resource): (i) the "dominance" hypothesis and (ii) the "plasticity in nest-site use" hypothesis. The "dominance" hypothesis predicts that subordinate species will decrease in density under scenarios

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of severe cavity reduction because dominant species take-over their nests when nesting opportunities are reduced (Aitken and Martin, 2008; Strubbe and Matthysen, 2009). This is particularly true when dominant and subordinate species share nest-site requirements and depend on specific types of cavities. According to the "plasticity in nest-site use" hypothesis, specialist species are more influenced by a reduction of suitable cavities than nestsite generalist species, as the former depend on rare specific types of cavities which are more likely to become even scarcer after cavity reduction (Aitken and Martin, 2008). Conversely, species with high plasticity in nest-site use can use a broad range of cavities, which enable them to cope with variation in cavity availability and to contend with intraspecific competition (Aitken and Martin, 2008). In addition to these hypotheses, indirect species interactions can also influence community structure (Blanc and Walters, 2008: Kappes and Davis, 2008: Norris and Martin, 2010). For example, through enlargement of excavated red-cockaded woodpecker (Picoides borealis) cavities, northern flickers (Colaptes auratus) provide nesting opportunities to large SCN such as American kestrels (Falco sparverius paulus) and eastern screech owls (Otus asio). This shows that both cavity creation and enlargement are crucial processes in maintaining the structure of the community (Blanc and Walters, 2008). Thus, different responses of SCN communities to the variation in cavity abundances are expected depending on species-specific characteristics and interactions among individual species.

Most previous experimental studies on population limitation in cavity-nesters have involved addition of nest-boxes (e.g. Caine and Marion, 1991; Bock and Fleck, 1995; Pöysä and Pöysä, 2002; Lõhmus and Remm, 2005; Loman, 2006; Sánchez et al., 2007; Lindenmayer et al., 2009; Cockle et al., 2010; Miller, 2010; Aitken and Martin, 2012), whereas few studies have manipulated the abundance of natural cavities, mostly by reduction of cavity numbers through cavity-blocking (Brush, 1983; Waters et al., 1990; Aitken and Martin, 2008; Blanc and Walters, 2008; Strubbe and Matthysen, 2009). Only Brush (1983) has previously performed simultaneous cavity-blocking and nest-box addition experiments. but only in one replicate per treatment. To our knowledge, no studies have performed a replicated before-after-control-impact (BACI; Underwood, 1994) experimental design in which the availability of cavities was both reduced and increased simultaneously in the same habitats. Such study approach can improve our knowledge on the influence of nest-sites on SCN populations and communities. In cavity-rich environments where only a small proportion of cavities are used for nesting, a decrease in nest density induced by blocking the access to the few cavities used for nesting would mean that birds were unable to use at least some of the remaining non-blocked cavities. This in turn would suggest that bird populations are limited by availability of suitable nest-sites, instead of the total amount of cavities, at least under a scenario of slight reduction in cavity numbers. However, a lack of effect of cavity blocking on nest density would show that populations were not limited by availability of suitable nest-sites. On the other hand, an increase in nest density associated with the addition of nest-boxes would indicate that bird populations are limited by availability of nest-sites, whereas the lack of effect of nest-box addition would show that either populations are not limited by nest-sites or nest-boxes were not suitable for the targeted bird species. Moreover, experiments based on nest-box addition may help assess whether nest-box provisioning is a suitable strategy for conservation of SCN populations and communities (Lindenmayer et al., 2009).

Pyrenean oak (*Quercus pyrenaica*) forest is endemic of the western Mediterranean area (Tárrega and Luis, 1990; Calvo et al., 1991). Even though the Iberian Peninsula has the largest area occupied by this forest in its distribution range, only 2.2% of the Pyrenean oak forest surface has been protected in Spain (Maldonado et al., 2001). This study aims to improve our understanding on the ecological factors that influence SCN community structure in this particular forest ecosystem to provide effective management measures for their conservation. In a previous study (Robles et al., 2011), we have found that the number of SCN species and their abundances are lower in intensively-managed young Pyrenean oak forests with few cavities than in cavity-rich old forests, which suggests that low numbers of cavities may limit SCN populations and communities in the former. However, the influence of cavity numbers on the community structure of SCN in cavity-rich Pyrenean oak forests remains unclear and deserves more research. We used a replicated before-after-control-impact design in which the availability of cavities was both experimentally reduced and increased to assess the influence of the abundance of cavities on a SCN community inhabiting cavity-rich Pyrenean oak forest tracts of the Cantabrian Mountains (NW Spain). We first aimed to examine the response of the community by pooling all the species of the SCN assemblage. Then, we assessed species-specific responses to cavity manipulation. We addressed these issues by blocking nesting cavities and by supplying nest-boxes. Based on our results, we proposed management measures for the conservation of SCN assemblages in cavity-rich Pyrenean oak forests.

#### 2. Methods

#### 2.1. Study sites and experimental design

Data were collected in a ca. 200 km<sup>2</sup> area in the southern Cantabrian Mountains (NW Spain, 42° 43' N, 5° 1' W). This area is dominated by Pyrenean oak forest, covering ca. 85% of the surface (Robles et al., 2007, 2011). Pyrenean oaks can be mixed with a small proportion (<5%) of other Quercus species (Quercus faginea, Quercus petraea and Quercus paucirradiata), and less frequently (<1%) with non-oak species (e.g. Pinus spp., Populus spp., Salix spp.). Other forested habitats (2%) are pine plantations (Pinus spp.), riverside (Populus spp., Salix spp., Fraxinus sp.) and holm oak (Ouercus rotundifolia) forests. The remaining 13% is formed by non-forest habitats, such as pastures, scrublands, cereal croplands, roads and urban areas. In Pyrenean oak forests, we identified eight secondary cavity-nesting bird species: blue tit (*Cyanistes caeruleus*,  $\sim 10$  g), great tit (*Parus* major,  $\sim$ 18 g), spotless starling (*Sturnus unicolor*,  $\sim$ 87 g), short-toed treecreeper (Certhia brachydactyla, ~8 g), Eurasian nuthatch (Sitta europaea,  $\sim$ 22 g), pied flycatcher (*Ficedula hypoleuca*,  $\sim$ 13 g), common redstart (Phoenicurus phoenicurus,  $\sim 16$  g) and green woodpecker (Picus viridis, ~180 g). Green woodpeckers acted as SCN in this area, as they used previously existing holes instead of creating their own cavities (Robles et al., 2011). We identified two cavity excavators: great (Dendrocopos major, ~78 g) and middle (Dendrocopos medius, ~55 g) spotted woodpeckers. However, most cavities in Pyrenean oak forests are created by other processes such as fungal decay or mechanical damage of branches by wind (92% of the cavities; authors' unpublished data).

The study was conducted in nine forest plots with an average size of 7.9 ha  $\pm$  0.9 SE (range = 4.7–13.9). These plot sizes are enough to hold several territories or nests of most SCN except for green woodpeckers. Forest plots were spaced  $\geq$  0.9 km and were subjected to traditional management systems that favor the development of large-diameter oaks. Traditional management of Pyrenean oak forests is associated with extensive grazing and little selective cutting for firewood extraction (Robles et al., 2007, 2011). In 2007 and 2008, the influence of cavity availability on SCN was studied by a replicated before-after-control-impact design, in which we experimentally reduced and increased the availability of cavities suitable for nesting. We reduced the availability of nest-sites by blocking all cavities used for nesting by SCN in spring-early summer 2007 in Download English Version:

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