# SUITABLE CAVITIES AS A SCARCE RESOURCE FOR BOTH CAVITY AND NON-CAVITY NESTING BIRDS IN MANAGED TEMPERATE FORESTS. A CASE STUDY IN THE IBERIAN PENINSULA

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SUMMARY.—*Suitable cavities as a scarce resource for both cavity and non-cavity nesting birds in managed temperate forests. A case study in the Iberian Peninsula.*

**Aims:** To ascertain whether cavity-nesting bird communities are limited by experimentally-manipulated hole availability at managed beech and pine forests in northern Spanish highlands and to study the responses of non-cavity-nesting birds.

**Location:** North of Navarre (Spain).

**Methods:** Bird censuses were taken at breeding and wintering periods in study plots during 2001, 2002 and 2003. Nest boxes were placed in half of the study plots, and plots with and without nest boxes were compared for variation in nesting guild abundance and richness.

**Results:** Results showed an increase in cavity-nesting bird abundance and species richness between two breeding periods and in abundance between two non-breeding periods in the plots where nest boxes were added in both types of forest. No difference in abundance or richness during breeding was observed for the non-cavity nesting birds in plots where there was an increase in the abundance of cavity-nesters. However, an increase in abundance of non-cavity nesters in non-breeding periods was observed in plots where nest boxes were added in pine forests.

**Conclusion:** Results suggest that cavity-nesting bird communities were limited by the availability of suitable natural holes in the two forest types studied and highlight the importance of cavities outside the breeding season as shelter or roosting places for both cavity and non-cavity nesting bird communities.

*Key words*: cavity nesting bird, hole availability, nest boxes, non-cavity nesting bird, managed beech and Scots pine forests, northern Spain.

RESUMEN.**—***La disponibilidad de oquedades es un recurso escaso tanto para aves trogloditas como no trogloditas en bosques templados manejados. Un caso de estudio en la península Ibérica.*

**Objetivos:** Comprobar experimentalmente si la comunidad de aves trogloditas se encuentra limitada por la disponibilidad de oquedades en hayedos y pinares manejados del norte de España, analizando también la respuesta de las aves no trogloditas a la manipulación experimental de la disponibilidad de oquedades.

**Localidad:** Norte de Navarra (España).

**Métodos:** Se realizaron censos de aves durante los periodos reproductivos e invernales de 2001, 2002 y 2003. Se añadieron nidales artificiales en la mitad de las parcelas de estudio, analizando la variación de riqueza y abundancia de aves en parcelas con y sin nidales.

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**Resultados:** Se observó un incremento en la riqueza y abundancia de las aves trogloditas entre los dos periodos reproductivos y de la abundancia entre los periodos invernales en las parcelas donde se añadieron los nidales en ambos tipos de bosque. La variación entre periodos reproductivos de los parámetros poblacionales de las aves no trogloditas no mostró ninguna diferencia significativa en las parcelas con y sin nidales, aunque aumentó la abundancia en las parcelas con nidales entre los periodos invernales en los pinares.

**Conclusiones:** Los resultados sugieren que la comunidad de aves trogloditas se ve limitada por la disponibilidad de cavidades naturales adecuadas en los dos tipos de bosques estudiados. Además, resaltan la importancia de las cavidades fuera del periodo reproductor como dormideros o refugios tanto para aves trogloditas como no trogloditas.

*Palabras clave*: aves trogloditas, aves no trogloditas, bosques templados manejados de hayas y pinos silvestres, disponibilidad de oquedades, nidales artificiales, norte de España.

INTRODUCTION

Most forests in the temperate regions of Europe have been managed for a long time and, consequently, have undergone significant changes as compared to primeval forests in the distribution of tree age classes, the extent of old-growth stands and the availability of dead wood (Cumming *et al.*, 1994; Hagan *et al.*, 1997). The change in age class distribution towards younger age classes along with the loss of old forest stands and a decrease in the number of snags and old trees have sometimes led to a decrease in species depending on late-successional stages (Holmes *et al.*, 1986; Keller *et al.*, 2003) and, on the other hand, to an increase in species associated to young forests (Haila *et al.*, 1980). Old trees are an essential component in forests, supplying forest animals with food resources and perching, roosting and nesting places. The presence of cavities in old trees also plays an important role in forest ecosystems, since they are used by animals (*e.g.*, mammals, herpetofauna and birds) as nesting and/or shelter places (Welsh, 1990; Camprodon and Plana, 2001).

Among birds, cavity nesters are the most vulnerable to the scarcity of holes in a forest, especially secondary cavity-nesting birds, which are not able to hollow out their own cavities and depend on those already created by primary hole-nesters or tree senescence. Several studies have shown the dependence of secondary cavity-nesting birds on tree holes (Von Haartman, 1957; Hildén, 1965; Brawn *et al.*, 1984; Raphael and White, 1984; Zarnowitz and Manuwal, 1985; Holt and Martin, 1997; Martin and Eadie, 1999), in particular in managed forests, where there are usually fewer cavities available than in unmanaged forests (Newton, 1994). Where natural holes are lacking, nest boxes have turned out to be an alternative breeding place for secondary cavity-nesting birds (Waters *et al.*, 1990; Purcell *et al.*, 1997).

Although the number of cavities could determine the maximum number of pairs that breed in an area (Von Haartman, 1957; Zarnowitz and Manuwal, 1985), their availability does not always limit the population size of cavity-nesters (Sandström, 1992; Welsh and Capen, 1992). In addition to cavity availability, the density of cavity-nesting birds could be affected by factors such as food availability, winter mortality, predation rates and/or inter- and intraspecific territoriality (Hildén, 1965; Cody, 1985; Brawn and Balda, 1988; Martin, 1988; Waters *et al.*, 1990; Li and Martin, 1991; Martin, 1995). Competition for resources other than cavities could also structure forest bird communities (Wiens, 1989). Competition could occur between con-specifics or inter-specifics and not only at the species level but also at the guild level (Garcia, 1983; Bock *et al.*, 1992; Holt and

Martin, 1997; Martin and Martin, 2001). All the factors mentioned above highlight the importance of having a pluralistic perspective on the processes and factors involved in shaping avian communities.

In this study, avian community parameters in two types of managed temperate forests, Scots pine *Pinus sylvestris* and beech *Fagus sylvatica* forests were investigated, since broad-leaved trees and conifers presumably differ in the availability of nesting holes (Sandstörm, 1992; Bunnel, 2002). The aim was twofold. First, it was necessary to know whether cavity availability acts as a limiting resource for cavity-nesting species, thus affecting their population size and community structure. Secondly, and more interesting, to investigate whether there is competition between cavity and non-cavity nesters, since there is some evidence that an increase in the number of cavity-nesting birds could have a detrimental effect on non-cavity nesters (Bock *et al.*, 1992). Knowledge of the ecology and limitations of bird communities in managed forests would allow developing effective conservation and management strategies for this group of animals.

To achieve these aims, the availability of cavities was manipulated by supplying nest boxes to forest plots, also leaving appropriate controls. The variation in bird community parameters over the short-term was then compared between experimental plots and controls. According to the above-mentioned literature, an increase in the number of cavity nesters was expected (i.e. cavity nesters would be limited by the number of cavities) and, therefore, an increase in the abundance and/or richness of this avian guild in experimental plots was expected when compared with controls. In addition, if the whole avian community was limited by food resources, a decrease was expected in the abundance and/or richness of non-cavity nesters in forest plots where densities of cavity-nesters had been increased. Comparisons were included not only between breeding periods, but also between winter periods, because

the role of cavities outside the breeding season (*e.g.*, shelter, roosting places) is not well-known but might be important.

MATERIAL AND METHODS

*Study plots*

Fieldwork was conducted in the northeast of Navarre (Spain) from April 2001 to July 2003. Three areas of Scots pine forest [Sierra de Leire (42º39' – 42º40' N, 1º6' – 1º9' W), Roncal (42º48'–42º49' N, 0º54'–0º55' W) and Vidángoz (42º48' – 42º49' N, 0º59' – 1º0' W)] and three areas of beech forest [Sierra de Urbasa (42º49' – 42º51' N, 2º4' – 2º9' W), Sierra de Aralar (42º57' – 42º58' N, 2º0' – 2º2' W) and Monte de Limitaciones (42º47' – 42º49' N, 2º8' – 2º14' W)] were studied. Twenty plots were selected in the three areas of pine forest, trying to maximize tree size variability among plots (mean diameter at breast height (DBH) ranged 10 - 35 cm and number of trees per plot ranged 60 - 280). Following the same selection criterion, other 19 plots were selected in the three areas of beech forest (mean DBH ranged 12 - 50 cm and number of trees per plot ranged 8 - 180). All 39 plots were part of large forest areas ranging 1500-16000 hectares, i.e., they were not in isolated fragments. All plots were also located far from forest edges (minimum distance to forest edge ranged 900 - 2900 m). Every plot was a 25 m radius circle separated from the nearest plot by at least 500 m. Tree vegetation inside the plots was sampled. All trees, dead or alive (≥ 10 – cm  diameter at breast height (DBH) and > 3 m tall), were counted and their height and DBH recorded. Height was measured with a clinometer.

In February 2002, 300 nest boxes were placed in 12 out of 20 plots of pine forest, and 225 nest boxes were placed in 9 out of 19 plots of beech forest. Plots with nest boxes were chosen in a way that most of the variability in tree size was present in the two types of plot

(with and without nest boxes). Consequently, differences in mean DBH and number of trees between plots with and without nest boxes were far from significant (Student t-tests; pine forests; DBH: $t_{18}$ = -0.68, $P$ = 0.51; number of trees: $t_{18}$ = -0.91, $P$ = 0.37; beech forests; DBH: $t_{17}$ = 0.14, $P$ = 0.89; number of trees: $t_{17}$ = 0.57, $P$ = 0.58). Twenty five nest boxes were placed in every plot using a pole. The minimum distance between nest boxes was 8 m and the height varied from 3 to 5 m. At the end of the 2002 breeding season, nest boxes were checked, cleaned and repaired. Nest boxes were supplied by the Spanish Ministry of the Environment.

*Bird censuses*

Bird censuses were taken at two different times of the year, corresponding to different periods in their life cycle: Reproduction 1 (2001 breeding season, May - June), Winter 1 (2001 - 2002 wintering season, November 2001 - February 2002), Reproduction 2 (2002 breeding season, May - June), Winter 2 (2002 - 2003 wintering season, November 2002 - February 2003), and Reproduction 3 (2003 breeding season, May - June).

The point-count method was used because it is the most appropriate method for forest birds in homogeneous but not very large plots (Reynolds *et al.*, 1980; Bibby *et al.*, 2000). This method has been used extensively for bird censuses in temperate forests (Poulsen, 2002; Groom and Grubb, 2002; Allombert *et al.*, 2005; Díaz *et al.*, 2005; Paquet *et al.*, 2006). Each observation period lasted 15 minutes. The observer waited for 5 minutes after arrival at the census point before beginning the recording period, during which the observer stood in the centre of the plot. Only birds either heard or seen inside the plot were recorded (i.e., ≤ 25 m away from the observer). Every bird was considered an observation regardless of its territorial status. Two censuses on different days were taken for each plot and period of the year

with the exception of the Roncal area during Winter 2, when only one census was taken per plot due to unfavourable weather. When data from two censuses were available, mean values were used for each plot and period. Observations were made in the morning (05:15 - 10:20 h GMT) by the same person (S. S.) and under similar weather conditions, discarding foggy, windy and rainy days. The study focused on species that were reliably detectable through vocal or visual cues and those whose home ranges were small enough so that a reasonable number of independent detections could be assured (Hutto *et al.*, 1986). This eliminated the sparrowhawk *Accipiter nisus*, the woodpeckers (*Dendrocopos major* and *Picus viridis*), the common cuckoo *Cuculus canorus*, the common woodpigeon *Columba palumbus*, the jay *Garrulus glandarius* and the carrion crow *Corvus corone*. Migratory cavity-nesting birds were not detected at the study plots, thus all cavity-nesting species were resident. Species included in the analyses and their abundances for the study periods considered (Reproduction 1, Reproduction 3, Winter 1, and Winter 2) are shown in the Appendix 1.

*Weather conditions*

Inter-year differences in mean daily temperature were calculated both between winter (December, January and February) and breeding periods (April, May and June). Data were obtained from the automatic meteorological stations of Sierra de Aralar and Sierra de Leire (Meteorological Service of the Government of Navarre, http://meteo.navarra.es). Data from February 19th to 28th were unavailable in 2002 at both stations. Data from December 28th 2001 to January 2nd 2002 and from April 5th to May 7th 2001 were unavailable at Sierra de Leire station. Winter 2 was significantly colder than Winter 1 in the pine forest area, but the difference did not reach the statistical significance in the beech forest area (paired Student t-tests;

beech forest area: $t_{79} = 1.78$, $P = 0.079$; mean (SE), Winter 1 = 1.54 ºC (0.43), Winter 2 = 0.33 ºC (0.43); pine forest area: $t_{73} = 2.34$; $P = 0.022$; mean (SE), Winter 1 = 2.11 ºC (0.49), Winter 2 = 0.64 ºC (0.44). There were no significant differences in mean daily temperature between Reproduction 3 and Reproduction 1 (beech forest area: $t_{57} = -0.66$, $P = 0.51$; mean (SE), Reproduction 1 = 11.89 ºC (0.71), Reproduction 3 = 12.42 ºC (0.87); pine forest area: $t_{57} = -0.73$; $P = 0.46$; mean (SE), Reproduction 1 = 13.82 ºC (0.69), Reproduction 3 = 14.36 ºC (0.88)).

*Statistical analysis*

Two bird community parameters were calculated: richness (mean number of avian species per plot, census and period) and abundance (mean number of individuals per plot, census and period), which were found to follow a normal distribution (Kolmogorov-Smirnov tests, $P > 0.2$ in all 8 cases). The variation in richness and abundance of bird species was calculated as the difference between their numbers before and after placement of nest boxes. Differences in richness and abundance were the dependent variables in the analyses.

Comparisons were made between Reproduction 3 (when some plots had boxes and other plots had not) and Reproduction 1 (all plots without boxes) periods, since we assumed that birds required a period of adaptation to learn to recognize nest boxes as a resource. That is, the Reproduction 2 period was not included in the comparisons. Winter seasons (Winter 2 – Winter 1) were also compared. To test the effect of the presence/absence of nest boxes on the variation of bird parameters, a backward stepwise GLM was run, including in the model the type of forest (beech *versus* pine) as a categorical variable, tree size and number of trees as covariates, and the interactions. Only terms associated with a $P$-value smaller than 0.1 were kept in the final model. When a significant interaction was found, separate analyses were run to find out the meaning of the interaction. Tree size was a PCA factor obtained from mean height and mean DBH of the trees in every plot. Tree size was included in the model because it is related to the potential for natural cavities and to the amount of food that trees can provide (Fan *et al.*, 2003). Number of trees (log-transformed to approach a normal distribution) was included in the model because tree density might influence bird community structure (Lawler and Edwars, 2002).

All statistical analyses, performed with the Stastistica (2001) Program, were two-tailed with a significance level of 0.05.

RESULTS

During the last breeding season of this study (Reproduction 3), four species bred successfully in nest boxes of beech forest plots: great tit *Parus major* (8 nests), blue tit *Parus caeruleus* (5 nests), coal tit *Parus ater* (1 nest), and nuthatch *Sitta europaea* (1 nest); and also four species bred in nest boxes of pine forest plots: coal tit (15 nests), great tit (14 nests), crested tit *Parus cristatus* (3 nests) and short-toed treecreeper *Certhia brachydactyla* (3 nests). Information about the use of nest boxes by birds in winter was not recorded.

The difference in abundance of cavity nesters in the two breeding periods and the two winter periods was influenced by the presence of nest boxes (Table 1). Plots where nest boxes were added showed an increase in the abundance of cavity-nesting birds as compared to plots without nest boxes (Fig. 1). However, the variation in richness of cavity nesters depended on the period considered. The effect of nest boxes on richness in winter was not significant, although there was a marginal effect. On the other hand, both the type of forest and the presence/absence of nest boxes explained the difference in richness between breeding pe-

TABLE 1

Results from backward stepwise General Linear Models with differences in abundance and richness between studied periods as dependent variables, presence/absence of nest-boxes (NB) and type of forest (F; beech *versus* pine) as categorical independent variables, and tree size and number of trees as covariates. The interactions were also included in the model. Only terms associated with *P*-values smaller than 0.1 were kept in the final models. Results are shown separately for cavity-nesting and non-cavity nesting birds.
*[Resultados de Modelos Linares Generales por pasos y hacia atrás con las diferencias en abundancia y riqueza entre los periodos de estudio como variables dependientes, presencia/ausencia de nidales y tipo de bosque (hayedo vs pinar) como variables categóricas independientes y el tamaño del arbolado y el número de árboles como covariables. Las interacciones también se incluyeron en el modelo. Sólo términos con un valor de P menor que 0.1 permanecieron en los modelos finales. Los resultados se muestran por separado para las aves trogloditas y las no trogloditas.]*

| | Difference in abundance | | | | | | Differences in richness | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Breeding periods | | | Winter periods | | | Breeding periods | | | Winter periods | | |
| | F | df | P | F | df | P | F | df | P | F | df | P |
| Cavity-nesting birds *[Aves trogloditas]* | | | | | | | | | | | | |
| Nest-box | 18.93 | 1,37 | < 0.001 | 6.89 | 1,37 | 0.012 | 19.51 | 1,36 | < 0.001 | 3.13 | 1,37 | 0.085 |
| Type of forest | - | - | - | - | - | - | 4.79 | 1,36 | 0.035 | - | - | - |
| Non cavity-nesting birds *[Aves no trogloditas]* | | | | | | | | | | | | |
| Nest-box | - | - | - | 3.37 | 1,35 | 0.075 | - | - | - | 3.30 | 1,37 | 0.077 |
| Type of forest | - | - | - | 9.29 | 1,35 | 0.004 | - | - | - | - | - | - |
| NB x F | - | - | - | 8.97 | 1,35 | 0.005 | - | - | - | - | - | - |
| Tree size | - | - | - | - | - | - | 5.21 | 1,37 | 0.028 | - | - | - |

riods (Table 1). Plots where nest boxes were added underwent an increase in the richness of cavity-nesting birds as compared to plots without nest boxes (Fig. 2). Moreover, bird richness during breeding increased in pine forests while it decreased in beech forests (mean difference in richness (SE); beech forest: -0.32 (0.22); pine forest: 0.37 (0.25).

The experimental addition of nest boxes had no significant effects on the difference in abundance or richness of non-cavity nesters between the two breeding periods. Number of trees and type of forest did not show a significant effect either, whereas tree size had a significant effect on the difference in richness of non-cavity nesting birds between breeding periods

(Table 1). Plots with bigger trees showed an increase of non-cavity nesting species ($\beta = 0.351$).

Both the type of forest and the interaction between forest type and presence/absence of nest boxes had significant effects on the difference in the abundance of non-cavity nesting birds between winter periods (Table 1). Abundance of non-cavity nesters did not differ between winter periods in beech forests while in pine forests there was a decrease in bird abundance, although the difference between types of forest was only marginally significant (Table 1) and exclusively due to plots without nest boxes (Fig. 3; see below). In order to understand the meaning of the interaction between forest type and presence/absence
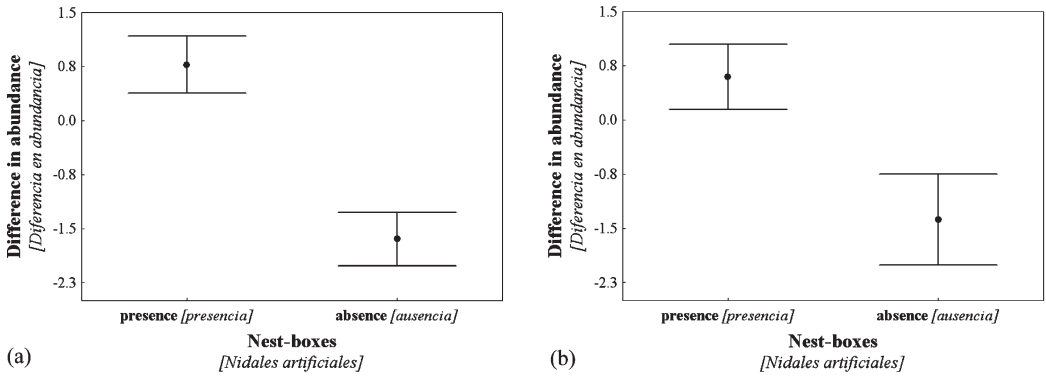
(a)

(b)

FIG. 1.—Mean ± SE variation in abundance of cavity–nesting birds between (a) breeding periods (Reproduction 3 – Reproduction 1) and (b) winter periods (Winter 2 – Winter 1) in forest plots with and without nest-boxes. For definition of periods see Methods.
*[Variación media (± error estándar) de la abundancia de aves trogloditas entre (a) periodos reproductores (Reproducción 3 – Reproducción 1) y (b) periodos invernales (Invierno 2 – Invierno 1) para parcelas de bosque con y sin nidales artificiales. Para la definición de los periodos, ver el apartado de Métodos.]*
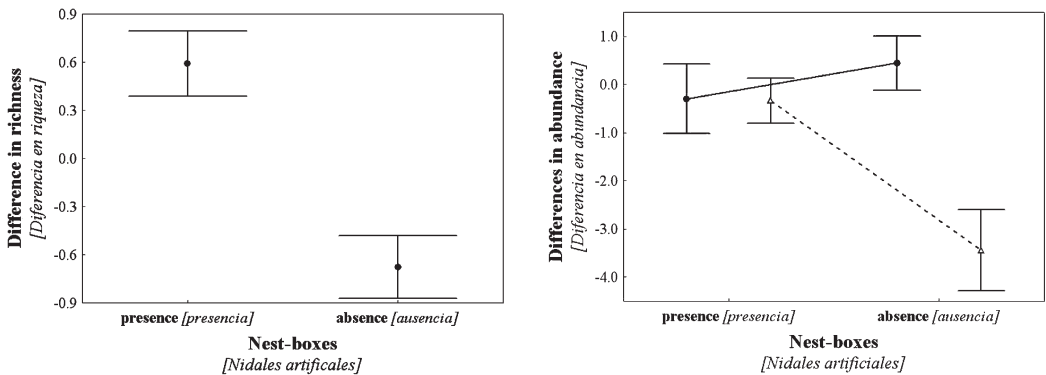


FIG. 2.—Mean ± SE variation in richness of cavity–nesting birds between breeding periods (Reproduction 3 – Reproduction 1) in plots with and without nest-boxes. For definition of periods see Methods.
*[Variación media (± error estándar) de la riqueza de aves trogloditas entre periodos reproductores (Reproducción 3 – Reproducción 1) para parcelas de bosque con y sin nidales artificiales. Para la definición de los periodos, ver el apartado de Métodos.]*
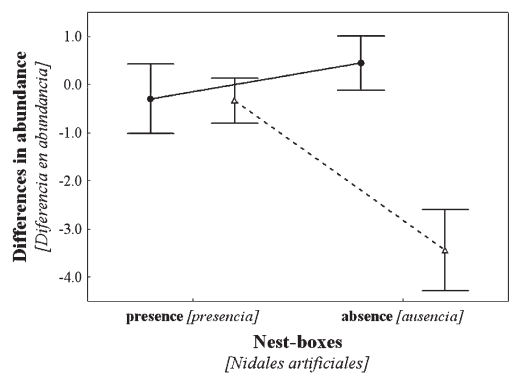
FIG. 3.—Mean ± SE variation in abundance of noncavity nesting birds, between winter periods (Winter 2 – Winter 1) in plots with and without nest-boxes. For definition of periods see Methods. Triangles and dotted lines represent pine forests and circles and solid lines represent beech forests.
*[Variación media (± error estándar) de la abundancia de aves no trogloditas entre periodos invernales (Invierno 2 – Invierno 1) para parcelas de bosque con y sin nidales artificiales. Para la definición de los periodos, ver el apartado de Métodos. Los triángulos y las líneas discontinuas representan los pinares mientras que los círculos y las líneas continuas los hayedos.]*

of nest boxes, separate analyses were performed for each type of forest. The presence/absence of nest boxes was found to have a significant effect on the variation in abundance of non-cavity nesters only in pine forests (beech forests: $F_{1,17} = 0.64$, $P = 0.43$; pine forests: $F_{1,18} = 12.17$, $P = 0.003$). While in beech forest plots without nest boxes the abundance of non-cavity nesters remained the same in both winter periods, pine forest plots without nest boxes underwent a decrease in the abundance of these birds (Fig. 3). Finally, the presence of nest boxes had a marginally non-significant effect on the variation in bird richness in the winter periods (Table 1).

DISCUSSION

After Von Haartman (1957) and Hilden (1965) pointed out that cavity availability is a limiting factor for cavity-nesting birds, other studies have also found the opposite, depending on the study area and the methodological approach. Some of the studies reporting that bird community is not limited by cavity availability were conducted in primeval or unmanaged forests (Walankiewicz, 1991; Wesolowski, 2003), where the availability of cavities is probably very high. Other studies showing the same results suggest that there is a large number of empty cavities in the forests studied and assume that bird populations are not limited by cavity availability (Waters *et al.*, 1990; Carlson *et al.*, 1998). However, a simple count of unoccupied cavities in a forest might overestimate cavity availability (Aitkinen *et al.*, 2002), since other factors such as their suitability (Lõhmus and Remm, 2005), and abundance and phenology of both inter- and intraspecific competitors (Nilsson, 1984; Ingold, 1989; Loeb and Hooper, 1997), could also influence their occupancy. In any case, it should not be assumed that cavity-nesting birds are always limited by hole abundance, so that this hypothesis has to be tested in every case. These results suggest that the breeding density of cavity-nesting birds was limited by the number and/or quality of natural nesting sites in the two types of forest studied.

Not only variation in abundance, but also in richness of cavity-nesting birds in the breeding periods was influenced by the presence of nest boxes in both types of forest. The increased richness in forest plots with nest boxes could be a consequence of competition for holes, in which dominant species may prevent individuals of subordinate species from obtaining a cavity. Thus, more cavities imply more individuals but also more species that may have access to this breeding resource, especially subordinate (usually smaller) species. Accordingly, East and Perrins (1988) found cavity limitation in mature forests, but only for certain species of cavity-nesting birds, depending on their habitat preferences and competition intensity within the bird community.

A significant effect of nest-box addition on the abundance of wintering birds was also found. There are at least two possible explanations for such an increase in cavity-nesting birds in the plots where nest boxes were added. Birds could be limited not only by natural nesting sites, but also by shelter sites if they use cavities year-round for roosting. In fact, there are some other studies showing the use of cavities by cavity-nesting birds outside of the breeding season (Raphael and White, 1984). Alternatively, if the populations are residents in the study area, the increase observed in the plots with nest boxes in winter could be caused by the population increase during the previous breeding period (see Results). As the birds in the study were not marked, it is not known whether the birds wintering in the study plots were the same individuals that bred there. Both alternatives are possible and non-exclusive.

Despite strong differences in breeding abundance and richness of cavity-nesting birds in forest plots with and without nest boxes, no significant differences were observed in the guild of non-cavity nesters be-

tween experimental and control plots during the breeding season. We predicted that if food resources were limiting, an increase in the abundance of cavity-nesting birds would have caused a decrease in non-cavity nesting birds. There are at least two studies that have shown a negative relationship between cavity- and non-cavity nesting birds because of competition for food resources after nest boxes increased the density of the first (Hogstad, 1975; Bock *et al.*, 1992). However, it seems that there was not much competition between the two guilds in the present study area. Bock and Fleck (1995), in a later study, did not find any evidence for competition between cavity- and non-cavity nesters after increasing the abundance of cavity-nesting birds, in spite of their previous findings (Bock *et al.*, 1992). Similarly, other studies (Brawn *et al.*, 1987; East and Perrins, 1988; Mönkkönnen *et al.*, 1990) also failed to find a decline in non-cavity-nesters after nest-box addition. Mönkkönnen *et al.* (1990) even found the opposite trend, supporting a process of heterospecific attraction rather than competitive interactions. The composition and structure of bird communities is probably affected by a range of processes interacting at different levels (Martin, 1988).

Interestingly, the addition of nest boxes had an effect on the guild of non-cavity nesting birds during winter. Although differences in richness between forest plots with and without nest boxes were marginally non-significant, differences in abundance were significant in pine forests (but not in beech forests). Pine forest plots where nest boxes were added underwent an increase in the abundance of wintering non-cavity nesting birds as compared to plots without nest boxes. It seems plausible that the birds used nest boxes as shelter or roosting places. Wesolowski (2003) reported that, in the Bialowieza forest, holes were used regularly by non-cavity nesters such as dunnocks *Prunella modularis* and robins *Erithacus rubecula*, although his study was conducted only during the breeding season. The present results suggest that the use of holes by this guild could be common, at least in winter. However, no significant effect of nest boxes on non-cavity nesting birds wintering in beech forests was found. Perhaps differences in food availability or weather conditions (2002/2003 winter season was colder than 2001/2002 winter season in pine forests, see 'Weather conditions' in 'Methods') between the two types of forest might have played a role. Microclimatic effects may have caused birds to become more prone to use the nest boxes as shelters in pine forests. Moreover, beech fructification usually shows high inter-year variability, with years of heavy fruit production followed by years of scarcity (Costa *et al.*, 2001). Since food availability was not recorded, it is only possible to speculate about the reasons for these differences in avian parameters between forests.

Contrary to expectations, the variation in cavity-nesting bird parameters in relation to the presence/absence of nest boxes was not influenced by tree size. Although a positive relationship between number of cavities and tree size has been found in other studies (Fan *et al.*, 2003), the effect of nest boxes on plots of mature forest (presumably with higher density of natural cavities than other plots) was not significantly different from the effect on plots of young forest. Therefore, these results suggest that, at least in our study area, the lack of suitable cavities could limit population sizes of cavity-nesting species even in mature forests. Sändström (1992), in a study of cavity occurrence in different kinds of forest, showed that in Scots pine forests only very old pines (more than 150 years) had cavities, whereas beech trees had an extremely low number of cavities, perhaps because beech trees do not show signs of senescence until the age of 300 years (Costa *et al.*, 2001). In the study area, forest management policy consists of harvesting pines at an age of 100 years and beech trees at 120 years. Therefore the oldest plots studied prob-

ably are not really mature enough and cavities are not abundant. Moreover, injured or diseased trees are removed in intermediate cuttings, thus reducing even more the likelihood of occurrence of natural holes. For non-cavity nesting birds, however, a positive effect of tree size on richness was found, although only in the breeding season. The bigger the trees, the larger the increase in the number of non-cavity nesting species, possibly because big trees provide a larger variety of resources and more stable conditions for this kind of birds than small trees (Poulsen, 2002).

This study may have implications in conservation biology, because forest harvest practices greatly affect the availability of holes in the forest. In our study area, a shortage of suitable cavities in managed forests seems to limit the abundance and richness of cavity-nesting birds. Practices that lead to an increase in the number of natural cavities should be encouraged to enhance bird abundance and diversity. As mentioned above, pine trees begin to form cavities at an age older than the current harvest (i.e., 100 years). Therefore, allowing some trees to complete their lifecycle would be beneficial to bird communities. Not removing snags could be also useful, because of the well known relationship between snags and cavities (Raphael and White, 1984). Although most studies dealing with cavity availability and cavity-nesting birds focus on the breeding period, this study shows that the availability of cavities outside the breeding season could also be important for bird communities and not only for cavity-nesting birds.

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APPENDIX 1 *[APÉNDICE 1]*

Mean abundance of cavity-nesting birds (CN) and non-cavity nesting birds (NCN) per plot of beech and pine forest at (a) the breeding periods (Reproduction 1 and Reproduction 3) and (b) the winter periods (Winter 1 and winter 2). Plots with and without nest-boxes are shown separately. Sample size (number of plots) is indicated in the table.

[*Apéndice. Abundancia media por parcela de aves trogloditas (CN) y no trogloditas (NCN) en hayedos y pinares en los diferentes periodos reproductores (Reproducción 1 y Reproducción 3) e invernales (Invierno 1 e Invierno 2). Se muestran por separado las parcelas con y sin nidales artificiales. El tamaño de muestra (número de parcelas) se indica en la tabla.*]

## a) Breeding periods *[Periodos reproductores]*

| | Beech forest | | | | Pine forest | | | |
| | Presence of nest-boxes | | | | Presence of nest-boxes | | | |
| | Yes (*n* = 10) | | No (*n* = 9) | | Yes (*n* = 12) | | No (*n* = 8) | |
| | Rep. 1 | Rep. 3 | Rep. 1 | Rep. 3 | Rep. 1 | Rep. 3 | Rep. 1 | Rep. 3 |
|---|---|---|---|---|---|---|---|---|
| *Lullula arborea* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 |
| *Anthus trivialis* (NCN) | 0.00 | 0.00 | 0.06 | 0.00 | 0.04 | 0.00 | 0.13 | 0.00 |
| *Troglodytes troglodytes* (NCN) | 0.65 | 0.30 | 0.78 | 0.22 | 1.42 | 0.75 | 1.13 | 0.69 |
| *Prunella modularis* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.54 | 0.29 | 0.19 | 0.13 |
| *Erithacus rubecula* (NCN) | 1.30 | 0.85 | 1.22 | 0.78 | 1.38 | 0.63 | 1.38 | 0.69 |
| *Turdus merula* (NCN) | 0.40 | 0.15 | 0.39 | 0.28 | 0.83 | 0.46 | 0.44 | 0.50 |
| *Turdus philomelos* (NCN) | 0.10 | 0.00 | 0.06 | 0.06 | 0.17 | 0.04 | 0.06 | 0.06 |
| *Turdus viscivorus* (NCN) | 0.05 | 0.05 | 0.17 | 0.00 | 0.13 | 0.04 | 0.00 | 0.00 |
| *Sylvia undata* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 |
| *Sylvia atricapilla* (NCN) | 0.50 | 0.20 | 0.50 | 0.50 | 0.79 | 0.38 | 0.75 | 0.25 |
| *Phylloscopus collybita* (NCN) | 0.05 | 0.00 | 0.39 | 0.33 | 0.25 | 0.17 | 0.44 | 0.19 |
| *Phylloscopus ibericus* (NCN) | 0.20 | 0.05 | 0.28 | 0.11 | 0.04 | 0.00 | 0.00 | 0.00 |
| *Phylloscopus bonelli* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.08 | 0.17 | 0.31 | 0.13 |
| *Regulus regulus* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.33 | 0.25 | 0.25 | 0.13 |
| *Regulus ignicapillus* (NCN) | 0.10 | 0.20 | 0.00 | 0.17 | 1.46 | 0.96 | 1.44 | 0.44 |
| *Parus palustris* (CN) | 0.20 | 0.20 | 0.17 | 0.28 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Parus cristatus* (CN) | 0.15 | 0.40 | 0.44 | 0.11 | 0.92 | 1.13 | 1.56 | 0.63 |
| *Parus ater* (CN) | 0.00 | 0.00 | 0.00 | 0.06 | 1.21 | 1.25 | 1.63 | 0.81 |
| *Parus caeruleus* (CN) | 0.40 | 0.80 | 0.39 | 0.39 | 0.00 | 0.04 | 0.31 | 0.00 |
| *Parus major* (CN) | 1.00 | 1.20 | 1.00 | 0.33 | 0.21 | 0.79 | 0.19 | 0.38 |
| *Aegithalos caudatus* (NCN) | 0.40 | 0.00 | 1.06 | 0.00 | 0.00 | 0.04 | 0.38 | 0.00 |
| *Sitta europaea* (CN) | 0.35 | 0.30 | 0.11 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Certhia brachydatcyla* (CN) | 0.40 | 0.30 | 0.56 | 0.22 | 0.25 | 0.21 | 0.50 | 0.44 |
| *Certhia familiaris* (CN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.04 | 0.13 | 0.00 |
| *Fringilla coelebs* (NCN) | 1.95 | 1.45 | 2.22 | 0.83 | 1.50 | 1.42 | 2.13 | 1.25 |
| *Serinus serinus* (NCN) | 0.00 | 0.00 | 0.06 | 0.00 | 0.08 | 0.04 | 0.00 | 0.00 |
| *Serinus citrinella* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 |
| *Carduelis chloris* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Pyrrhula pyrrhula* (NCN) | 0.10 | 0.00 | 0.06 | 0.00 | 0.04 | 0.17 | 0.00 | 0.00 |
| *Loxia curvirostra* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.13 | 0.17 | 0.06 | 0.00 |

APPENDIX 1 *[APÉNDICE 1]* (CONT.)

**b) Winter periods** *[Periodos invernales]*

| | Beech forest | | | | Pine forest | | | |
|---|---|---|---|---|---|---|---|---|
| | Presence of nest-boxes | | | | Presence of nest-boxes | | | |
| | Yes (*n* = 10) | | No (*n* = 9) | | Yes (*n* = 12) | | No (*n* = 8) | |
| | Win. 1 | Win. 2 | Win. 1 | Win. 2 | Win. 1 | Win. 2 | Win. 1 | Win. 2 |
| *Troglodytes troglodytes* (NCN) | 0.20 | 0.00 | 0.17 | 0.17 | 0.58 | 0.46 | 0.56 | 0.31 |
| *Prunella modularis* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.13 | 0.00 | 0.00 |
| *Erithacus rubecula* (NCN) | 0.45 | 0.20 | 0.50 | 0.17 | 0.25 | 0.42 | 0.25 | 0.38 |
| *Turdus merula* (NCN) | 0.15 | 0.20 | 0.22 | 0.11 | 0.33 | 0.25 | 0.56 | 0.31 |
| *Turdus philomelos* (NCN) | 0.05 | 0.15 | 0.11 | 0.06 | 0.04 | 0.04 | 0.06 | 0.00 |
| *Turdus viscivorus* (NCN) | 0.05 | 0.10 | 0.06 | 0.06 | 0.75 | 0.46 | 0.69 | 0.13 |
| *Sylvia undata* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Sylvia atricapilla* (NCN) | 0.00 | 0.00 | 0.00 | 0.06 | 0.00 | 0.00 | 0.00 | 0.06 |
| *Phylloscopus collybita* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.06 |
| *Phylloscopus ibericus* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Regulus regulus* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 | 0.75 | 0.00 |
| *Regulus ignicapillus* (NCN) | 0.05 | 0.05 | 0.06 | 0.06 | 0.46 | 0.67 | 0.88 | 0.19 |
| *Parus palustris* (CN) | 0.35 | 0.50 | 0.50 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Parus cristatus* (CN) | 0.35 | 0.45 | 0.94 | 0.72 | 1.00 | 0.83 | 1.31 | 1.00 |
| *Parus ater* (CN) | 0.20 | 0.10 | 0.06 | 0.11 | 1.17 | 0.92 | 1.50 | 0.56 |
| *Parus caeruleus* (CN) | 0.90 | 1.45 | 1.39 | 0.50 | 0.13 | 0.21 | 0.19 | 0.00 |
| *Parus major* (CN) | 0.90 | 1.50 | 0.78 | 1.00 | 0.13 | 0.33 | 0.25 | 0.19 |
| *Aegithalos caudatus* (NCN) | 0.55 | 0.00 | 0.06 | 0.00 | 0.29 | 0.04 | 0.56 | 0.00 |
| *Sitta europaea* (CN) | 0.15 | 0.40 | 0.11 | 0.44 | 0.00 | 0.04 | 0.13 | 0.13 |
| *Certhia brachydatcyla* (CN) | 0.30 | 0.10 | 0.56 | 0.17 | 0.29 | 0.33 | 0.25 | 0.19 |
| *Certhia familiaris* (CN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Fringilla coelebs* (NCN) | 1.00 | 1.45 | 0.50 | 1.33 | 0.54 | 0.96 | 0.31 | 0.75 |
| *Serinus serinus* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Serinus citrinella* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 |
| *Carduelis chloris* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.25 | 0.00 |
| *Carduelis spinus* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.42 | 0.00 | 0.63 | 0.00 |
| *Pyrrhula pyrrhula* (NCN) | 0.00 | 0.05 | 0.06 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Loxia curvirostra* (NCN) | 0.00 | 0.00 | 0.00 | 0.00 | 0.25 | 0.46 | 0.13 | 0.00 |