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The abundance of tree holes and their utilization by hole-nesting birds in a primeval boreal forest of Mongolia

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Abstract. The natural tree holes and nest holes of hole-nesting birds were surveyed in four forest types in the west Khentii Mountains of NE Mongolia. The utilization patterns of species, size and condition of trees, as well as hole types, were investigated. The average density of tree holes in the study area approached 30 holes/ha, while that of hole-nesting birds was 2.4 nests/ha only. The riparian mixed forest had the greatest number of species and individuals of hole-nesting birds, while the spruce-fir forest had the lowest numbers. Excavating bird species preferred larger, deciduous trees, and snags. Non-excavators did not select holes according to tree species or size, but preferred holes in living trees and branch holes. In view of the low occupancy of holes among the four habitats, we suggest that the density of secondary hole-nesting birds is not limited by availability of holes in the study area.

Key words: boreal forest, tree holes, hole-nesting birds, nest-site selection, cavity nesters

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INTRODUCTION

Owing to the expansion of forestry practices all over the world, forest bird communities have been dramatically re-shaped (Hobson & Schieck 1999, Sekercioglu 2002). Hole-nesting birds are considered as one of the most susceptible groups to such impacts due to their strong dependence on trees (Angelstam & Mikusiński 1994, Martin & Eadie 1999, Imbeau et al. 1999, 2001). It has been suggested that the availability of nesting holes limits the population density of such birds in many managed forests (von Haartman 1957, Johnson 1994, Newton 1994, Semel & Sherman 2001, Twedt & Henne-Kerr 2001, Pöysä & Pöysä 2002). Since the 1990s, with the emergence of ecological forestry, there is an increasing need to improve our understanding of biodiversity and its maintenance in natural forests, so that such knowledge can be incorporated into management guidelines (Hansen et al. 1991, Fujimori 2001). Though hole-nesting birds have received much attention, studies based on natural holes

or conducted in primeval forest are relatively few (van Balen et al. 1982, Nilsson 1984, Alatalo et al. 1988, Wesołowski 1989, Sandström 1992, Sachslehner 1995, Wesołowski & Stańska 2001). Also few studies (Walankiewicz 1991, Sandström 1992) have quantitatively surveyed the forest structure and the availability of natural holes, yet such studies are essential to demonstrate that nest holes are indeed limiting.

The aim of this study was to quantify the forest structure, abundance of natural holes and densities of hole-nesting birds in different types of primeval boreal forests, and to investigate the utilization of trees and holes by all hole-nesting birds.

STUDY AREA

The study area was located in the west Khentii Mountains (49°04'N, 107°24'E), NE Mongolia. The climax vegetation of this region is taiga, with Siberian Pine *Pinus sibirica* and Siberian Spruce *Picea obovata* as the dominant tree species. However,

these forests are heterogeneous due to variation in topography and fire history. Scots Pine *Pinus sylvestris* occupies steep slopes, and stands of Siberian Fir *Abies sibirica* cover stream valleys. In the most widespread post-fire secondary forest, the dominant tree species are Whitespire Birch *Betula platyphylla* and Siberian Larch *Larix sibirica*. The riparian forest is

dominated by Laurel Poplar *Populus laurifolia*, Birch, Scots Pine or Willow *Salix* spp.

Considering the representative forest types and their accessibility, four habitats were selected:

1) Mature birch-larch forest (Fig. 1a) — a deciduous forest dominated by large birches. Canopy is rather open with scattered emergent old larches.



Fig. 1. Habitats sampled in the study. a — mature birch-larch forest, b — young birch-larch forest, c — riparian mixed forest,

2) Young birch-larch forest after recent fire on a steep slope (Fig. 1b) — the dominance of birch is similar to that in the previous habitat, but is composed of smaller and closely spaced stems. Large Scots pines patchily dominate the upper slopes. Over 95% of all living stems, even the young ones, were scarred by fire. Density of standing dead trees is high.

3) Riparian mixed forest along the river (Fig. 1c) — tree species composition and forest structure are diverse. Birch, poplar and pine are dominant species, while willow, larch and spruce are also common in some patches. Shrub layer is well developed.

4) Spruce-fir coniferous forest (Fig. 1d) — a dense coniferous forest dominated by spruce, fir, siberian pine, birch and old larch are scattered, with scots Pine forming patches on upper slopes. Deadfalls (dead wood on the ground) are abundant.

METHODS

In each habitat, five 1 ha plots (50 × 200 m) were selected. Two points were taken systematically in each plot for taking habitat measurements. At each point, standing stems (≥ 5 cm diameter at breast height (DBH)) were sampled by the plotless method with the help of a dendrometer (Grosenbaugh 1952). This method was used instead of the fixed-area plot sampling because the probability a tree being sampled is proportional to its DBH in the former method. So it is more efficient in collecting the information of large trees, especially in heterogeneous natural forest where the occurrence probability of a tree is usually negatively correlated to its DBH. The data at each sample point can be projected to per unit area based information without bias. For each sampled tree, we recorded: (1) tree species, (2) DBH, and (3) tree condition, the latter categorised as living, recently died or snag with broken top (after Gunn & Hagan 2000).

Each sampled standing stem was also searched for holes by examining from the ground in autumn 2002, when deciduous trees had lost their leaves. Each tree was observed from at least three directions with the help of binoculars. Trees with holes found were referred as hole trees. Holes were classified into one of the following types: 1) woodpecker holes, excavated by woodpeckers for nesting or roosting, 2) other bird-induced holes, including all other excavated holes that were apparently not the nesting or roosting holes of woodpeckers, 3) branch holes, which originating from fallen limbs

and showed no signs of processing by birds, and 4) bark crevices, formed under loose bark (after Carlson et al. 1998). In the study area, woodpecker holes were excavated by the Black Woodpecker *Dryocopus martius*, the Grey-headed Woodpecker *Picus canus*, the Great Spotted Woodpecker *Dendrocopos major*, the White-backed Woodpecker *D. leucotos*, the Lesser Spotted Woodpecker *D. minor* or the Three-toed Woodpecker *Picoides tridactylus*. "Other bird-induced holes" included holes excavated by the Willow Tit *Parus montanus* for nesting and holes of any origin but followed by the destruction of woodpeckers. The former two types of holes were referred as excavated holes, and the others as non-excavated holes. The six woodpecker species and Willow Tit were referred as excavators, and other secondary hole-nesting species as non-excavators.

Data of hole-nesting birds were collected from the third decade of April to the first decade of July in 2002 and 2003. Each plot was visited intensively to search for the occupied holes. The behaviour of all hole-nesting bird species was observed and their territories were outlined to help locate their nests. A hole was classified as occupied when an adult bird was observed bringing in nesting material or food. Trees with occupied hole were referred as nest trees. For each occupied hole, the species, DBH and condition of the nest tree (as described above), as well as the type of the nest hole (as one of the four types described above), were recorded.

RESULTS

Abundance of holes

The average density of tree holes in the study area approached 30 holes/ha (Table 1). The hole density was lowest in the spruce-fir forest due to less branch holes in this habitat, and was highest in the riparian mixed forest due to more woodpecker nests. Branch holes were the most common type of holes, except in the spruce-fir forest, while bark crevices were the scarcest hole type. Because the abundance of holes varied greatly among the plots in the same habitat, only the density of non-excavated holes in the young birch-larch forest and that in the spruce-fir forest showed a significant difference (Mann-Whitney U-test = 22.0, df = 1, $p < 0.05$).

Abundance of hole-nesting birds

A total of 24 hole-nesting bird species have been recorded in the study area. In the study

Table 1. Density (mean \pm SD) of each type of hole (per ha) in each habitat: Woodpecker — woodpecker holes, Other — other bird-induced holes, Branch — branch holes, Crevices — bark crevices.

Habitat	Type of holes				Total
	excavated		non-excavated		
	Woodpecker	Other	Branch	Crevices	
Mature birch-larch forest	1.2 \pm 2.7	8.0 \pm 10.6	15.0 \pm 10.6	0.0 \pm 0.0	24.2 \pm 22.0
Young birch-larch forest	2.7 \pm 6.1	9.2 \pm 12.0	22.2 \pm 12.6	2.8 \pm 5.5	36.9 \pm 15.9
Riparian mixed forest	10.3 \pm 9.4	7.2 \pm 8.0	18.9 \pm 11.0	2.9 \pm 2.9	39.3 \pm 18.8
Spruce-fir forest	1.2 \pm 2.0	8.9 \pm 13.5	7.9 \pm 5.2	0.0 \pm 0.0	18.1 \pm 18.0
All	3.9 \pm 4.3	8.3 \pm 0.9	16.0 \pm 6.1	1.4 \pm 1.6	29.6 \pm 10.1

duration, nest of 13 species were found in the sampling plots (20 ha in total), and 49 and 48 nest holes were observed in 2002 and 2003 respectively (Table 2). Neither the number of nests or species in each habitat showed significant differences between years, so data for both years were pooled.

Table 2. Density of nests and hole-nesting species (mean per ha \pm SD) and hole occupancy (%) by non-excavators in each habitat.

Habitat	Nests (N)	Species (N)	%
Mature birch-larch forest	2.6 \pm 0.8 (26)	2.4 \pm 0.8 (8)	7.0
Young birch-larch forest	2.6 \pm 1.3 (26)	2.4 \pm 1.0 (9)	4.6
Riparian mixed forest	3.5 \pm 1.5 (35)	3.1 \pm 1.3 (9)	5.6
Spruce-fir forest	1.0 \pm 0.7 (10)	1.0 \pm 0.7 (2)	3.3
All	2.4 \pm 1.0 (97)	2.2 \pm 0.9 (13)	5.2

The density of hole-nesting birds varied from 1.0 nest/ha in the spruce-fir forest to 3.5 nests/ha in the riparian mixed forest. The spruce-fir forest had fewer individuals and species than the other three habitats (Mann-Whitney U-test, $p < 0.01$ for each other habitat), while there were no significant differences among the three deciduous habitats. Species composition of the three deciduous habitats was quite similar (Sorenson index of similarity = 0.67–0.71), while the spruce-fir forest was distinct from the others (Sorenson index = 0.36–0.40).

Hole occupancy was estimated by dividing the mean density of holes by that of non-excavators in each habitat. The overall occupancy in the study area was 5.2%, which is highest in the mature birch-larch forest and lowest in the spruce-fir forest (Table 2).

Utilization of trees and holes

As no significant differences were found in any of the nest parameters between years, the data for 2002 and 2003 were pooled.

Tree species. Because the tree species composition differed significantly among habitats (Table 3, $\chi^2 = 719.4$, $df = 27$, $p < 0.001$), each habitat was considered separately. Within each habitat, excavators and non-excavators showed no significant differences in their selection of different tree species for nesting and were thus combined.

In each habitat, trees species were not selected according to their relative abundance (Table 3, Pearson χ^2 , $p < 0.001$ in each habitat). Birch served most often as the nest tree in all habitats. In the riparian mixed forest, poplar was strongly over-used. In the spruce-fir forest, where spruce, fir and Siberian pine comprised most of the standing stems, no nests were found in these dominant tree species.

When further taking into account the supply of holes, the species distribution of holes trees (Table 3) was not significantly different from that of nest trees in each habitat. Holes in different tree species were utilized in proportion to their availability, and the utilization rate of a tree species was in proportion to the occurrence rate of holes in this species. Holes occurred more frequently in poplar than in any other species, and more frequently in birch than in pine, fir and spruce (Pearson χ^2 , $p < 0.05$ between each tree pairs), and this gave rise to the utilization pattern of tree species.

DBH. Both the DBH distribution of nest trees of excavators and that of non-excavators differed significantly from that of trees sampled systematically (Fig. 2, $\chi^2 = 60.4$, $df = 2$, $p < 0.001$ for excavators; $\chi^2 = 227.2$, $df = 2$, $p < 0.001$ for non-excavators). Larger trees were overused by both categories of birds, but non-excavators used

Table 3. Species composition of trees (percentage) in studied plot, trees contained holes and trees with nests in each habitat.

Species	Trees		
	In plot	With holes	With nest
Mature birch-larch forest			
	(174)	(28)	(26)
<i>Betula platyphylla</i>	48.0	100.0	84.6
<i>Larix sibirica</i>	52.0	0	15.4
Young birch-larch forest			
	(204)	(28)	(26)
<i>Populus tremula</i>	0.5	0	11.5
<i>Betula platyphylla</i>	66.9	74.5	80.8
<i>Larix sibirica</i>	24.1	24	3.8
<i>Pinus sylvestris</i>	8.5	1.5	3.8
Riparian mixed forest			
	(180)	(75)	(35)
<i>Sorbus spp.</i>	11.5	0	0
<i>Salix spp.</i>	5.7	3.1	5.7
<i>Populus laurifolia</i>	6.0	78.0	37.1
<i>Betula platyphylla</i>	45.9	16.4	42.9
<i>Larix sibirica</i>	1.0	2.6	0
<i>Pinus sylvestris</i>	24.9	0	14.3
<i>Picea obovata</i>	5.0	0	0
Spruce-fir forest			
	(305)	(26)	(10)
<i>Betula platyphylla</i>	14.2	57.7	80.0
<i>Larix sibirica</i>	1.7	32.1	20.0
<i>Pinus sylvestris</i>	4.4	10.2	0
<i>P. sibirica</i>	16.8	0	0
<i>Abies sibirica</i>	25.8	0	0
<i>Picea obovata</i>	37.1	0	0

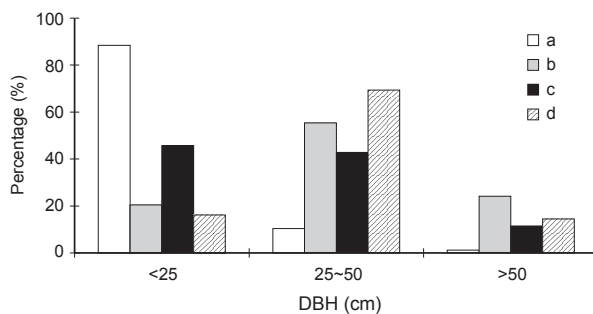


Fig 2. DBH of trees systematically sampled in plots (a, N = 863), trees with holes (b, N = 157), nest trees of excavators (c, N = 35) and nest trees of non-excavators (d, N = 62).



Fig 3. Tree condition of trees systematically sampled in plots (a, N = 863), trees with holes (b, N = 157), nest trees of excavators (c, N = 35) and nest trees of non-excavators (d, N = 62).

larger trees more than excavators ($\chi^2 = 10.1$, $df = 2$, $p < 0.01$). The DBH of trees used by non-excavators was not significantly different from that of hole trees (Fig. 2).

Tree condition. Both excavators and non-excavators placed their nests most often in living trees (Fig. 3). However, in relation to their occurrence in the forest, living trees were underused and dead trees were overused by both categories of birds ($\chi^2 = 76.6$, $df = 2$, $p < 0.001$ for excavators; $\chi^2 = 9.8$, $df = 2$, $p < 0.01$ for non-excavators). Moreover excavators preferred snags more than non-exca-

vators ($\chi^2 = 11.2$, $df = 2$, $p < 0.01$). Given their relative abundance (Fig. 3), holes in snags were underused by non-excavators, while holes in living trees were overused by these birds ($\chi^2 = 14.5$, $df = 2$, $p < 0.001$).

Hole type. Excavators mostly used holes excavated by themselves or other excavators, while in few cases *Parus montanus* also used branch holes (Table 4). The vast majority (71%) of the nests of non-excavators were established in branch holes, and 18% in woodpecker holes. In comparison to their relative frequency in the forest, branch holes

Table 4. Availability and occupation (in %) of different hole types.

Holes type	Holes available	Occupation of holes	
		by excavators	by non-excavators
woodpecker holes	13.0	20.0	17.7
other bird-induced holes	28.1	68.6	6.5
branch holes	54.1	11.4	71.0
bark crevice	4.8	0.0	4.8
	100 (N = 157)	100 (N = 35)	100 (N = 62)

were overused by non-excavators, while other bird-induced holes were underused by these birds ($\chi^2 = 12.5$, $df = 3$, $p < 0.01$).

DISCUSSION

Abundance of holes

The densities of holes reported in the literature vary widely from 0.08 to 72.0 holes/ha (van Balen et al. 1982, Wesołowski 1989, Noeke 1990, Waters et al. 1990, Walankiewicz 1991, Sandström 1992, Carlson et al. 1998), and the density in our study area (30 holes/ha) is among the highest reported. Comparisons are approximate as the definitions of holes and survey methods varied substantially. The abundance of holes is also strongly influenced by tree density, age of trees and tree species composition, and high densities were mainly recorded in natural forests. The most comparable study to the present one was conducted in natural forests in Sweden (Sandström 1992), where the hole density was 41.0 (2–72) holes/ha. One possible reason for the higher value in Sweden than in Mongolia is the absence of hole-rich oaks in the latter. If conspecific or congeneric trees of these two sites are compared, the pattern is strikingly similar (Sweden in brackets): the proportion of stems with holes was 1% (2%) in *Pinus sylvestris*, 5% (9%) in *Betula* spp., 34% (30%) in *Populus* spp. and 0% (0.5%) in *Picea* spp.

Lower hole densities in coniferous forests than in deciduous ones has been widely documented, with densities in the former ranging from 0.7 to 16.0 holes/ha (summarised from Waters et al. 1990 and Sandström 1992). The slightly higher value for our study spruce-fir plots (18 holes/ha) might have resulted from the presence of scattered birch and the pristine state of our plots.

Abundance of hole-nesting birds and occupancy of holes

In the present study, the density of hole-nesting birds was lowest in the spruce-fir forest (1.0 nest/ha), and highest in the riparian mixed forest (3.5 nests/ha). This corresponded to the densities in other natural forests (0.4–1.7 pairs/ha in coniferous forests, 1.1–6.0 in deciduous forests), and was higher than that of managed forests (0.2–1.1 in coniferous forests and 1.3–2.0 in deciduous forest, Noeke 1989, Wesołowski 1989, Waters et al. 1990, Walankiewicz 1991, Sandström 1992, Carlson et al. 1998).

The riparian mixed forest had both highest densities of holes and hole-nesting birds and the spruce-fir forest was lowest in both parameters. These trends raise the issue of whether the availability of breeding holes acts as a limiting factor on bird density. Although the average occupancy rate of holes by non-excavators was only 5.2%, which indicated a large proportion of unoccupied holes, the quality of these holes was unknown and thus, many may have been unsuitable. However, if assuming the proportion of unsuitable holes was the same among habitats, some clues could be drawn through the comparison of hole occupancy. Between the mature and young birch-larch forests, which had similar forest composition, the latter possessed more tree holes than the former, but the density of hole-nesting birds was identical in both habitats, which resulted in a lower occupancy in the latter. Thus there might be another factor limiting bird populations in the young birch-larch forest. On the other hand, if hole availability limited the density of non-excavators, competition should be strongest in the spruce-fir forest, where tree holes were most scarce. Yet the occupancy rate in this habitat was the lowest, suggesting that other factors suppressed the bird density.

The occupancy rate in the study area was similar to that of Swedish natural forest (5.3–9.1%), in which the inner dimension of all holes were measured, and more than 50% of them were considered as suitable for nesting (Carlson et al. 1998). Other studies in the primeval temperate forest also suggested that the density of hole-nesting birds was limited by factors other than tree hole availability (Wesołowski 1989, Walankiewicz 1991).

Utilization of trees and holes

Consistent with other studies, excavators in this study preferred larger, deciduous trees and snags, which have softer sapwood and easier for excavating (Aulén 1988, Sandström 1992, Stenberg 1996, Rolstad et al. 2000). Non-excavators also overused larger and deciduous trees. But given the relative abundance of tree holes, they were not selective on holes according to tree species or size. This implicated that their overuse of larger and deciduous trees was not really a preference on large diameter or certain tree species, but simply reflected the higher availability of holes in these trees. In the primeval forest of Poland, Wesołowski (1989) also suggested that tree species and size were not important factors influencing their nest-site selection. However, non-excavators showed preferences for holes in living trees, which was also observed in Poland. In

our study area, some nests were observed to be lost due to the predation by Great Spotted Woodpecker or the nest tree falling, and such events happened almost exclusively on snags. Security could be an important advantage of nesting in a living tree. The more stable microclimate inside holes within living trees might be another consideration (Wiebe 2001).

Of the hole types studied, branch holes were preferred by non-excavators. The underuse of other bird-induced holes was partly related to the fact that such holes occurred mostly in snags. As woodpecker holes were used in proportion to their occurrence, our study does not support the generally accepted doctrine that woodpeckers are keystone species for supporting non-excavators. The percentage of non-excavators' nests in branch holes (71%) and woodpecker holes (18%) was similar to that found in Sweden (65% and 22%, respectively; Carlson et al. 1998).

Implications for conservation and management

From the viewpoint of nest site management for hole-nesting birds, poplar and birch are good candidates for wildlife trees. Poplar is highly preferred by excavators, and it also possesses natural holes most common for serving non-excavators. In practice birch is valuable because it is widespread in secondary forests and can also scatter into conifer stands. Snags are important resources for excavators, and the artificial creation of snags through girdling or topping is helpful to enrich the nest sites for excavators in managed forests (Parks et al. 1999, Brandeis et al. 2002). However, non-excavators would not benefit from such practices, as they prefer holes in living trees. Setting nest boxes is not an ideal solution for non-excavators, because it might alter their breeding ecology, biological interactions and the community structure (Møller 1989, 1994, Purcell et al. 1997, Wesolowski & Stańska 2001). The retention of living old trees is important for non-excavators.

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[Obfitość dziupli i ich wykorzystanie przez ptaki w pierwotnym lesie tajgowym Mongolii]

Badania prowadzono w okresie od końca kwietnia do początku lipca lat 2002 i 2003 w górach Khentii (NE Mongolia), obejmując nimi cztery typowe dla tego regionu środowiska leśne (Fig. 1): stary i młody las brzoźowo-modrzewiowy, mieszany las nadrzeczny oraz bór świerkowo-jodłowy. W każdym z tych środowisk wyznaczono po 5 powierzchni po 50 × 200 m, na których liczono drzewa i ich martwe pnie, określano gatunek i stan drzewa, mierzono pierśnicę (DBH), badano dziuple — ich rodzaj, pochodzenie i wykorzystanie przez ptaki.

Średnie zagęszczenie dziupli dla wszystkich badanych powierzchni wyniosło 30/ha i było najniższe w borze świerkowo-jodłowym (Tab. 1), w którym było też najniższe zagęszczenie i bogactwo gatunkowe ptaków gnieźdzących się w dziuplach (Tab. 2). Ogółem stwierdzono wykorzystanie różnych rodzajów dziupli i szczelin w pniach drzewnych przez 13 gatunków ptaków a średnie zagęszczenie wykorzystanych przez nie dziupli wyniosło 2.4 gniazd/ha.

We wszystkich środowiskach dziuple w brzoźach były częstsze niż w innych gatunkach drzew (Tab. 3). Ptaki wykuwające dziuple (dziuplaki pierwotne) najczęściej gnieździły się w topolach i brzoźach, a najrzadziej w drzewach szpilkowych. Ptaki te wybierały też częściej duże drzewa, natomiast dziuplaki wtórne wykorzystywały dziuple różnych rodzajów i wielkości oraz w różnych gatunkach drzew — proporcjonalnie do ich dostępności (Fig. 2). Dziuplaki pierwotne chętniej wybierały pnie drzew martwych (Fig. 3), a dziuplaki wtórne — wypróchniałe dziuple po martwych gałęziach, natomiast szczeliny pni były wykorzystywane najrzadziej (Tab. 4).

Badane tereny były, w porównaniu do danych z piśmiennictwa, stosunkowo bogate pod względem obfitości dziupli. Zagęszczenie dziuplaków było porównywalne z innymi naturalnymi lasami, a znacznie wyższe niż w lasach zagospodarowanych. Autorzy wnioskujeją, że na badanym terenie dostępność dziupli nie była czynnikiem ograniczającym liczebność dziuplaków wtórnych.