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Nest-site characteristics of hole-nesting birds in a primeval boreal forest of Mongolia

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Abstract. Nest sites of nine common hole-nesting bird species were studied in the West Khentey Mountains, NE Mongolia. Among three excavators, the Great Spotted Woodpecker used more aspens, larger trees, and more living or intact dead trees than the Lesser Spotted Woodpecker or the Willow Tit. Among non-excavators, the Nuthatch used mainly old holes of the Great Spotted Woodpecker, and the Red-throated Flycatcher frequently used those of the Willow Tit. Thus, the nest site characters of these two species resembled those of the original excavators, and their nests were placed higher than those of other non-excavators. The Coal Tit and the Great Tit used mostly branch holes in living trees. With respect to nest site use, the Daurian Redstart behaved as a generalist while the Common Treecreeper specialized in long slits. The nest site selection of excavators might be governed by body size, territory size and their different abilities of excavation. The non-excavators were best differentiated by their preferred hole type, and their tree use and nest site characters were mainly a consequence of the location of such holes. Interspecific competition did not appear to be important in the nest site use of hole-nesting birds in the study area.

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

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INTRODUCTION

Due to their close association with trees and tree holes, hole-nesting birds are highly sensitive to forest structure (Angelstam & Mikusiński 1994, Imbeau et al. 1999, 2001, Hausner et al. 2003, Wübbenhorst & Südbeck 2003). Though the plantation of conifers, fragmentation of landscape and installation of nest boxes do cause the expansion of some species which inhabit coniferous stands, prefer forest edges or are well adapted to nest boxes, many hole-nesting bird species suffer from modern forestry due to the lack of suitable nest sites, lack of suitable foraging substrates or increased competition with edge species (Pettersson 1985, Mikusiński 1995, Wesołowski 1995, Mikusiński & Angelstam 1997, Koenig 2003). Therefore, they are intensively studied for conservation and management purposes.

Many studies on hole-nesting birds have been conducted using nest boxes or in managed forests (e.g. Minot 1981, Willner et al. 1983, Pogue & Schnell 1994, Krištín & Žilinec 1997, Huhta & Jokimaki 2001). However, some authors have questioned the applicable range of nest-box data (van Balen et al. 1982, Nilsson 1984a, Alatalo et al. 1988, Møller 1989, Walankiewicz 1991, Wesołowski & Stańska 2001). Nest boxes may differ from natural holes in their microclimate, shape, dimensions and density in the habitat. Recent comparative studies have found that laying date, clutch size, predation rate, main predator species, parasite loads, breeding success and population fluctuations differed between nest box populations and those breeding in natural holes (Purcell et al. 1997, Czeszczewik et al. 1999, Wesołowski & Stańska 2001, Evans et al. 2002, Mitrus 2003, Czeszczewik 2004), and the response differed from species to species. There are also substantial differences between managed forests and primeval conditions. Managed forests usually have impoverished snag density and hole abundance (Moriarty & McComb 1983, Newton 1994, Graves et al. 2000). Predator abundance and potential predator species may also differ between managed forests and natural ones. Even in unmanaged forest fragments surrounded by modified landscape, forest edge species usually dominate hole-nesting birds communities (Johnsson et al. 1993), and the extent and the pattern of predation may differ from that under natural conditions (Sandström 1991, Walankiewicz 2002, Wesołowski 2002).

Although the nest-site selection of hole-nesting birds has received much attention, most studies focused only on single species (e.g. Korol & Hutto 1984, Dow & Fredga 1985, Belthoff & Ritchison 1990, Daily 1993, Smith 1997, Rolstad et al. 2000). These efforts resulted in detailed information valuable for setting up individual conservation guidelines, the interspecific relationships were, however, largely ignored. Thus there is a call for approaches at community level, which is critical for demonstrating ecological links among species and drawing up comprehensive conservation plans (Stauffer & Best 1982, Martin & Eadie 1999, Bednarz et al. 2004).

While great research efforts have been placed in the study of hole-nesting birds in Europe and North America, the information from other parts of the world is largely lacking. This study was a first attempt to investigate the nest-site selection of hole-nesting birds in the boreal forest of Mongolia. The objectives were to characterise the nest sites of common hole-nesting species, compare their nest site preferences, and discuss the relationships between species.

STUDY AREA AND METHODS

The field work was conducted in the West Khentey mountains (49°04'N, 107°24'E), NE Mongolia. The landscape is a mosaic of steppes and forests. The forests are composed of Siberian Pine *Pinus sibirica*, Siberian Spruce *Picea obovata* and Siberian Fir *Abies sibirica* in coniferous parts, of Whitespire Birch *Betula platyphylla* and Siberian Larch *Larix sibirica* in post-fire parts, and of Laurel Poplar *Populus laurifolia*, birch, spruce, Scots Pine *Pinus sylvestris* or Willow *Salix* spp. in riparian patches (for detailed habitat descriptions, see Bai et al. 2003).

Nests of all hole-nesting bird species were searched from the last week of April to the first week of July in 2002 and 2003. Given the northern latitude, harsh winter and late-coming spring of the study area, most hole-nesting birds did not begin nesting until the first week of May. This was analogous to the phenology of hole-nesting birds in the boreal forests of Fennoscandia (Carlson et al. 1998) and Canada (Martin et al. 2004).

Nest holes were spotted from the ground by observing breeding behaviour, listening to excavating adults or begging chicks and scratching or knocking hole trees. A nest hole was defined when an adult bird was observed bringing in nesting material or food. The observations of birds displaying or defending a hole were not considered as signs of hole occupancy (Wesołowski 1989, Martin & Eadie 1999). A tree with a nest hole was referred as the nest tree, and the part of trunk or branch in which the nest hole was located was referred as the substrate. The total area surveyed covered approximately 150 ha, not all nests in the area were located.

For each nest, we recorded: 1) characters of the nest tree, including tree species, tree diameter at breast height (DBH) and tree condition (categorised as living, dead tree with intact top or snag with broken top; after Gunn & Hagan 2000) and 2) characters of the nest hole, including hole type, hole height above ground, substrate diameter, substrate condition (categorised as living or dead), hole opening length and hole opening width.

Hole type was classified into woodpecker holes, other bird-induced holes, branch holes or others (after Carlson et al. 1998). Woodpecker holes referred to the holes excavated by woodpeckers for nesting or roosting. In the study area, these might be constructed 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 all other excavated holes that were apparently not the nest or roost sites of woodpeckers. This category included holes excavated by the Willow Tit *Parus montanus* for nesting. These holes could be confusable with those of the Lesser Spotted Woodpecker. But from preliminary observations, most could be told by that the openings of the formers were usually not exactly round and had rough edges. Holes made by woodpeckers other than nest or roost sites were also placed in this category. Because many of them, which might be a deep feeding hole or a beginning of future nest or roost site, resembled the holes of the Willow Tit for observers on the ground. Some of these holes could also previously originate through other causes but then further excavated by woodpeckers for feeding. Branch holes referred to the holes originating from fallen limbs and showing no signs of processing by birds. The category “others” covered all other less common nest sites, which encountered in this study included crevices under loose bark, hollows on broken top (chimneys), holes originated from side fire and vertical slits in trunk due to the shear force when the snag broke.

The hole height was measured from the ground to the middle of the hole opening with a dendrometer. The substrate diameter, hole opening length and hole opening width were estimated from ground using the size of adult birds as a reference (Peters & Grubb 1983). The ratio of opening length to opening width was calculated as an index of opening shape. The opening shape of a hole was termed “slit-like” when the ratio was larger than 1.25, “flat” when the ratio was smaller than 0.8, and “round” for an intermediate value.

Data from both years were pooled, and the repeat use of holes was not excluded. Comparisons were conducted between bird species to reveal their relative preferences. For continuous variables, Mann-Whitney U test was applied for pairwise comparisons. F test was applied to compare the variance, which indicated the niche breadth. For categorical variables, χ^2 test was used.

After checking each variable separately, the cluster analysis was applied to summarise the overall nest site similarity among species (Jobson 1992). Categorical variables were manipulated as dummy variables. The discriminant function analysis with backward stepwise selection was then performed to select the variables which maximised separation among bird species (Jobson 1992).

RESULTS

257 nests of 16 hole-nesting bird species were recorded in the study period. Due to the limitation of sample size, only nine species were analysed, including three excavators, the Great Spotted Woodpecker, the Lesser Spotted Woodpecker, the Willow Tit, and six non-excavators, the Daurian Redstart *Phoenicurus auroreus*, the Red-throated Flycatcher *Ficedula albicilla*, the Coal Tit *Parus ater*, the Great Tit *P. major*, the Nuthatch *Sitta europaea* and the Common Treecreeper *Certhia familiaris*.

Tree species

In the utilisation of tree species, three bird species showed patterns distinct from others (Table 1). Beside the Great Spotted Woodpecker, the Nuthatch and the Common Treecreeper, all other six species established most of their nests in Birch. Among the six species, the Lesser Spotted Woodpecker differed from the Willow Tit in that it used relatively less Birch but more Aspen (χ^2 = 11.2, df = 4, p < 0.05). The Common Treecreeper differed from all others except the Nuthatch in that it placed 64% of its nests in Larch. The Great Spotted Woodpecker also differed from all others except Nuthatch in its high preference for Aspen. The Nuthatch used both Larch and Aspen frequently, and differed from all others except the Great Spotted Woodpecker and the Common Treecreeper (χ^2 test, all cases p < 0.05).

DBH and substrate diameter

The DBH of nest trees ranged from 12 cm in the Willow Tit to 91 cm in the Coal Tit (Table 2). The Willow Tit differed from all other species in that they placed their nests in smallest trees (U-test, all cases p < 0.05). The Red-throated Flycatcher, the Lesser Spotted Woodpecker, the

Table 1. Species composition (in %) of nest trees used by each bird species.

Bird species	Tree species						N
	Salix spp.	*Populus tremula*	*Populus laurifolia*	*Betula platyphylla*	*Larix sibirica*	*Pinus sylvestris*	
Dendrocopos major	-	53.8	-	30.8	-	15.4	13
D. minor	-	15.4	7.7	69.2	7.7	-	13
Phoenicurus auroreus	4.3	-	4.3	73.9	17.4	-	23
Ficedula albicilla	-	4.0	-	96.0	-	-	25
Parus ater	-	1.9	3.8	86.8	3.8	3.8	53
P. major	-	-	18.8	81.3	-	-	16
P. montanus	3.1	-	12.5	81.3	3.1	-	64
Sitta europaea	-	23.8	-	19.0	38.1	19.0	21
Certhia familiaris	-	9.1	-	18.2	63.6	9.1	11

Table 2. Mean (± SD) of nest tree DBH, nest substrate diameter and nest hole height above ground of each bird species.

Bird species	DBH (cm)	Substrate diameter (cm)	Hole height (m)	N
D. major	38.5 ± 7.2	27.2 ± 5.4	8.4 ± 2.2	13
D. minor	33.2 ± 9.9	20.9 ± 4.5	8.8 ± 3.6	13
P. auroreus	35.0 ± 11.5	30.6 ± 13.6	4.4 ± 3.0	23
F. albicilla	28.1 ± 7.8	17.2 ± 5.8	9.2 ± 3.5	25
P. ater	34.0 ± 15.5	30.5 ± 15.1	4.2 ± 3.2	53
P. major	35.1 ± 8.5	27.1 ± 6.7	5.0 ± 2.7	16
P. montanus	24.6 ± 11.1	15.7 ± 7.5	7.3 ± 4.6	64
S. europaea	46.9 ± 14.5	29.1 ± 6.8	11.3 ± 3.9	21
C. familiaris	46.5 ± 10.6	41 ± 14.1	4.3 ± 3.6	11

Coal Tit, the Great Tit and the Daurian Redstart nested in trees of intermediate DBH, among them the nest trees of Red-throated Flycatcher were smaller than those of the Great Tit (U = 109.5, df = 1, $p < 0.05$) and the Daurian Redstart (U = 383.0, df = 1, $p < 0.05$). The Great Spotted Woodpecker, the Nuthatch and the Common Treecreeper never utilised trees with DBH smaller than 25 cm. The nest trees of the Nuthatch and the Common Treecreeper were larger than that of all other six species, and the nest trees of the Great Spotted Woodpecker were larger than that of the Lesser Spotted Woodpecker (U = 126.5, df = 1, $p < 0.05$), the Coal Tit (U = 501.0, df = 1, $p < 0.05$), the Red-throated Flycatcher (U = 276.0, df = 1, $p < 0.001$) and the Willow Tit (U = 745.0, df = 1, $p < 0.001$).

The substrate diameter ranged from 6 cm in the Willow Tit to 96 cm in the Coal Tit. The Common Treecreeper nested in thickest parts of trees than all other species (Table 2). The Lesser Spotted Woodpecker, the Red-throated Flycatcher and the Willow Tit utilised holes in thinner parts of trees than all others. Among the three species, the Red-throated Flycatcher and the Willow Tit further used thinner parts than the Lesser Spotted Woodpecker (U = 230.0, df = 1, $p < 0.05$, U = 656.0, df = 1, $p < 0.01$, respectively). Other five species utilised holes in substrates of intermediate diameter and were similar to each other.

Height above ground

The height of nest holes varied between 0.1 m in the Daurian Redstart and 20 m in the Nuthatch. The three excavators as well as the Nuthatch and the Red-throated Flycatcher nested in higher holes than other four species (Table 2). Among them, the Nuthatch nested higher than the Great Spotted Woodpecker (U = 75.0, df = 1, $p < 0.05$) and the Willow Tit (U = 336.0, df = 1, $p < 0.001$), and the Red-throated Flycatcher higher than the Willow Tit (U = 1024.5, df = 1, $p < 0.05$). The Great Spotted Woodpecker, the Lesser Spotted Woodpecker and the Nuthatch never nested in holes lower than 4 m. The Daurian Redstart, the Coal Tit, the Great Tit and the Common Treecreeper utilised lower holes and showed no difference between each other. The Willow Tit could use holes with more variable height than the Great Spotted Woodpecker (F = 4.4, $p < 0.01$), the Daurian Redstart (F = 2.4, $p < 0.05$), the Coal Tit (F = 2.1, $p < 0.01$) and the Great Tit (F = 3.0, $p < 0.05$).

Tree condition and substrate condition

The Coal Tit and the Great Tit highly preferred living trees (Table 3). The strong preference for living tree of the Coal Tit made it distinct from all other species except the Great Tit. The Great Tit, with its smaller sample size, significantly differed from the Lesser Spotted Woodpecker ($\chi^2 = 10.2$, df = 2, $p < 0.01$), the Daurian Redstart ($\chi^2 = 6.7$, df = 2, $p < 0.05$) and the Willow Tit ($\chi^2 = 10.9$, df = 2, $p < 0.01$). In another extreme, the Lesser Spotted Woodpecker and the Willow Tit established most of their nests in broken snags. The nest tree condition of the Lesser Spotted Woodpecker significantly differed from that of the Coal Tit and the Great Tit as well as the Great Spotted Woodpecker ($\chi^2 = 6.5$, df = 2, $p < 0.05$) and

Table 3. Condition of nest trees and nest substrates (in %) used by each bird species.

Bird species	Tree condition			Substrate condition		N
	living	fresh dead	snag	living	dead	
D. major	61.5	30.8	7.7	38.5	61.5	13
D. minor	30.8	15.4	53.8	-	100.0	13
P. auroreus	47.8	13.0	39.1	39.1	60.9	23
F. albicilla	52.0	16.0	32.0	8.0	92.0	25
P. ater	96.2	3.8	-	96.2	3.8	53
P. major	87.5	6.3	6.3	62.5	37.5	16
P. montanus	43.8	4.7	51.6	15.6	84.4	64
S. europaea	61.9	33.3	4.8	42.9	57.1	21
C. familiaris	45.5	27.3	27.3	45.5	54.5	11

Table 4. Type of nest holes (in %) used by each bird species.

Bird species	Hole types				N
	woodpecker holes	other bird-induced holes	branch holes	others	
D. major	100.0	-	-	-	13
D. minor	100.0	-	-	-	13
P. auroreus	17.4	21.7	56.5	4.3	23
F. albicilla	32.0	56.0	12.0	-	25
P. ater	-	-	100.0	-	53
P. major	-	-	100.0	-	16
P. montanus	1.6	84.4	14.1	-	64
S. europaea	85.7	-	14.3	-	21
C. familiaris	-	-	-	100.0	11

the Nuthatch (χ^2 = 10.8, df = 2, $p < 0.01$). The Willow Tit differed from the previous two tit species as well as the Great Spotted Woodpecker (χ^2 = 13.5, df = 2, $p < 0.01$), the Nuthatch (χ^2 = 20.8, df = 2, $p < 0.001$) and the Common Treecreeper (χ^2 = 7.1, df = 2, $p < 0.05$). The nest tree condition of other five species could be further viewed as two groups. The Great Spotted Woodpecker and the Nuthatch utilised living trees and intact dead trees more often and used broken snags only seldom. The Daurian Redstart, the Red-throated Flycatcher and the Common Treecreeper also placed most of their nests in living trees, while, in contrast to the former group, snags were often used. Among the five species, only the Daurian Redstart and the Nuthatch differed significantly in their nest tree condition (χ^2 = 8.1, df = 2, $p < 0.05$).

The Coal Tit differed from all other species in their high preference for holes in living parts of trees, while the Lesser Spotted Woodpecker, the Red-throated Flycatcher and the Willow Tit nested mainly in holes in dead parts (Table 3). The Lesser Spotted Woodpecker excavated exclusively in dead substrates. The Willow Tit also used only dead substrates when excavating by itself, but all its nest holes that were not self-excavated occurred in living substrates. The comparison of substrate condition with nest tree condition indicated that the Red-throated Flycatcher and the Willow Tit preferred a broken top or a dead branch when using a living tree (χ^2 = 9.5, df = 1, $p < 0.01$, χ^2 = 10.8, df = 1, $p < 0.01$, respectively). Other five species used holes in living or dead substrates more evenly and showed no difference to each other.

Hole type

The preferences for hole types were distinct among most bird species (Table 4). Woodpecker species were persistent in using woodpecker holes. Though being an excavator as well, only 84% of the Willow Tit constructed nest holes by their own. One out of the 64 nests of the Willow Tit were found in a woodpecker hole after the entrance modified by the Nuthatch, and nine were found in branch holes on which no sign of further excavating was observed. The Nuthatch preferred woodpecker holes, the Red-throated Flycatcher placed most of its nests in other bird-induced holes, and the Coal Tit and the Great Tit used exclusively branch holes. The Common Treecreeper utilised special hole types: eight of the nests found were located in crevices under loose bark, two in vertical slits in trunk due to the shear force when the snag broke, and one in trunk fissure originated from side fire. The Daurian Redstart was the only species that utilised holes of all categories. Except among the two woodpecker species and the Nuthatch, and between the Coal Tit and the Great Tit, the hole type utilisation pattern differed in all pairwise comparisons between species (χ^2 test, all cases $p < 0.05$).

Dimension and shape of hole opening

The length of hole opening varied greatly, ranging from 2.4 cm in the Red-throated Flycatcher to 74 cm in the Common Treecreeper (Table 5). The Lesser Spotted Woodpecker, the Red-throated Flycatcher and the Willow Tit utilised holes with smallest opening length, while the Common Treecreeper utilised those with largest opening length. The Nuthatch used holes with the opening length similar to that of the Great Spotted Woodpecker, the Coal Tit and the Great Tit, but it minimised the opening length to the smallest of all. The Common Treecreeper could utilise holes with most variable length (F test, $p < 0.001$ with each of the other species), while the Great Spotted Woodpecker and the Lesser Spotted Woodpecker were most strict in opening length (F test, $p < 0.01$ with each of the other species).

Table 5. Nest hole openings characteristics of each bird species. † — measurements after the minimisation by *S. europaea*.

Bird species	Shape of hole openings (%)			Opening length (cm)	Opening width (cm)	N
	flat	round	slit-like			
D. major	-	100.0	-	4.7 ± 0.3	4.7 ± 0.3	13
D. minor	-	100.0	-	3.4 ± 0.3	3.4 ± 0.3	13
P. auroreus	17.4	26.1	56.5	8.1 ± 4.6	6.5 ± 3.2	23
F. albicilla	8.0	88.0	4.0	3.8 ± 1.0	3.9 ± 0.8	25
P. ater	7.5	15.1	77.4	6.2 ± 3.1	3.1 ± 0.7	53
P. major	12.5	18.8	68.8	7.0 ± 3.0	4.1 ± 1.3	16
P. montanus	6.3	79.7	14.1	3.5 ± 0.9	3.4 ± 0.5	64
S. europaea	-	90.5	9.5	5.1 ± 0.7 3.0 ± 0.2†	4.9 ± 0.3 3.1 ± 0.2†	21
C. familiaris	-	-	100	18 ± 20.7	3.1 ± 0.9	11

The width of hole opening showed less variability than length (Table 5), ranging from 2 cm in the Coal Tit, the Willow Tit and the Common Treecreeper to 18 cm in the Daurian Redstart. The Daurian Redstart bred in holes with widest opening, and was the only species utilising holes with opening wider than 8 cm. The Great Spotted Woodpecker and the Nuthatch utilised holes with similar opening width, which was wider than that of other six species. The Nuthatch then minimised the opening width to one of the smallest, similar to that of the Coal Tit and the Common Treecreeper. The holes used by the Daurian Redstart had the largest variance in opening width (F test, $p < 0.001$ with each of the other species), while those of the Great Spotted Woodpecker, the Lesser Spotted Woodpecker and the Nuthatch showed least variance (F test, $p < 0.05$ with each of the other species).

The preference for hole opening shape showed two distinct patterns: the Great Spotted Woodpecker, the Lesser Spotted Woodpecker, the Red-throated Flycatcher, the Willow Tit and the Nuthatch preferred holes with round openings, while others utilised mostly slit-like holes (Table 5). Holes with flat opening shape were seldom used by any species.

Results of multivariate statistics

The overall similarity of nest sites among bird species was summarised and visualised in the cluster tree (Fig. 1). Greatest similarity occurred between the Red-throated Flycatcher and the Willow Tit, while the nest site of the Common Treecreeper was distinct. Four groups could be identified: the Great Spotted Woodpecker with the Nuthatch, the Lesser Spotted Woodpecker with the Red-throated Flycatcher and the Willow

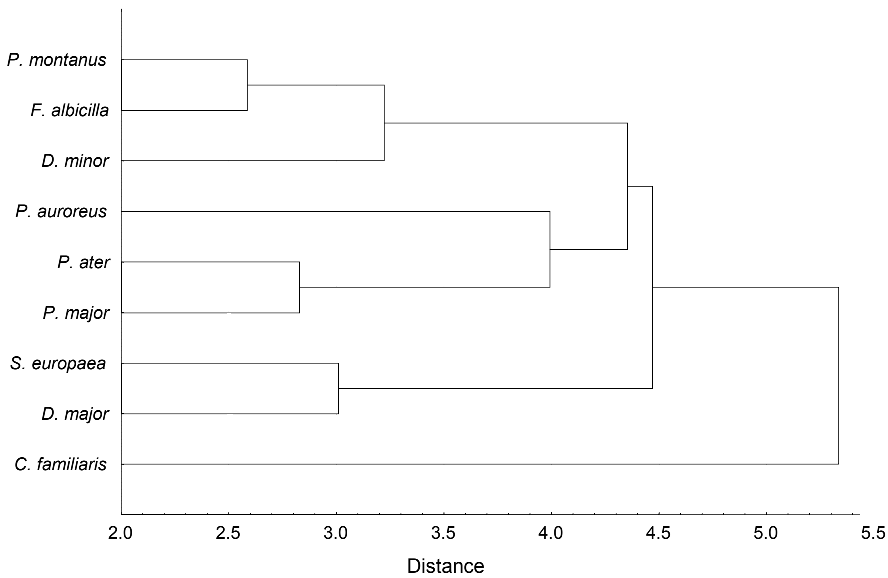

Fig. 1. The nest site similarity among bird species.

Table 6. Reclassification matrix from discriminant function analysis based on hole type and hole opening width.

Observed	Classified									Accuracy (%)
	D. major	*D. minor*	*P. auroreus*	*F. albicilla*	*P. ater*	*P. major*	*P. montanus*	*S europaea*	*C. familiaris*	
D. major	0	0	0	0	0	0	0	13	0	0.0
D. minor	0	12	0	0	0	0	0	1	0	92.3
P. auroreus	0	0	8	0	6	1	3	4	1	34.8
F. albicilla	0	2	0	0	3	0	14	6	0	0.0
P. ater	0	0	0	0	53	0	0	0	0	100.0
P. major	0	0	2	0	12	2	0	0	0	12.5
P. montanus	0	1	0	0	8	1	54	0	0	84.4
S. europaea	0	0	0	0	2	0	0	18	0	90.0
C. familiaris	0	0	0	0	0	0	0	0	11	100.0

Tit, the Daurian Redstart with the Coal Tit and the Great Tit, and the Common Treecreeper alone.

In the discriminant function analysis, a full model with all 15 variables resulted in 67% of correct classification. When a backward stepwise selection was applied, the three hole type variables and the hole opening width alone reached an accuracy of 66%, i.e. over 98% of the discriminant power of the full model. From the reclassification matrix (Table 6), the nest sites of the Great Spotted Woodpecker and the Nuthatch were indistinguishable. The nest sites of the Daurian Redstart overlapped with that of the Coal Tit, the Great Tit, the Willow Tit and the Nuthatch. The nest site of the Red-throated Flycatcher was mainly confounded with that of the Willow Tit, but also with the Lesser Spotted Woodpecker, the Coal Tit and the Nuthatch. The nest site of the Great Tit was highly confounded with that of the Coal Tit.

DISCUSSION

Nest site selection relative to resource availability

In the study area, the forest structure and hole abundance of different forest types were surveyed and reported in another study (Bai et al. 2003). The area covered in the present study was larger and included all the plots of the previous study. Though similar efforts for nest search were made in each forest type, these patches did not contribute equally to the data set, due to different bird density and different field work efficiency (resulted from, e.g. slope, shrub density, tree density) in different sites. Thus, the pooled nest data could not be statistically compared with the tree and hole availability. Yet, some clues could be drawn through simple comparisons.

In the area, Birch comprised 14% to 67% of the standing stems across different forest types (Bai et al. 2003). Thus, the very high use rates of Birch by the Daurian Redstart, the Red-throated Flycatcher, the Coal Tit, the Great Tit and the Willow Tit suggested the use over availability. Larch, comprising 1% to 52% of the standing stems, was used by the Common Treecreeper overproportionally. Poplar, which occurred only in riparian areas and constituted about 6% of the trees there, was overproportionally used by the Great Tit and the Willow Tit. Aspen formed small patches, and its reported availability (0–0.5%) could be biased due to its patchy distribution. Yet the high use rates of Aspen by the Great Spotted Woodpecker, the Lesser Spotted Woodpecker and the Nuthatch indicated overproportional use. Spruce, Fir and Siberian Pine occurred mainly in the spruce-fir forest and altogether comprised 80% of the trees there, but no nest was found in them. The Lesser Spotted Woodpecker, the Daurian Redstart and the Great Tit were never observed in this habitat, and the Red-throated Flycatcher occurred only very seldom. For other species, these three conifers were underused. Taking hole availability into consideration, overall 58% (16–100% across different habitats) of the tree holes were located in Birch, 26% (0–78%) in Poplar, and no hole was found in Spruce, Fir and Siberian Pine (Bai et al. 2003). Thus, the tree species utilisation pattern of most non-excavators might simply reflect the different hole availability. The preference for holes regarding tree species occurred in that the Common Treecreeper used holes in Larch and the Nuthatch used those in Aspen more frequently.

The percentages of trees of DBH < 25 cm, 25–50 cm and > 50 cm were 88.4%, 10.4% and 1.2%, respectively (Bai et al. 2003). Thus, all bird species used large trees overproportionally. Tree holes also occurred more frequently in larger trees, with 20.5%, 55.4% and 24.1% of the holes in trees of

DBH < 25 cm, 25–50 cm and > 50 cm, respectively. Therefore except the Red-throated Flycatcher, all non-excavators appeared to use trees of different size according to hole availability. The Red-throated Flycatcher used holes in smaller trees more frequently.

Living trees, intact dead trees and broken snags comprised approximately 85%, 10% and 5% of the standing stems, respectively (Bai et al. 2003). Thus, all species except the Coal Tit and the Great Tit used living trees underproportionally. 51%, 10% and 39% of the tree holes were found in living trees, intact dead trees and broken snags, respectively. Therefore, the Coal Tit and the Great Tit appeared to select holes in living trees, the Nuthatch preferred holes in intact dead trees, and all these three species avoided holes in broken snags. Other non-excavators were not selective to holes according to tree condition.

Nest site use of excavators

Aspen, Poplar and Birch were important nest tree species for the three excavators studied. The relative preference for *Populus* species over Birch was the Great Spotted Woodpecker, the Lesser Spotted Woodpecker and the Willow Tit in descending order. *Populus* spp. are susceptible to heartrot, which provides a soft substrate for excavation, while retains a firm sapwood shell, that gives stability for the hole (Conner et al. 1976, Hart & Hart 2001). Thus, the preference for Aspen shown by woodpeckers has been frequently documented (Wesołowski & Tomiałojć 1986, Sandström 1992, Martin & Eadie 1999, Martin et al. 2004). However, the nests of the Willow Tit were rarely found in Aspen. This might be partly due to the difference in their territory size and the patchy distribution of Aspen in the study area. The Great Spotted Woodpecker and the Lesser Spotted Woodpecker usually utilised any suitable Aspen in their Birch-dominated territory, while the small territory of the Willow Tit would limit its acquisition to this scarce resource. The firm sapwood of *Populus* might also cause higher excavation burden to the smaller Lesser Spotted Woodpecker and Willow Tit. The high preference for *Populus* of the Great Spotted Woodpecker could also be related to its larger body size. *Populus* had much larger mean diameter than Birch in the study area, which could support the spacious nest hole of the Great Spotted Woodpecker.

All the three excavators preferred large trees, and the association with large trees formed again the descending order of the Great Spotted Woodpecker, the Lesser Spotted Woodpecker and the Willow Tit. Large trees have higher structural stability, and it is possible to nest higher in larger trees. However, suitable large trees might be rare. Thus, the Willow Tit could have limited acquisition to these trees in its small territory. The Great Spotted Woodpecker utilised largest trees, reflecting its needs of building more spacious holes. The same constraints were also reflected in the nest substrate diameter, as the Great Spotted Woodpecker excavated in the thickest substrate and the Willow Tit utilised the thinnest. By nesting in thinner part of trees, nests could be placed higher, but there might be a disadvantage of reduced thermal isolation due to thinner walls. Building in thinner substrate may also reduce the effort of excavating through thick bark and cambium.

Living trees were used underproportionally by all excavators. The Great Spotted Woodpecker preferred intact dead trees presumably as a compromise between structural stability and the burden of excavation (Stenberg 1996). As weaker excavators, the Lesser Spotted Woodpecker and the Willow Tit highly preferred broken snags. Trees with broken tops are often more heavily decayed, because a broken top exposes the heartwood to the invasion of decay fungi and often accumulates rain water which further promotes decomposition process (Lehmkuhl et al. 2003). The condition of nest substrate also reflected the difference in excavating ability. About 40% of the Great Spotted Woodpecker excavated in living part of trees, with the cost of heavier excavation burden and the benefit of lower predation rate and more stable microclimate (Wiebe 2001, Wesołowski 2002). The Lesser Spotted Woodpecker and the Willow Tit, when excavating by itself, were limited to dead substrates.

The nest holes of these three excavators showed no difference in their height above ground. And their nests were in general located higher than that of non-excavators, which is usually explained as an adaptation against nest predation. Nest predation rate was found to decrease with hole height (Nilsson 1984b, Li & Martin 1991). Higher nests are less likely to be found by predators from ground, and have an increased energy cost for predators to reach them. Higher nests also raise the ability of parents to detect and deter potential predators (Martin & Li 1992). However, predation might not be the only explanation. Excavating low in a tall snag would largely reduce the structural stability of the tree and lead to a high risk of tree break at the hole location. The downward decay due to fungi invading from the broken top may also make excavating close to the more heavily decayed broken top energetically profitable (Jackson & Jackson 2004).

Excavators usually build their hole opening as small as possible, just fitting to their own body size. This could decrease the detection and access by predators as well as minimise the energy cost of excavation (Peterson & Gauthier 1985, Sandström 1991). The opening shape was close to round, which is the most efficient shape.

In summary, these three excavators had some adaptations in common, i.e. holes high above ground with round and minimised opening. While they also showed different adaptations in nest tree and nest substrate selection, which were shaped by their different excavation ability, body size and territory size.

Nest site use of non-excavators

Nuthatch. In the study area, the Nuthatch showed highest preference for woodpecker holes compared to other non-excavators. More than 80% of the Nuthatch nested in woodpecker holes, higher than the rates documented in Europe (Wesołowski 1989). This might be partially due to the release from competition with the Starling *Sturnus vulgaris*, which is the dominant secondary user of middle-sized woodpecker holes in Europe especially in forest edges.

Since the Nuthatch nested mainly in middle-sized woodpecker holes, which in the study area were mostly excavated by the Great Spotted Woodpecker, the nest site of the Nuthatch consequently resembled that of the Great Spotted Woodpecker. The Nuthatch used holes in Aspen overproportionally, which largely reflected the hole location of the Aspen-preferring Great Spotted Woodpecker, instead of direct selection on tree species of the Nuthatch. It also used more intact dead trees, placed its nest higher than all other non-excavators, and bred mainly in holes with round opening, which were all characteristic for the Great Spotted Woodpecker. The only difference between the Nuthatch and the Great Spotted Woodpecker nest sites was that on average the Nuthatch nested higher than the Great Spotted Woodpecker. This was probably because that the Nuthatch selected higher holes from available old woodpecker holes, with the advantage of reduced predation of higher nests (Nilsson 1984b). In Europe, the Nuthatch was often reported as one of the non-excavators which had highest nest sites (van Balen et al. 1982, Nilsson 1984b, Wesołowski 1989).

Red-throated Flycatcher. Similar to the Nuthatch, the Red-throated Flycatcher also nested mainly in excavated holes, mostly those from the Willow Tit. As a consequence, the nest tree and nest hole characters of the Red-throated Flycatcher largely resembled those of the Willow Tit. Thus among the six non-excavators studied, it used the smallest trees, nested in holes higher than all others except the Nuthatch, and most of its nest holes located in dead substrate and had round openings. On average, the Red-throated Flycatcher bred in higher holes than the Willow Tit did, indicating that the Red-throated Flycatcher might select higher holes from the available ones, presumably an adaptation against predation (Nilsson 1984b).

Until few years ago, the Red-throated Flycatcher was considered as a subspecies of the Red-breasted Flycatcher *Ficedula parva*, with *F. p. parva* in west Palearctic and *F. p. albicilla* in east Palearctic. They were then separated into two species based on that the latter has different winter quarters, lighter weight, almost unspotted white eggs, different song, a more complete pre-breeding moult leading to the appearance of the orange patch in males at their first spring, and this orange patch in the latter never reaches the breast (O. Bourski, pers. com.). These two closely related species also use completely different nest sites. In consistence with the present study, studies in Central Siberia also documented the Red-throated Flycatcher as an excavated hole user, using mostly Willow Tit holes, sometimes woodpecker holes and seldom branch holes (Rogacheva et al. 1991). In contrast, the Red-breasted Flycatcher used mainly chimneys and half holes, with relatively low nest height above ground (Miera 1978, Glutz von Blotzheim & Bauer 1993, Mitrus & Soćko 2004). What might be the selection force leading to the distinct nest site use of these two closely related species? Hole availability may play an important role. The Willow Tit is numerous in Siberia, and almost no other species competes with the Redthroated Flycatcher to be a secondary user (O. Bourski, pers. com.).

Coal Tit and Great Tit. Opposite to above two species, the Coal Tit and the Great Tit behaved as branch hole specialists. They were not selective with respect to tree species or tree diameter, as they frequently use deciduous trees and large trees, following the higher availability of holes in such trees. However, they showed high preference for holes in living trees and in living substrates. Non-excavating tit species breeding almost exclusively in living trees were also reported in Europe (Wesołowski 1989, 1996, Günther & Hellmann 1995). Living trees have higher structural stability and are less prone to fall. Nests placed in living parts of trees suffer less predation (Albano 1992, Christman & Dhondt 1997, Wesołowski 2002), as larger predators that could not reach the nest through hole entrance usually destroy the hole wall, which is less likely to happen to holes surrounded by sound wood. Microclimate inside holes in living substrates may also be more stable. Holes in decayed substrates reach higher maximum temperatures and have greater daily fluctuations than those in harder wood (Wiebe 2001).

The nest hole characters of the Coal Tit and the Great Tit, as branch hole specialists, followed the appearance of such holes. These holes usually occurred lower in thicker parts of trees, which had undergone a longer time for holes to develop. Branch holes also mostly had slit-like opening shape, due to the nature of branch fall and wood texture. Such nest site characters of non-excavating tit species were frequently documented in Europe (van Balen et al. 1982, Wesołowski 1989, 1996, Sandström 1992).

Common Treecreeper. Distinct from all others, the Common Treecreeper specialised in long slits, and most of its tree use could be explained by the availability of such holes. It preferred Larch as long crevices mostly occurred behind the thick bark of Larch. It nested in larger trees since bark crevices occurred mainly in old trees, and old larch trees could develop very large diameters. When slits were formed in smaller trees, as encountered in this study due to fire fissure and shear force when snags broke, it utilised small trees as well.

Daurian Redstart. The Daurian Redstart behaved as a generalist in many aspects. It utilised tree species, tree DBH and tree condition according to hole availability, indicating that it was not selective to these tree attributes. It was the only non-excavator utilising all four types of tree holes, even nesting in ground holes at the river bank was observed. The Daurian Redstart also used holes of most variable opening dimensions and opening shape. The Common Redstart *Phoenicurus phoenicurus* in Europe also appeared less selective in nest site use compared to other hole nesters (van Balen et al. 1982, Glutz von Blotzheim & Bauer 1993). Using diverse nest sites could be more likely to appear in such later breeding migrants.

As demonstrated by the discriminant function analysis, hole type was an important variable for distinguishing species. We did not measure the inner dimension of holes, which was suggested to be an important factor of hole occupancy and often differs among species (van Balen et al. 1982, Johnsson et al. 1993, Carlson et al. 1998). Different types of natural holes could reflect difference in inner dimensions to certain extent. Except the Daurian Redstart, all non-excavators had specific preference for a certain hole type, and their nest tree use and nest site characters followed mainly the occurrence of such holes. This emphasised that the attributes of natural holes are usually diverse and correlated, very different from nest boxes, which tend to be uniform.

Niche overlap and role of competition

Among the excavators, the two smaller species, the Lesser Spotted Woodpecker and the Willow Tit, were not likely to suffer from competition with the Great Spotted Woodpecker, since the preferred nest tree species and nest tree condition of the latter were distinct. The Great Spotted Woodpecker was also confined to using substrates above certain diameter and thus needed larger trees. The nest sites of the Lesser Spotted Woodpecker and the Willow Tit, as dead wood specialists, were similar to some extent. However, on average, the Willow Tit used smaller trees and excavated in thinner substrates. It also appeared to associate with more heavily decayed wood than the Lesser Spotted Woodpecker. Snag availability in the study area was not likely to be a limiting factor for these two species, and competition for nest sites between them was never observed in the study period.

Among non-excavators, the Common Treecreeper bred earliest, and it utilised unique niche, thus it was basically free from interspecific nest site competition. The Nuthatch, also an early breeder, encountered little nest site competition from other species as well. Its nest-site, mostly in living or intact dead large trees, placed high up with the hole opening minimised by itself, seemed an optimum in terms of both reduced predation and favourable microclimate.

The specialisation in branch holes of the Coal Tit and the Great Tit did not appear to be forced by the competition with the Nuthatch. There were always some usable woodpecker holes left for the later-coming Daurian Redstart and Red-throated Flycatcher. Moreover, in fact, without the ability of minimising hole opening, middle-sized woodpecker holes were not likely to be a good breeding place. In Poland, the nests of the Marsh Tit *P. palustris* in woodpecker holes were depredated more often than those in branch holes (Wesołowski 2002). It is interesting that both the Coal Tit and the Great Tit never used the old nests of the Willow Tit, which were a plentiful resource and located high with small opening. The Coal Tit and the Great Tit had to make the choice of nesting lower in living or at least more intact substrate, or nesting high in decayed wood, and they gave the priority to the former.

Perrins (1979) explained the low nesting height of the Great Tit by preferred foraging sites in the breeding season. However, this did not fit to the Coal Tit, which usually foraged high in thin twigs (Glutz von Blotzheim & Bauer 1993). Competition was most likely to occur between these two tit species. Though on average the Coal Tit used holes of smaller opening than the Great Tit, some overlap existed. In the literature, the Great Tit used holes with larger and deeper chambers than the Coal Tit (van Balen et al. 1982), but in the present study the inner dimension of holes was not measured. Competition for nest sites between them were observed a few times during the study. The density of the Great Tit in the study area was relatively low, approximately 1–3 pairs/10 ha, while that of the Coal Tit was 6–10 pairs/10 ha. The low density of the dominant competitor, the Great Tit, should not be due to nest site competition, since many holes were left for the Coal Tit. In addition, for the Coal Tit, the nest site use was more likely to be influenced by intraspecific territoriality rather than interspecific competition.

The Red-throated Flycatcher, facing the same choice of nesting in branch holes or excavated holes, preferred the latter. It was possible that, for this latest-breeding migrant, most of the favourable branch holes were already occupied by the Coal Tit and the Great Tit. However, this pattern might also reflect the different trade-offs of different species. As a canopy fly-catcher, nesting high would be advantageous for reduced exposure of adult birds and nest sites to predators. Since branch holes were rare in higher parts of trees, the Red-throated Flycatcher used more woodpecker holes and the Willow Tit holes. Despite the distinct nest sites of the Red-breasted Flycatcher in Europe, other two European hole-nesting flycatchers, the Collared Flycatcher *F. albicollis* and the Pied Flycatcher *F. hypoleuca*, often nest high above ground when they use natural holes (Sachslehner 1995, Czeszczewik & Walankiewicz 2003, but Nilsson 1984b).

The Daurian Redstart, being a nest site generalist, had certain extent of overlap with most of other non-excavators, as indicated by the confounding results of discriminant function analysis. The nest-site use of this species was most likely to be shaped by interspecific competition, as it often utilised holes with unnecessarily large openings. Nevertheless, its density might not be limited by the availability of holes, since many holes occupied by the later-coming Red-throated Flycatcher could be usable for the Daurian Redstart as well. Experimental manipulation would be necessary to learn whether its nest site use was shaped by ongoing competition, or was simply less selective as a late breeding migrant.

In general, the role of interspecific competition in shaping nest-site selection and limiting population density appeared much less important than that reported in most studies. Many studies could arise from impoverished nest site availability in managed forests (Brawn & Balda 1988). Moreover, many of the superior competitors in these studies were edge species or introduced species, with the association of human activities. In the Netherlands, competition with the Starling shaped nest-site use and population size of the Great Tit (van Balen et al. 1982). In Sweden, the dominance of the Jackdaw *Corvus monedula* forced other users of Black Woodpecker holes to use shallower and lower ones, and made Stock Doves *Columba oenas* move deeper into forest (Johnsson et al. 1993). In the United States, the nest niche of the introduced European Starling and House Sparrow *Passer domesticus* overlapped with native Bluebirds *Sialia* spp., and caused great decline of their populations (Erskine & McLaren 1976, Sedgwick 1997). The competition with the Starling also limited the Tree Swallow *Tachycineta bicolor* to smaller holes and nest sites farther from woodland edges (Rendell & Robertson 1989, Dobkin et al. 1995). The aggressiveness of the Starling could exert selection on other species to shift their nesting phenology and behaviour (Koenig 2003). The present study supports the argument of Wesołowski (1989) that interspecific competition, though playing some role in nest hole selection, could be less important in natural forests than in managed forests.

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STRESZCZENIE

[Miejsca gniazdowe dziuplaków w pierwotnym lesie tajgowym Mongolii]

Badania prowadzono w górach Khentii (NE Mongolia) w latach 2002–2003. Dziuple uznawano za zajęte, gdy obserwowano ptaki dorosłe przynoszące materiał gniazdowych lub pokarm dla piskląt. Dla każdego gniazda opisywano: gatunek drzewa z dziuplą, jego pierśnicę, kondycję, rodzaj dziupli, grubość i kondycję fragmentu drzewa zawierającego dziuplę oraz wielkość otworu wejściowego. Znaleziono łącznie 257 dziupli 16 gatunków ptaków. Ze względu na wielkość próby w pracy zawarte są dane o dziuplach 9 gatunków ptaków: trzech dziuplaków pierwotnych (samych wykuwających dziuple) — dzięcioła dużego *Dendrocopos major*, dzięciołka *D. minor* oraz sikory czarnogłowej *Parus palustris*, oraz 6 gatunków dziuplaków wtórnych (korzystających z istniejących dziupli) — bogatki *P. major*, sosnówki *P. ater*, pleszki chińskiej *Phoenicurus auroreus*, muchołówki rdzawogardłej *Ficedula albicilla*, kowalika *Sitta europaea*, pełzacza leśnego *Certhia familiaris*. Dokładną charakterystykę miejsc gniazdowych tych gatunków zawierają tabele 1–5. Na podstawie analizy wszystkich branych pod uwagę cech, podjęto próbę stwierdzenia trafności przypisania dziupli do poszczególnych gatunków. Stwierdzono, że dziuple dzięcioła dużego i kowalika były nierozróżnialne, zaś całkowicie różne od pozostałych są dziuple pełzacza. W przypadku pozostałych gatunków biorąc pod uwagę miejsca ich umieszczenia były w pewnym stopniu podobne między gatunkami (Tab. 6). Podobieństwo miejsc umieszczenia dziupli zajmowanych przez poszczególne gatunki może być związane z układami dziuplaki pierwotne-wtórne. Wyróżniono 3 takie grupy gatunków: dzięcioł duży — kowalik, dzięciołek i muchołówka rdzawogardła, sikora czarnogłowa oraz pozostałe gatunki sikor i pleszka. Osobną grupę stanowiły dziuple pełzacza leśnego (Fig. 1). Zebrane wyniki autorzy porównują z publikowanymi danymi zebranymi w Europie, zwracając uwagę na podobieństwa nisz gniazdowych i konkurencję międzygatunkową w tej grupie ptaków.

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