

The Importance of Dead-Wood Supply for Woodpeckers in Estonia

ASKO LÕHMUS*, RIHO KINKS AND MIHKEL SOON

Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, EE-51014 Tartu, Estonia

*corresponding author; E-mail: asko.lohmus@ut.ee

Lõhmus, A., Kinks, R. and Soon, M. 2010. The Importance of Dead-Wood Supply for Woodpeckers in Estonia. *Baltic Forestry*, 16 (1): 76-86.

Abstract

We explored which species of woodpeckers depend on the supply of standing dead trees (snags) in Estonia and how that dependence relates to their invertebrate prey base. In a 900-km² area in east-central Estonia, we described the snag supply within a radius of 600 m around 73 nests of six woodpecker species and in 30 random transects representing the available forest landscape. We modelled woodpecker habitat preferences as differences between the snag supply around their nests and in random transects, analysed the incidence of woodpecker foraging signs in terms of dead-wood characteristics, and estimated the abundance of arthropods in bark samples collected from snags in late winter. The results confirmed the division of woodpeckers into 'snag specialist' and generalist species. Characteristically, the abundant snag supply in the nesting territories of the three specialised species – White-backed Woodpecker (*Dendrocopos leucotos*), Lesser Spotted Woodpecker (*D. minor*) and Three-toed Woodpecker (*Picoides tridactylus*) – included many alders and Norway spruces and few Scots pines, which generally followed the frequency of use and arthropod abundance in these trees. The scarcity of arthropods in the bark samples from birch coincided with a low frequency of foraging signs on its trunks; however, birch was not avoided around the nests and may host important prey base in its abundant fungal fruit-bodies. Larger snags tended to have more arthropods per unit of bark area but their importance for woodpeckers was not clear. We concur with previous suggestions that the requirements of specialised woodpeckers can be used for deriving tentative targets of snag-retention. In this study, their nesting probability increased from 25% to 75% when snag densities (≥ 5 cm diameter, ≥ 0.5 m height; pine snags excluded) increased from 100 to 200 trunks per hectare. However, snag management should be spatially explicit, because such levels can hardly be sustained all over the landscape, and also consider at least epixylic fungi and specific insects, which require different types of snags than woodpeckers.

Key words: dead wood, forest management, habitat selection, snag, woodpecker

Introduction

In recent decades, rare species dependent on dead wood have received considerable interest by forest scientists and managers. This is because intensive forest management significantly reduces the supply of dead wood and, thereby, may threaten a large part of forest biodiversity (Siitonen 2001, Grove 2002). Thus, an important question for developing ecologically sustainable modifications or alternative approaches in forestry is: how much, and which kind of dead wood should be left in forests in order to avoid species extinctions.

Woodpeckers hold a special position in dead-wood research and management for three reasons. First, several woodpecker species are narrowly specialised to feed upon wood-inhabiting invertebrates at least seasonally, and those species are threatened with extinction in intensively managed regions (e.g. Roberge et al. 2008a). Second, because most woodpeck-

ers are year-round resident birds that are relatively well detectable, they may act as focal taxa for the conservation management of large parts of forest biodiversity, such as the less conspicuous wood-inhabiting insects and cryptogams (Martikainen et al. 1998, Roberge et al. 2008b) or forest birds in general (Mikusiński et al. 2001). Finally, because of their large home-ranges, woodpeckers are particularly informative on large (landscape-planning) scales, where the effects on small organisms are more difficult to monitor and may be less expressed (e.g. Angelstam et al. 2004, Roberge et al. 2008b).

To be effectively used as focal species for management, woodpeckers' requirements for dead wood should be described quantitatively on proper spatial scales and understood causally (e.g. Drapeau et al. 2009). The causal links are particularly important when habitat use of the species differs geographically (e.g. Väli et al. 2004), as reported also for some European specialised woodpecker species with re-

spect to forest types used (Angelstam et al. 2004). Such variation includes the large-scale patterns created by climate: in areas experiencing thick and lasting snow cover, most downed wood remains inaccessible in winter and standing dead trees (hereafter 'snags') become crucial for woodpeckers (Aulén 1991, Bull et al. 1993). Interestingly, a recent study found relatively weak relationships between snag supply and woodpecker abundance in four species in south-central Lithuania, which was attributed to the narrow range of conditions studied (Roberge et al. 2008a). Hence, additional Baltic studies are needed, particularly from northern (hemiboreal) areas, with an emphasis on which kind of snags, and why, are crucial. That would mean measuring the actual supply of invertebrate prey in snags in relation to snag characteristics – a rare type of studies in general and not undertaken in hemiboreal Europe to our knowledge. In hemiboreal environments, winter food base is critical for woodpeckers, and in this season the specialist species actually use dead trees most (Pettersson 1983, Aulén 1988).

In this study we explore which species of woodpeckers depend on the supply of snags in Estonia, how that dependence might be related to the winter abundance of invertebrates in those trees, and how the incidence of woodpecker nesting in relation to snag supply could be used for informing forest management. Obviously, the abundance of invertebrates in snags generally follows snag abundance, but we ask whether the species and size of the trees also matter. Thus, we (1) relate, using multifactor logistic regression modelling, the incidence of nesting territories of woodpeckers to the abundance of various fractions of snags; (2) compare the snags of four common taxa – Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), birches (*Betula* spp.) and black alder (*Alnus glutinosa*) – both in terms of their use by woodpeckers and the abundance of wintering arthropods; (3) test for tree-size effects to explore a possible conflict with forestry – arthropods may be most abundant in large snags (Grove 2002, but see Lindhe et al. 2005), while such snags are particularly rare in managed forest landscapes (Lõhmus 2003, Lõhmus et al. 2005). We expect that the types of snags having the highest arthropod abundance are most used for foraging by woodpeckers and such snags are also most influential for the birds' nesting territory selection. We also expect that these patterns are most pronounced for previously distinguished 'snag specialist' woodpecker species (Roberge et al. 2008a), which then could be collectively used for informing forest management.

Materials and methods

Study area and sampling design

The study was carried out in a 900-km² area in east-central Estonia (58°25' N, 26°20' E). The terrain is flat. Forest land covers 49%, agricultural land 36%, mire 8%, flood-plains 2%, rivers and lakes 2% and settlements 3% of the area. Half the forests grow on wet soils. Most forests feature a single-aged tree layer (because of a long clear-cutting history) and consist, on average, of 46% birch, 17% Scots pine, 15% Norway spruce, 9% aspen (*Populus tremula*), 7% grey alder (*Alnus incana*), 6% black alder and 1% other tree species. The area includes nature reserves as well as different production forests (four State forest districts as well as a large number of private owners), reflecting the management regimes as well as landscape composition typical of Estonia. That similarity includes about 40% of forest land being developed during the twentieth century, a low proportion of old unmanaged forests (2% of forest land), mostly natural regeneration resulting in mixed stands, and a low intensity of thinnings (see Lõhmus 2002, Lõhmus and Lõhmus 2005, Lõhmus et al. 2005).

The sampling scheme was based on the locations of (1) woodpecker nests and (2) randomly distributed transects all over the forest land (forest and clear-cuts) to reveal the general situation 'available' for woodpeckers. The latter comprised 30 long (2 km), straight transects marked in the field (see Lõhmus et al. 2005 for a map and further details). Woodpecker nests were sought systematically in 1999–2001 in the nesting territories previously mapped using playback techniques in early spring (see Lõhmus et al. 2000 for preliminary results) and a combination of several other standard methods (forest birds of the study area have been the subject of intensive long-term surveys; e.g. Lõhmus 2004, 2005).

Fieldwork and laboratory work

Two datasets on dead-wood abundance and use by woodpeckers were collected between 2000 and 2004. First, snags were counted along strip transects of 10 m width (five metres to both sides of the transect line). In addition to the random transects (see above), three 'nest-site transects' were delineated around each woodpecker nest. The nest-site transects were straight, 600 m long each, and maximally spaced out while staying in forest as much as possible. Hence, when the nest was completely surrounded by forest, the transects were 120° apart from each other, but when the nest was situated at forest edge, the transects were not directed to the open land and were distributed more densely. The nest-site transects were planned on the

map prior to fieldwork and, thus, randomly sampled the forests in woodpecker territories. In order to maintain observational independence, only one nest from each nesting territory was described, and nesting territory (or random transect) was used as the sample unit instead of individual trees or nest-site transects. To optimize field effort, only a random selection of the nests of the most common species, the Great Spotted Woodpecker (*Dendrocopos major*), were described. Altogether, 73 nests of six species of true woodpeckers were included – in addition to the Great Spotted Woodpecker also the White-backed Woodpecker (*Dendrocopos leucotos*), Lesser Spotted Woodpecker (*D. minor*), Black Woodpecker (*Dryocopus martius*), Grey-headed Woodpecker (*Picus canus*) and Three-toed Woodpecker (*Picoides tridactylus*).

In the random-transect and nest-site-transect strips, the same observer (R. K.) counted all snags at least 0.5 m tall and 5 cm diameter at breast height (or at the top in case of lower stumps). In nest-site transects, the data were separately collected for 100-m sections from the nest up to 600 m. That total distance corresponds to typical nesting-territory size of woodpeckers (see Hagemeyer and Blair 1997), while the sections were used to detect the scale of habitat selection of the birds. For each of the 46 061 snags recorded, the species (six taxa distinguished: Scots pine, Norway spruce, *Betula* spp., *Alnus* spp., aspen, other), height class (three categories: 1, 0.5–3 m; 2, reaching subcanopy; 3, large tree reaching upper canopy) and presence of any signs of woodpecker foraging were recorded. The most common tree species in the category 'other' was European ash (*Fraxinus excelsior*).

A supplementary dataset was collected by another observer (P. Lõhmus) to explore woodpeckers' intensive use of dead-wood items of particular qualities, including downed dead wood. For that, all large snags (diameter at breast height (DBH) ≥ 10 cm; over 1.5 m tall) and downed wood (diameter of the thickest end ≥ 20 cm; ≥ 50 cm long) were mapped on the random transects (see Lõhmus et al. 2005 for general results). The 2573 items found were characterized by tree species, diameter, decay stage, and extensive breakage by woodpecker activity; snags were also divided into those with bark (over 20% of surface covered with bark) and without.

To estimate the abundance of arthropods wintering in the snags, 80 trees of four common species (Scots pine, Norway spruce, birch and Black alder) were sampled on ten transects by M. S. The transects were selected according to the co-occurrence of the tree species there to minimize the effects of surrounding habitats. In late March to early April 2004 and 2005,

bark samples were collected from two dead trunks of each tree species in each transect and year using a modified method of Powell et al. (2002). Only trunks having relatively intact wood (approximately 1 cm could be penetrated by knife) and extensive bark cover were considered, and size differences between the trees of different species were avoided. From each trunk, bark was removed at two 15×15 cm square plots (facing north and south, respectively) at approximately 1 m height. After the bark removal, xylem gallery entrances of wood-boring insects were counted in each exposed plot. The bark samples were dissected in laboratory and all arthropods found were determined to order and counted. In case of Collembola, only individuals >5 mm long were recorded. Because most gallery entrances had been made by beetles, the index of beetle abundance was derived as the sum of individuals found and the entrances (Powell et al. 2002).

Data analysis

The data analysis comprised three parts: (1) distinguishing the characteristic features of the snag supply around specialist-woodpecker nest-sites as compared with the situation generally available (random transects) or around generalist woodpecker nest-sites; (2) relating the incidence of woodpecker foraging to the characteristics and location (around nest-sites vs. in random transects) of dead trees; (3) testing for tree species and diameter effects on the abundance of arthropods in the bark samples. The analyses were carried out using STATISTICA 8.0 software. In case of parametric tests, Kolmogorov-Smirnov test was used to check the normality of distributions, and logarithmic transformations were used by necessity in part (3).

For part (1), eleven candidate variables were used: diversity of the snag supply (Shannon index calculated from the relative frequencies of the trees in the 18 taxon×size categories), total density of snags, and its subsets – snag densities of the three height categories and six taxon categories. The densities were obtained by standardising snag count results of random and nest-site transects (all three transects of each nest-site pooled) to trees-per-hectare units. Two nests in cemeteries were omitted from the analyses as outliers. Then, confirmative one-way analyses of variance of total snag density and snag composition were carried out to explore the expected grouping of the species as specialists and generalists. The expectation was that the snag supply around the nest-sites of specialist species tends to be more abundant and compositionally different from random transects. Those differences of each nest site and random transect from each other were measured in cluster analysis as Euclidean

distances using ten variables (omitting the total density). Finally, the characteristic features of the nest-sites of specialist species were extracted using multivariate logistic regression (separately for the comparison with generalists and the random transects). Because of many redundant variables, we first made preliminary univariate screening of the variables. The best explanatory models with those variables having univariate $p < 0.1$ were then built using both forward and backward stepwise procedure.

In part (2), two basic analyses were carried out. First, the incidence of intensive foraging (see above) was related to tree species and tree diameter using logistic regression. Second, analyses of variance (ANOVA) were conducted to check whether the proportion of snags carrying any signs of woodpecker foraging differed according to their location around woodpecker nests vs. random transects, tree taxa and height categories. For those ANOVAs, the sample unit was either a random transect or a nest-site, and the proportions of use for different tree taxa or height categories were treated as repeated measures in each transect. Only the proportions based on at least five snags observed were considered.

For the arthropod analysis (part 3), the sample unit was a tree species in one transect, i.e. the abundance values of each major arthropod taxon group from the two snags \times two bark samples of each tree species were averaged. The effects of tree species and tree diameter were then explored using conventional univariate tests depending on the variable distribution (ANOVA, Kruskal-Wallis ANOVA, Spearman correlation).

Results

Snags around woodpecker nests and in random transects

The general analysis of the supply of snags around woodpecker nests and on the random transects strongly supported the ecological groups of specialist and generalist species among woodpeckers. The total density of snags differed among woodpecker species and the random transects (ANOVA: $F_{6,96} = 2.4$, $p = 0.035$), with the three expected specialist species (White-backed Woodpecker, Lesser Spotted Woodpecker, Three-toed Woodpecker) nesting in most snag-rich forests (Fig. 1a). The values observed (Fig. 1a) indicate that values exceeding 150 dead trunks per hectare result in a rapid increase in the probability of nesting of those species. The same species consistently differed most from the random transects in terms of snag composition (Fig. 1b).

The total density of snags did not vary along with the distance from woodpecker nests within the 600 m

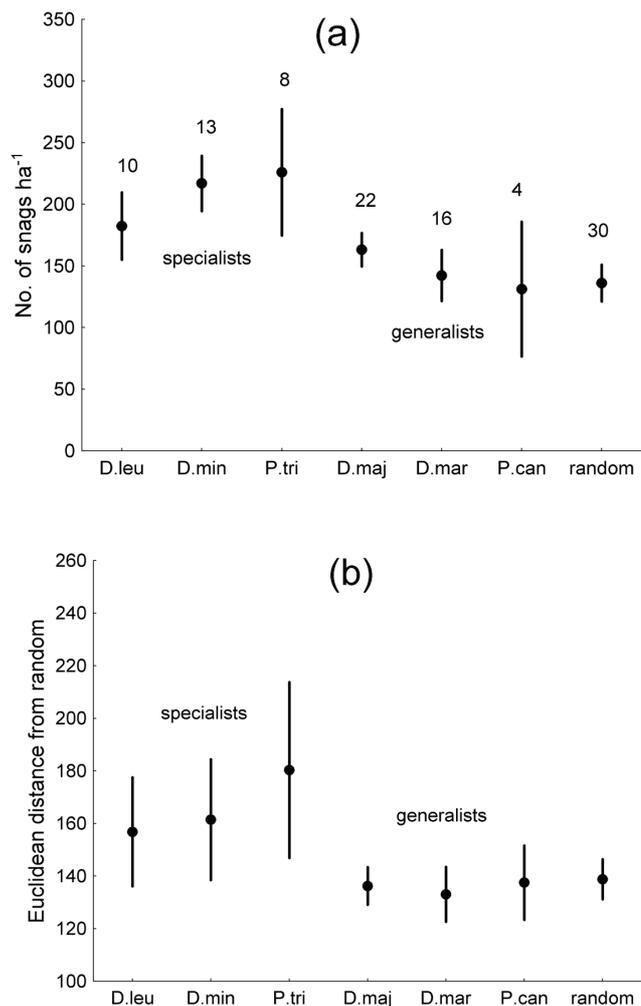


Figure 1. Mean (\pm SE) density of snags (a) and difference from the snag composition of random transects (b) in the nesting territories of six species of woodpeckers and the random transects. Species: D. leu – *Dendrocopos leucotos*, D. maj – *D. major*, D. min – *D. minor*, D. mar – *Dryocopus martius*, P. can – *Picus canus*, P. tri – *Picoides tridactylus*. The numbers are sample sizes. In part (b), ‘random transects’ denote the mean difference of random transects from all other random transects

considered (Repeated measures ANOVA for the six 100-m distance classes: $F_{5,345} = 0.3$, $p = 0.90$). However, the difference between specialist and generalist species ($F_{1,69} = 4.8$, $p = 0.032$) was most pronounced within 200 m (Fig. 2a) even though the distance \times woodpecker type interaction was not significant ($F_{5,345} = 0.9$, $p = 0.51$).

Of eleven variables considered for distinguishing the snag supply around the nests of specialist species and the random transects (Table 1), three (densi-

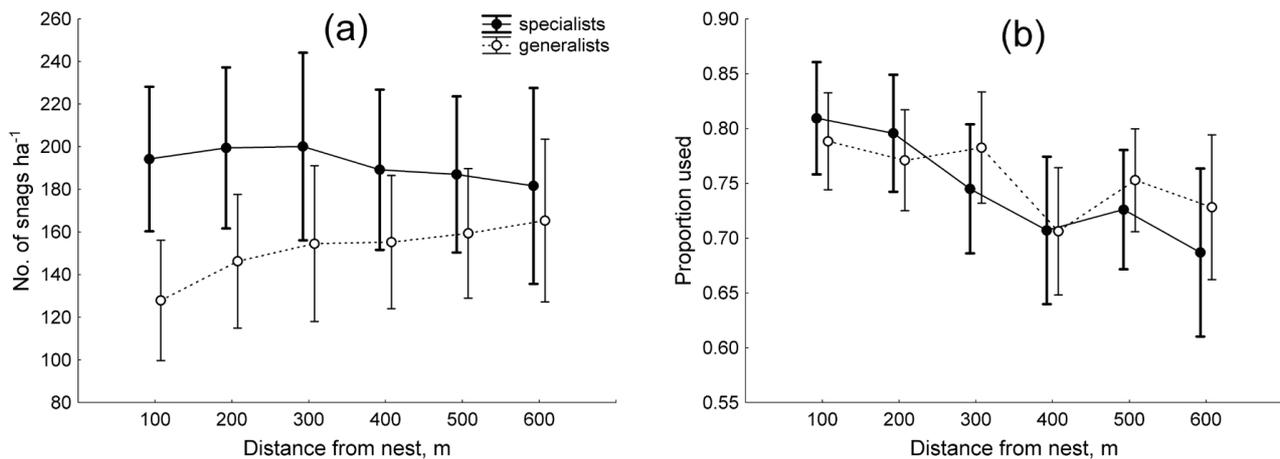


Figure 2. Mean (\pm 95% CI) density of snags (a) and the proportion carrying signs of woodpecker foraging (b) along with the distance from woodpecker nests (100-m distance intervals; generalist and specialist species distinguished, cf. Fig. 1)

Table 1. Characteristics of the snag supply in the forests around woodpecker nests and in random transects

Variable	Median (quartile range)		
	Specialist species ^a (n = 31)	Generalist species ^b (n = 42)	Random transects (n = 30)
General statistics			
Total density of snags, no. ha ⁻¹	195 (150–235)	145 (92–204)	119 (68–196)
Shannon index of diversity	1.8 (1.6–2.0)	1.8 (1.7–1.9)	1.7 (1.5–2.1)
Tree-species composition			
Snags of <i>Pinus sylvestris</i> , no. ha ⁻¹	0 (0)	0 (0–51)	1 (0–36)
Snags of <i>Picea abies</i> , no. ha ⁻¹	24 (5–39)	10 (5–28)	9 (2–21)
Snags of <i>Betula</i> spp., no. ha ⁻¹	60 (18–98)	31 (16–82)	19 (8–69)
Snags of <i>Alnus</i> spp., no. ha ⁻¹	81 (41–112)	29 (13–79)	31 (3–47)
Snags of <i>Populus tremula</i> , no. ha ⁻¹	5 (0–13)	3 (0–9)	1 (0–5)
Snags of other tree species, no. ha ⁻¹	5 (1–9)	2 (0–5)	2 (0–7)
Size composition			
Snags 0.5–3 m tall, no. ha ⁻¹	101 (68–141)	74 (41–123)	55 (26–92)
Medium-height snags, no. ha ⁻¹	83 (55–108)	54 (37–87)	59 (30–87)
Large dead trees, no. ha ⁻¹	5 (3–10)	5 (3–8)	5 (2–8)

a *Dendrocopos leucotos*, *D. minor*, *Picoides tridactylus*

b *Dendrocopos major*, *Dryocopus martius*, *Picus canus*

c calculated from the relative abundances of 18 types (6 taxa \times 3 height classes)

ty of ‘other’ tree species and large trees; diversity of the snag supply) were not significant ($p > 0.1$) at the univariate screening stage. Among the remaining variables, only two were significant after controlling for the total density of snags (likelihood-ratio test: $\chi^2 = 9.5$, $p = 0.002$): the densities of spruce (positive; $\chi^2 = 7.4$, $p = 0.006$) and pine (negative; $\chi^2 = 14.5$, $p < 0.001$). A full type-III model with those three variables retained all of them as significant (Table 2); this was also the best model among all possible three-variable models, and no other variable could be added to retain all variables significant at $p < 0.05$.

Of eleven variables considered for distinguishing the snag supply around the nests of specialist and generalist species, four (density of birch, aspen, large snags, and the diversity of the snag supply) were not significant ($p > 0.1$) at the univariate screening stage and two more variables (densities of low- and medium-height snags separately) did not contribute to the total density of snags. However, such independent contributions were detected for the densities of alders (positive; $\chi^2 = 3.8$, $p = 0.05$), spruce (positive; $\chi^2 = 4.6$, $p = 0.031$), ‘other’ tree species (positive; $\chi^2 = 4.3$, $p = 0.039$) and pine (negative; $\chi^2 = 12.0$, $p < 0.001$). Because these

Table 2. The best multivariate logistic regression models separating the snag supply around the nests of specialist woodpecker species ($n = 31$) from the snag supply in random transects ($n = 30$) and around the nests of generalist woodpeckers ($n = 41$). Note the two alternative models for the specialists vs. generalists contrast. LL – log-likelihood of the variable

Variable	Estimate	SE	LL	χ^2_1	p
Specialists vs. random transects (model log-likelihood -28.3, $p < 0.0001$)					
Total density of snags, no. ha ⁻¹	0.012	0.004	-33.1	9.4	0.0021
Snags of <i>Pinus sylvestris</i> , no. ha ⁻¹	-0.061	0.035	-33.8	10.9	0.0010
Snags of <i>Picea abies</i> , no. ha ⁻¹	0.034	0.020	-30.3	3.9	0.0497
Specialists vs. generalists, model I (model log-likelihood -38.1, $p < 0.0001$)					
Snags of <i>Picea abies</i> , no. ha ⁻¹	0.040	0.015	-42.3	8.4	0.0037
Snags of <i>Alnus</i> spp., no. ha ⁻¹	0.014	0.005	-42.6	8.9	0.0028
Snags of other tree species, no. ha ⁻¹	0.083	0.046	-41.2	6.1	0.0133
Specialists vs. generalists, model II (model log-likelihood -40.1, $p < 0.0001$)					
Total density of snags, no. ha ⁻¹	0.008	0.004	-43.2	6.2	0.0130
Snags of <i>Pinus sylvestris</i> , no. ha ⁻¹	-0.046	0.026	-46.1	12.0	0.0005

variables tended to lose their significance in a full type-III model (obviously because of redundancy-related confounding effects to each other), additional approaches were used to find the best explanatory sets. First, both forward and backward stepwise procedures extracted the densities of alder and spruce snags as explanatory variables, while the forward procedure also included the density of ‘other’ tree species (i.e., mostly *Fraxinus excelsior*) (Table 2). Second, exploration of the best subsets indicated that, although the model extracted in the previous approach was the best three-variable subset, the best two-variable subset was actually formed by the two variables left out. Therefore, the model comprising the total density of snags (positive) and pine snags (negative) should be considered an alternative (Table 2).

Because the specialist woodpeckers so clearly avoided pine snags (see also Table 1), a simple practical logistic model was elaborated to illustrate their nesting probability in relation to the density of all non-pine snags. That relationship (Fig. 3) indicated that when the density of such snags increased from 150 to 300 snags ha⁻¹ the probability of specialist woodpecker nesting increased approximately from 50% to 90%. While there appeared an up to 25% theoretical probability of woodpecker nesting even at snag densities below 100 snags ha⁻¹ (Fig. 3), it should be reminded that 75% of the nest-sites found actually had at least 150 snags ha⁻¹ (Table 1).

Woodpeckers' foraging signs on dead trees

In the random transects, thirty-five (2.0%) of the 1724 snags described (including 2.1% of the 1324 trees with bark, and 1.8% of the 400 trees without bark), but no downed tree ($n = 849$), were intensively used by woodpeckers for foraging. Such intensive use by woodpeckers depended significantly on tree species (likelihood-ratio test: $p < 0.0001$), with Scots pine being used significantly less often (Wald test: $p = 0.032$) and black alder significantly more often ($p < 0.0001$)

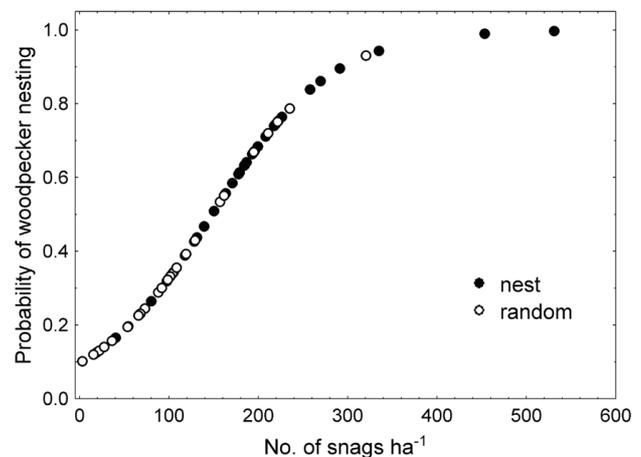


Figure 3. Predicted probabilities (y-axis) and observed incidence (31 nest-sites vs. 30 random transects) of the nesting of specialised woodpeckers in relation to the total density of snags other than those of Scots pine. The parameters of the logistic equation are: coefficient = 0.015 ± 0.004 SE ($\chi^2_1 = 18.4$, $p < 0.0001$), intercept -2.226 ± 0.707

than ‘other’ tree species. In contrast, tree diameter was not related to the incidence of woodpecker foraging neither as the main effect (likelihood-ratio test: $p = 0.44$) nor when nested within tree species ($p = 0.91$).

In addition to those extensively used trees, most snags carried at least some signs of woodpecker foraging. Such snags formed, on average, $71 \pm 16\%$ (SD) of the snags on the 30 random transects, which did not differ significantly from $75 \pm 12\%$ around 42 nests of generalist woodpeckers and $74 \pm 12\%$ around 33 nests of specialized woodpeckers (ANOVA: $F_{2,102} = 1.0$, $p = 0.38$). However, there still was a clear within-territory decrease in the proportion of snags used along with the distance from the nest (Repeated measures ANOVA for the six 100-m sections: $F_{5,330} = 6.7$, $p < 0.0001$): snags were most frequently used within 200–300 m of woodpecker nests (Fig. 2b). That tendency did not differ between generalist and specialist species (woodpecker \times section interaction: $F_{5,330} = 1.0$, $p = 0.44$).

The use of snags differed among height categories (Repeated measures ANOVA: $F_{2,148} = 25.8$, $p < 0.0001$) with dead trees reaching the upper canopy being used significantly more frequently (Tukey test: $p < 0.0001$) than the two lower height classes. The frequency of use of the latter was similar (Tukey test: $p = 0.88$). That height-dependency was similar on random transects and around nest-sites (transect type \times height category interaction: $F_{4,148} = 0.6$, $p = 0.70$).

Analyses of tree-species dependent use by woodpeckers were complicated because only a few tree species co-occurred in reasonable numbers in the same transects or around the same nest-sites. Yet, highly consistent pairwise tree-species effects (mean values compared within the sample units) confirmed three main patterns in the average values (Fig. 4). First, the use of birch was less frequent than any other common species. Compared with alders (Repeated measures ANOVA: $F_{1,83} = 70.6$, $p < 0.0001$), spruce ($F_{1,75} = 20.1$, $p < 0.0001$) and aspen ($F_{1,44} = 6.2$, $p = 0.017$) the less frequent use of birch was similar around the nests and in random transects. Secondly, the difference between birch and pine ($F_{1,28} = 10.6$, $p = 0.0030$) was only pronounced in the random transects (Tukey test: $p = 0.002$), not around the nests of either generalist (Tukey test: $p = 0.99$) or specialist woodpeckers (Tukey test: $p = 0.76$; the interaction term in general: $F_{2,28} = 4.1$, $p = 0.028$). That tendency of less frequent use of pines around woodpecker nests than in the random transects (Fig. 4) was also seen when analysed separately (One-way

ANOVA: $F_{2,30} = 4.4$, $p = 0.021$; but note the very small sample size for specialist woodpeckers). Third, there were no significant differences in the overall use frequency between any other main tree taxa.

Insects in and under the bark

From the bark samples, altogether 719 arthropods were caught: 373 Diptera (of those 275 Nematocera under the bark of one spruce tree), 216 beetles, 73 spiders, 44 Hymenoptera, 5 Lepidoptera, 3 Collembola, 2 Heteroptera, 1 Psocoptera and 1 Homoptera. Of the 647 insects, 508 were adults, 137 were larvae and two (Lepidoptera) were pupae. The average number of gallery entrances under the 450 cm² bark collected from one tree varied from one to six in case of different tree species and years.

The abundance of two major taxon groups varied significantly among tree species and, in both cases, birch had the lowest abundance of individuals. In beetles, that effect (ANOVA: $F_{3,36} = 4.4$, $p = 0.010$) included a contrast between the beetle-rich spruce and beetle-poor birch (Tukey test: $p = 0.007$). In case of spiders ($F_{3,36} = 12.7$, $p = 0.005$), their low abundance in birch contrasted with a high abundance in black alder (Tukey test: $p = 0.008$). The latter pattern was significant also in each year separately, while the result on beetles was not significant in 2004. The abundance of Diptera collected showed no clear variation among tree species (Kruskal-Wallis test: $H_3 = 4.9$, $p = 0.18$).

Among major taxon groups, the abundance increased significantly with tree diameter (tree species pooled, $n = 40$) in case of beetles ($r_s = 0.41$, $p = 0.008$) and Diptera ($r_s = 0.32$, $p = 0.042$), but not in spiders ($r_s = -0.11$, $p = 0.51$). However, in Diptera that correlation was greatly influenced by one individual-rich large tree (see above), after the omission of which the relationship appeared only marginal ($r_s = 0.31$, $n = 39$, $p = 0.055$).

Discussion and Conclusions

Woodpeckers in relation to snags and insects

Our study confirmed, on the basis of snag densities in nesting territories, the division of woodpeckers into specialist and generalist species. The same 'snag specialist' species as White-backed Woodpecker, Lesser Spotted Woodpecker and Three-toed Woodpecker were distinguished for boreal and north-temperate Europe also by Roberge et al. (2008a). Such specificity explains the observations in the cut areas of Estonia, where those species only occasionally nest, while other woodpeckers (Great Spotted Woodpecker, Black Woodpecker and Grey-headed Woodpecker) are regular breeders in the presence of retention trees (Rosenvald and Lõhmus 2007). Apparently, the rela-

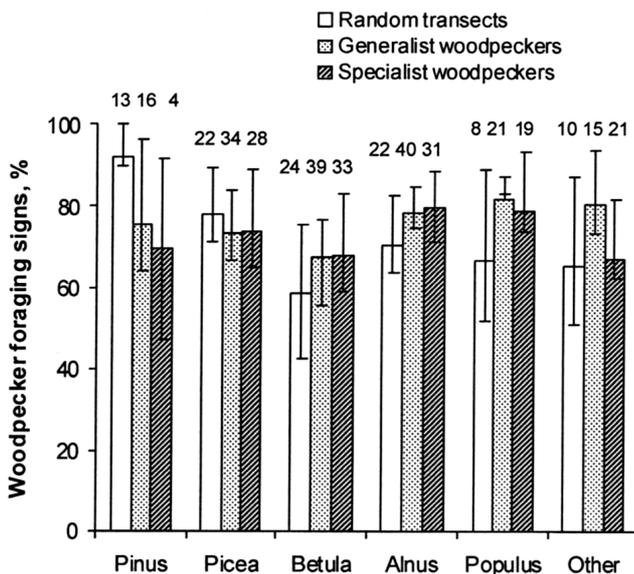


Figure 4. Mean (\pm quartile range) share of snags with the signs of woodpecker foraging in relation to tree species and location (random transects or woodpecker nesting territories). The numbers refer to sample sizes (the transects or territories with at least five trees observed)

tively abundant supply of harvesting slash and logs does not compensate the scarcity of snags in cut areas (see Lõhmus et al. 2005), probably because the downed dead wood is inaccessible in winter. The lack of extensive use of downed wood by woodpeckers was also documented in our study.

In general, our study supported the idea that snags vary in their quality for woodpeckers, and that variation is at least partly related to invertebrate abundance. In particular, specialised woodpeckers nested in areas with abundant snags of Norway spruce and black alder – the tree species hosting the highest numbers of wintering beetles and spiders, respectively. Black alder also was the tree species most extensively pecked by woodpeckers. The observations on the quality of Scots pine, birches, and snags of different sizes require additional explanations, however.

Three independent datasets indicated an avoidance of Scots pine snags by specialist woodpeckers: the logistic regression models revealing those snags as the only type actually avoided around nests (also different from the nest-sites of generalist woodpeckers), their generally low frequency of use there (Fig. 4), and the rare incidence of extensive use by woodpeckers. Such avoidance does not contradict the fact that, at the same time, the bark samples from pine snags did not appear particularly arthropod-poor. This is because the supply of Scots pine snags in our study area, differently from any other tree species, mostly contains decorticate trunks (Lõhmus and Lõhmus 2001). Hence, the total abundance of hibernating arthropods per trunk is still lowest in pine snags. Moreover, typical pine stands are situated in nutrient-poor sites, which may have a poor food base for woodpeckers in general. These ideas are supported by summer window-trapping of insects on the same four tree species in our random transects: the lowest numbers of insects were trapped on pines with no difference between dead and live trunks (in other tree species, dead trees were generally more insect-rich) and the general arthropod composition on pine snags differed from that on the snags of all other tree species (Soon 2004).

Birch had fewest arthropods per bark area in winter and also fewest woodpecker foraging signs. Those findings may be related to the relatively smooth bark of birch, which offers less cover for hibernating arthropods. However, woodpeckers did not avoid birch around their nests, and the trapping study cited above (Soon 2004) actually recorded the highest insect abundance in summer on dead birch. One explanation to such pattern is that the value of birch snags for woodpeckers is due to the rich insect fauna inhabiting their characteristically abundant fruit-bodies of *Fomes fomentarius* (Aulén 1991). That importance may have been

missed because woodpecker foraging was usually recorded based on the pecking of the trunks only (old fruit-bodies seemed to be damaged for various reasons). Additionally, the abundance of birch around the woodpecker nests may result from the actual preference by them for insect-rich black alders, which usually grow in mixed stands with birch in our study area.

In terms of tree size, a novel finding was that the density of insects (at least beetles) per surface area was larger in larger-diameter trees. As a result, the total per-tree insect abundance may increase disproportionately to tree size; for example, because of a thicker or coarser bark of larger trees. This contrasts with an intuitive idea that, in case of equal volumes, smaller dead trees would provide more habitats for surface-dwelling organisms (Kruys and Jonsson 1999). Such complex relationships could not be explored with our data, but the window-trapping of insects in summer typically also yielded more individuals from larger-diameter snags (Soon 2004) and the tallest snags were more frequently used by woodpeckers (similar evidence from North America: Hutto 1995, Gunn and Hagan 2000). Nevertheless, the real value of such snags for woodpeckers in Estonia was apparently minor because they were rare (Table 1), the incidence of extensive foraging by woodpeckers was not related to tree diameter, and distinguishing the size fractions never improved the models of woodpeckers' nest-site preferences. Given also that the actual responses of insects to snag size may be highly species-specific (Lindhe et al. 2005), the significance of small snags and stumps should not be forgotten while establishing snag conservation targets, which usually have considered large snags only (e.g. Bütler et al. 2004).

Implications for forest management

We concur with the previous suggestions that the requirements of specialist woodpeckers can be used for deriving tentative targets of snag-retention in forestry (Bütler et al. 2004, Roberge et al. 2008a). In this study, their nesting probability increased from 25% to 75% when the densities of snags of >5 cm in diameter (pine snags excluded) increased from 100 to 200 trunks per hectare. It should be stressed that those numbers represent the environments sustaining viable woodpecker populations: the trends for all the three specialist species have been either stable or increasing since the 1970s in Estonia (Elts et al. 2009). This is a different situation than in several intensively managed forest regions where the woodpeckers are declining or have even gone locally extinct (Roberge et al. 2008a). Interestingly, in the breeding areas of a Norwegian viable population of White-backed Woodpeckers the average abundance of dead trees (154 trees >5 cm in

diameter per ha; Hogstad and Stenberg 1994) was almost identical to that recorded by us (Fig. 1a). However, that population also used Scots pine, which was avoided in our study area.

Another finding of management value was the scale of the most pronounced preferences and snag-use around the woodpecker nests, i.e. 200–300 m radius (Fig. 2). This suggests a minimum size of habitat patches for the specialised species. However, because the actual home-ranges of the woodpeckers are much larger, particularly in winter (Angelstam et al. 2004), there should be a network of such snag-rich patches in forest landscapes. In this respect, a good connectiveness of our study area was revealed by considerable snag densities and frequency of their use by woodpeckers in the random transects.

The target patches for snag management (particularly when enhancing landscape connectivity) are not necessarily mature stands only because woodpeckers appeared to frequently use snags of all sizes. In the absence of thinnings, considerable quantities of snags spontaneously develop even in first-generation mid-aged forests, such as alder and birch stands on abandoned agricultural lands (Lõhmus and Lõhmus 2005). Moreover, several insectivorous woodpecker species, including the Three-toed Woodpecker, are adapted to use naturally disturbed areas, such as post-fire communities (Hutto 1995). Hence, in addition to appropriate planning of set-aside stands and thinnings, ecologically sound snag retention guidelines should also be elaborated for final fellings and for the salvage logging of fire- or storm-disturbed areas (Hutto 2006). A promising technique is to retain dead and dying trees in small patches or at the edges of the harvested area because decayed snags are easily destroyed by the machinery in the main cutting area. Where natural snags are lacking, purposeful creating of high stumps during conventional harvesting operations is a promising technique (Lindbladh and Abrahamsson 2008).

We propose that, in addition to woodpeckers, two other taxon groups with distinct requirements should be considered for integrated snag management: (1) epixylic lichenized and non-lichenized fungi and (2) mono- or oligophagous insects. The first taxon group requires decorticate snags (Holien 1996, Lõhmus and Lõhmus 2001) – differently from the bark-covered snags important to woodpeckers for their invertebrate fauna in or under the bark (Aulén 1991). Combining those requirements highlights the importance of retaining large snags, which more probably have both bark-covered and decorticate patches and also persist longer to enable passively dispersing species to colonize them (Lõhmus and Lõhmus 2001). Snag persistence and large size are also crucial for vertebrates nesting

there (e.g. Lõhmus 2003). Insect communities in snags vary according to tree species, decay stage, the decomposing fungal species and canopy closure (e.g. Kaila et al. 1994, 1997, Saint-Germain et al. 2007, Lindbladh and Abrahamsson 2008). For this taxon group, diverse snag supply should be provided on the landscape scale (Lindbladh and Abrahamsson 2008) – a requirement different from that of woodpeckers, which primarily benefited from abundance, not the diversity or location of snags.

Finally, we draw attention to that dead wood also includes dead branches in the crowns of old live trees, which were not considered in our study but may provide important prey for specialist woodpeckers (Pettersson 1983, Smith 2007). Such trees are relatively rare in forests managed with clear-cuttings but they may play a substantial role for dead-wood dependent organisms in uneven-aged silvicultural systems and traditional cultural landscapes (note the two woodpecker pairs nesting in cemeteries in our study as well). Hence, senescent trees should be included when considering snag-retention targets for uneven-aged systems.

Acknowledgements

We thank Piret Lõhmus for the supplementary dead-wood dataset and Jaanus Remm for planning the transects and marking them in the field. The comments by Piret Lõhmus, Raul Rosenvald and two anonymous reviewers helped to improve the manuscript. Valentina Krivtsova prepared the Russian summary. The research was supported by the Estonian Science Foundation (grants 5257 and 7402), the Estonian Ministry of Education and Science (project SF0180012s09) and the European Union through the European Regional Development Fund (Centre of Excellence FIBIR).

References

- Angelstam, P., Roberge, J. M., Lõhmus, A., Bergmanis, M., Brazaitis, G., Dõnz-Breuss, M., Edenius, L., Kosinski, Z., Kurlavičius, P., Lärmanis, V., Lūkins, M., Mikusiński, G., Račinskis, E., Strazds, M. and Tryjanowski, P. 2004. Habitat modelling as a tool for landscape-scale conservation – a review of parameters for focal forest birds. *Ecological Bulletins* 51: 427–454.
- Aulén, G. 1988. Ecology and distribution of white-backed woodpecker (*Dendrocopos leucotos*) in Sweden. Doctoral thesis, Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Uppsala.
- Aulén, G. 1991. Increasing insect abundance by killing deciduous trees: a method of improving the food situation for endangered woodpeckers. *Holarctic Ecology* 14: 68–80.
- Bull, E. L. and Holthausen, R. S. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. *The Journal of Wildlife Management* 57: 335–345.

- Bütler, R., Angelstam, P. and Schlaepfer, R. 2004. Quantitative snag targets for the three-toed woodpecker *Picoides tridactylus*. *Ecological Bulletins* 51: 219–232.
- Drapeau, P., Nappi, A., Imbeau, L. and Saint-Germain, M. 2009. Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. *Forestry Chronicle* 85: 227–234.
- Elts, J., Kuresoo, A., Leibak, E., Leito, A., Leivits, A., Lilleleht, V., Luigujõe, L., Mägi, E., Nellis, R., Nellis, R. and Ots, M. 2009. Eesti lindude staatus, pesitsusaegne ja talvine arvukus 2003–2008 [Status and numbers of Estonian birds, 2003–2008]. *Hirundo* 22: 3–31, (in Estonian with English summary)
- Grove, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* 33: 1–23.
- Gunn, J. S. and Hagan J. M., III. 2000. Woodpecker abundance and tree use in uneven-aged managed, and unmanaged, forest in northern Maine. *Forest Ecology and Management* 126: 1–12.
- Hagemeijer, W. J. M. and Blair, M. J. (Editors) 1997. The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. T & AD Poyser, London. 903 p.
- Hogstad, O. and Stenberg, I. 1994. Habitat selection of a viable population of white-backed woodpeckers *Dendrocopos leucotos*. *Fauna Norvegica Series C Cinclus* 17: 75–94.
- Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* 9: 1041–1058.
- Holien, H. 1996. Influence of site and stand factors on the distribution of crustose lichens of the caliciales in a suboceanic spruce forest area in central Norway. *The Lichenologist* 28: 315–330.
- Hutto, R. L. 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. *Conservation Biology* 20: 984–993.
- Kaila, L., Martikainen, P., Punttila, P. and Yakovlev, E. 1994. Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. *Annales Zoologici Fennici* 31: 97–107.
- Kaila, L., Martikainen, P. and Punttila, P. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodiversity and Conservation* 6: 1–18.
- Kruys, N. and Jonsson, B. G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Canadian Journal of Forest Research* 29: 1295–1299.
- Lindbladh, M. and Abrahamsson, M. 2008. Beetle diversity in high-stumps from Norway spruce thinnings. *Scandinavian Journal of Forest Research* 23: 339–347.
- Lindhe, A., Lindelöw, Å. and Åsenblad, N. 2005. Saproxylic beetles in standing dead wood: density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation* 14: 3033–3053.
- Lõhmus, A. 2002. The lack of old-growth forest – a threat to Estonian biodiversity. Proceedings of the Estonian Academy of Sciences, *Biology/Ecology* 51: 138–144.
- Lõhmus, A. 2003. Do Ural owls suffer from the lack of nest sites in managed forests? *Biological Conservation* 110: 1–9.
- Lõhmus, A. 2004. Breeding bird communities in two Estonian forest landscapes: are managed areas lost for biodiversity conservation? Proceedings of the Estonian Academy of Sciences, *Biology/Ecology* 53, p. 52–67.
- Lõhmus, A. 2005. Are timber harvesting and conservation of nest sites of forest-dwelling raptors always mutually exclusive? *Animal Conservation* 8: 443–450.
- Lõhmus, A. and Lõhmus, P. 2005. Coarse woody debris in mid-aged stands: abandoned agricultural versus long-term forest land. *Canadian Journal of Forest Research* 35: 1502–1506.
- Lõhmus, A., Elts, J., Evestus, T., Kinks, R., Kulpsoo, L., Leivits, A., Nellis, R. and Väli, Ü. 2000. Rähnide arvukusest Eestis [Numbers of breeding woodpeckers in Estonia]. *Hirundo* 13: 67–81, (in Estonian with English summary)
- Lõhmus, A., Lõhmus, P., Remm, J. and Vellak, K. 2005. Old-growth structural elements in a strict reserve and commercial forest landscape in Estonia. *Forest Ecology and Management* 216: 201–215.
- Lõhmus, P. and Lõhmus, A. 2001. Snags, and their lichen flora in old Estonian peatland forests. *Annales Botanici Fennici* 38: 265–280.
- Martikainen, P., Kaila, L. and Haila, Y. 1998. Threatened beetles in white-backed woodpecker habitats. *Conservation Biology*, 12: 293–301.
- Mikusiński, G., Gromadzki, M. and Chylarecki, P. 2001. Woodpeckers as indicators of forest bird diversity. *Conservation Biology* 15: 208–217.
- Pettersson, B., 1983. Foraging behaviour of the middle spotted woodpecker *Dendrocopos medius* in Sweden. *Holarctic Ecology* 6: 263–269.
- Powell, H. D., Hejl, S. J. and Six, D. L. 2002. Measuring woodpecker food: a simple method for comparing wood-boring beetle abundance among fire-killed trees. *Journal of Field Ornithology*, 73: 130–140.
- Roberge, J.-M., Angelstam, P. and Villard, M.-A. 2008a. Specialised woodpeckers and naturalness in hemiboreal forests – Deriving quantitative targets for conservation planning. *Biological Conservation* 141: 997–1012.
- Roberge, J.-M., Mikusiński, G. and Svensson, S. 2008b. The white-backed woodpecker: Umbrella species for forest conservation planning? *Biodiversity and Conservation* 17: 2479–2494.
- Rosenvald, R. and Lõhmus, A. 2007. Breeding birds in hemiboreal clear-cuts: tree retention effects in relation to site type. *Forestry* 80: 503–516.
- Saint-Germain, M., Drapeau, P. and Buddle, C. M. 2007. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. *Ecography* 30: 737–748.
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49: 11–41.
- Smith, K. W. 2007. The utilization of dead wood resources by woodpeckers in Britain. *Ibis* 149, Suppl. 2: 183–192.
- Soon, M. 2004. Putukate arvukus ja koosseis surnud puudel sõltuvalt puu liigist ja jämedusest [Abundance and composition of insects on snags depending on tree species and size]. BSc thesis, University of Tartu, Estonia, (in Estonian with English summary)
- Väli, Ü., Treinys, R. and Lõhmus, A. 2004. Geographical variation in macrohabitat use and preferences of the lesser spotted eagle *Aquila pomarina*. *Ibis* 146: 661–671.

Received 18 October 2009

Accepted 15 March 2010

ЗНАЧЕНИЕ СУХОСТОЯ ДЛЯ ДЯТЛОВ В ЭСТОНИИ

Аско Лыхмус, Рихо Кинкс, Михкель Соон

Резюме

Мы исследовали, какие виды дятлов зависят от сухостоя в Эстонии и как эта зависимость связана с их кормовой базой беспозвоночных. На территории площадью 900 км² в восточно-центральной Эстонии было изучено количество сухостоя в радиусе 600 м вокруг 73 гнезд шести видов дятлов и на 30 случайным образом расположенных трансект, которые характеризуют данный лесной ландшафт. Мы (1) вывели модель предпочтения места обитания дятлами, сравнив характеристики сухостоя вокруг гнезд дятлов и случайно расположенных трансект, (2) по наличию признаков добычи корма дятлами проанализировали, какие характеристики древесины дятлы предпочитают, и (3) определили численность членистоногих по собранной в конце зимы коре сухостоя. Было характерно, что обилие сухостоя на территориях гнездования трех видов-специалистов - белоспинного дятла (*Dendrocopos leucotos*), малого пестрого дятла (*D. minor*) и трехпалого дятла (*Picoides tridactylus*) - выражается в большом количестве ольх и елей, и только в нескольких соснах, что в общем соответствовало относительной частоте поиска пищи дятлами и многочисленности членистоногих в этих видах деревьев. Малочисленность членистоногих в коре березы совпала с низкой частотой признаков добычи пищи на их стволах; однако дятлы не избегали березу около гнезд, и она может быть важной из-за насекомых в многочисленных плодовых телах грибов. Более крупные стволы имели больше членистоногих на единицу коры, но их значимость для дятлов не была ясна. Мы согласны с предыдущими предположениями, что потребности дятлов-специалистов могут быть использованы для создания руководств по сохранению сухостоя. В этом исследовании вероятность гнездования дятлов-специалистов увеличилась от 25% до 75%, когда количество сухостоя (≥ 5 см диаметром, ≥ 0.5 м в высоту; сосны не учитывались) выросло от 100 до 200 стволов на гектар. Однако сохранение сухостоя должно быть запланировано на ландшафтном уровне, поскольку такое количество стволов на гектар невозможно поддерживать на всей территории. Помимо дятлов следует учитывать также грибы-эпифиты и специфических насекомых, которые нуждаются в других типах сухостоя.

Ключевые слова: дятел, лесное хозяйство, предпочтения места обитания, сухостой