

Woodpecker foraging activity in oak-dominated hill forests in Hungary

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Abstract We documented the foraging activities of woodpeckers on selected trees in an established conservation-oriented management study in five oak-dominated forests in Hungary. We examined the tree species preference of woodpeckers as a group and the impact of specific tree characteristics on the habitat use of woodpeckers. We estimated the percentage of visible foraging signs on the trunks and upper limbs of selected trees through the winter and early spring of 2019–2020. Based on the Jacobs’ index, woodpeckers preferred oak species for foraging and most foraging signs were on limbs rather than trunks. Foraging signs on trunks were more frequent on those of larger diameters and greater heights. It was also found that the lower the tree, the greater the effect of its diameter on the occurrence of signs.

Keywords: woodpecker ecology, woodpecker foraging signs, conservation, nature conservation management

Összefoglalás Kutatásunkban hazai harkályfajok táplálkozási nyomait mértük fel egy természetvédelmi erdőkezelési kutatás alapállapot felméréseként tölgy dominálta gazdasági erdőkben. Vizsgáltuk a harkályok fajaj-preferenciáját, valamint a fák egyes jellemzőinek hatását a harkályok élőhely-használatára. 2019–2020 tele és kora tavasza között mértük fel a kijelölt fákön megfigyelhető táplálkozási nyomok százalékos előfordulását a fák törzsén és a lombkoronában. Eredményeink alapján a harkályfajok leginkább a különböző tölgyfajokat preferálták, ezen belül is legnagyobb mértékben a kocsánytalan tölgyet, emellett pedig nagyobb eséllyel találtunk táplálkozási nyomokat az ágakon, mint a fák törzsén. A detektált táplálkozási nyomok a nagyobb törzstátmérőjű és magasabbak fákön voltak gyakoribbak. Minél alacsonyabb a fa, annál nagyobb hatása van a mellmagassági átmérőnek a táplálkozási nyomok előfordulására, a felsőbb magassági kategóriákban az átmérő hatása mérsékeltebb.

Kulcsszavak: harkály ökológia, harkály táplálkozási nyomok, természetvédelem, természetvédelmi erdőkezelés

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Introduction

The ecological impact of woodpecker species in wooded ecosystems is important for numerous reasons. They are considered umbrella species because through their presence they can support many other species (Melletti & Penteriani 2003, Garmendia *et al.* 2006, Puverel *et al.* 2019). They provide nesting and roosting site for various cavity-dwelling species, including invertebrates, mammals and birds such as tits (Paridae), flycatchers (*Ficedula* spp.), nuthatches (*Sitta* spp.), treecreepers (*Certhia* spp.) and some owls (Strigidae) and ducks (Anatidae)

(Gorman 2004). Certain woodpeckers can also be regarded as keystone species (Mikusiński *et al.* 2001, Virkkala 2006), for example, Black Woodpecker (*Dryocopus martius*) in Europe (Gorman 2011, Puverel *et al.* 2019) and Red-cockaded Woodpecker (*Dryobates borealis*) in North America (Jusino *et al.* 2015). The most abundant European species, the Great Spotted Woodpecker (*Dendrocopos major*), is often categorized as a keystone species, especially in sub-optimal habitats, where there is invariably a lack of natural cavities (Pasinelli 2007). However, this species is a major nest predator of cavity-nesting songbirds and therefore, its keystone role is sometimes considered as controversial (Wesolowski 2007, Ónodi & Winkler 2016).

Woodpeckers are particularly suitable as indicator organisms (Virkkala 2006, Drever *et al.* 2008). First, most of them are year-round resident and mostly easily detectable (Lõhmus *et al.* 2010). Second, they have large home ranges (e.g. Bocca *et al.* 2007, Charman *et al.* 2010, Champion *et al.* 2020), hence they can provide information on large areas. Third, this is the only bird family in the Western Palearctic that can forage for insects within the inner layers of wood, which are threatened with extinction in intensively managed regions so that they can be monitored relatively easily (Lõhmus *et al.* 2010). They are also highly susceptible to habitat change (Mikusiński *et al.* 2001, Thompson *et al.* 2003, Mikusiński 2006). Finally, they provide identifiable foraging signs that are often specific to the group (Gorman 2015).

Many studies on the habitat and nesting requirements of woodpecker and cavity-nesting species in general have been published (Wesolowski & Tomialojc 1986, Hardersen 2004, Pasinelli 2007, Kosinski *et al.* 2017). There has been less focus on foraging habitat needs and on foraging signs. This is especially true for species-specific observations, especially in managed, commercial stands (Czeszczewik 2009, St-Amand *et al.* 2018, Aszalós *et al.* 2020). Woodpeckers that forage on bark may choose trees with different characteristics for foraging than they do for nesting, and thus, habitats appropriate for nesting may fail to include suitable foraging sites (Swallow *et al.* 1988, St-Amand *et al.* 2018). The motivation for studying artificially created snags usually relates to nesting (Brandeis *et al.* 2002, Kilgo & Vukovich 2014, Barry *et al.* 2018). Few studies examine this subject in the context of foraging needs (Aulén 1991, Farris & Zack 2005, Arnett *et al.* 2010, Aszalós *et al.* 2020).

In this study, the following questions were posed. Which tree species are preferred for foraging by woodpeckers in the studied oak forests? Does the diameter or height of trees affect how they are used? Which attributes of the studied trees influence the presence of woodpecker foraging signs? What determines, and to what extent, the number of foraging signs observed on the studied trees?

Materials and Methods

Study sites

This study was part of a detailed, conservation-oriented management project (LIFE 4 Oak Forests Project, LIFE16NAT/IT/000245), the purpose of which was to structurally enrich certain oak-dominated woodlands in Hungary through various management techniques. Within this framework, we designated ten 80×80 m (0.64 ha) square plots in 5 study sites,

in which artificial standing and downed deadwood and the opening of canopy gaps will be created in the near future. The present study was a baseline research carried out prior to the planned management. Therefore, all the trees surveyed would be selected for management activities, and, in addition, control trees that would not be managed, were also selected. In the forthcoming winter of 2021–2022, there will be a follow-up survey of both the managed and control trees. Therefore, all trees selected for this study were living specimens at the time of data collection. On 10 square plots in the 5 study sites, we measured a total of 1,471 individual trees. In these study plots, we surveyed all trees with diameters of more than 10 cm at breast height (DBH). *Table 1* summarizes the data of the trees measured (species, height, diameter).

Table 1. Numbers, mean diameter, and height of the surveyed trees by species (QC – *Quercus cerris*, RP – *Robinia pseudoacacia*, C – *Crataegus* sp., CB – *Carpinus betulus*, QR – *Quercus robur*, QP – *Quercus petraea*, AC – *Acer campestre*, FE – *Fraxinus excelsior*, QPU – *Quercus pubescens*, FO – *Fraxinus ornus*, QRU – *Quercus rubra*)

1. táblázat A vizsgált faegyedek száma, átlagos átmérője és magassága fafajok szerint bemutattva (QC – *Quercus cerris*, RP – *Robinia pseudoacacia*, C – *Crataegus* sp., CB – *Carpinus betulus*, QR – *Quercus robur*, QP – *Quercus petraea*, AC – *Acer campestre*, FE – *Fraxinus excelsior*, QPU – *Quercus pubescens*, FO – *Fraxinus ornus*, QRU – *Quercus rubra*)

tree species	QP	QR	QC	QPU	QRU	CB	FE	FO	AC	RP	C
number of individuals	616	71	750	7	1	11	1	1	11	1	1
mean DBH_cm	28.1	37.09	33.24	32.2	32.5	22.87	15.3	15.6	13.7	30.6	12.6
mean height_m	20.3	23.34	23.5	18.56	25.86	17.82	19.33	12.05	13.11	19	10.67



Figure 1. Location of the study sites

1. ábra Vizsgáló területek elhelyezkedése

All study areas were within hill ranges in north-east Hungary (Figure 1). The first study site is located in the Duna-Ipoly National Park, specifically in the Börzsöny Hills near the settlement of Nagyoroszi (65°08'20"N-29°62'40"E, 250 m a.s.l., 10–15° slope, 80–99 years old stands). The studied forest was dominated by sessile oak (*Quercus petraea*) – Turkey oak (*Quercus cerris*) and hornbeam (*Carpinus betulus*). The second and third sites were situated in the Cserhát Hills, which are part of the East-Cserhát Landscape Protection Area. The second site, near the settlement of Buják (68°84'36"N-28°55'10"E, 300 m a.s.l., 10° slope, 80–99 years old stands), is a Turkey oak-pedunculate oak (*Quercus robur*) forest with a high scrub layer. The other site, in the vicinity of Garáb (69°48'84"N-29°32'60"E, 500 m a.s.l., 20–25° slope), is a 60–79-year-old deciduous woodland with sessile oak, hornbeam, beech (*Fagus sylvatica*) and Turkey oak. The final two study sites were located in the Bükk Hills (Bükk National Park) near the settlements of Cserépfalu (76°32'78"N-29°29'00"E, 250-350 a.s.l., 5–10° slope, 80–99-year-old stands) and Bükkzsérc (75°67'58"N-29°23'50"E, 350–450 m a.s.l., 10–15° slope, 40–59 and 80–99-year-old stands). Both sites are predominantly covered by Turkey oak-sessile oak forests.

Woodpecker foraging activity surveys

In the course of previous point count surveys, we detected the presence of the Great (*Dendrocopos major*), Middle (*Leiopicus medius*), Lesser Spotted (*Dryobates minor*), Black (*Dryocopus martius*), Eurasian Green (*Picus viridis*) and Grey-headed Woodpeckers (*Picus canus*) within the study sites. In most cases, it was not possible to accurately distinguish between the foraging marks that the different species made, as most are not diagnostic (Gorman 2015). From the species present in the study areas, only the black woodpecker's foraging marks are generally identifiable to species, owing to its large bill size. Therefore, we decided not to attempt to identify signs and marks to species level, but rather the wood layers that the birds accessed. The percentage of visible foraging signs on the trunks and limbs of the surveyed trees were estimated using binoculars and naked eyes through the winter and early spring of 2019–2020. The survey differentiated four depth categories for presumed woodpecker foraging signs on trees: marks on the bark, bark scaling, excavation marks in the sapwood, excavation marks in the heartwood. 'Marks on the bark' means that birds had searched for prey by only superficial pecking. 'Bark scaling' means that birds had peeled off sections of bark and foraged beneath it. We also identified deeper excavation marks: ones that penetrated only into the sapwood and others that entered deeper into the heartwood. Heartwood was recognized by its distinctive (usually reddish) colour. We also differentiated between marks on trunks (with an estimated diameter greater than 15 cm) and on limbs (with an estimated maximum diameter of 15 cm).

Data analyses

We calculated the frequency and distribution of woodpecker foraging signs according to tree species and categories of diameter at breast height (10–20; 20.1–40 and above 40 cm) and tree height (0.5–15; 15.1–25, and above 25.1 m). Jacobs' preference index values (Jacobs

1974) were calculated using frequency data from a previous vegetation survey in the study sites. This index represents a -1 to $+1$ scale from avoidance to the examined variable's preference, respectively.

We used a mixed linear model with zero-inflated beta distribution and logit link. Since beta distribution is defined on interval $[0, 1]$, the zero-inflation part models the probability of occurrence of foraging signs. The conditional part models the area of signs when they occur. Our models included tree species, DBH, and height as fixed effects and research plots as a random factor. Main effects were tested by Type II Wald's chi-square test. Because of the limited data due to the limited availability of secondary tree species, only the pedunculate oak, sessile oak, and Turkey oak were included in the model. Analyses were done in the R statistical environment (version 4.0.2 R Development Core Team 2020) using the glmmTMB (version 1.0.2.1, Brooks *et al.* 2017), emmeans (version 1.5.4, Lenth 2021), multcomp (version 1.4-16, Hothorn *et al.* 2018) and effects (4.2-0, Fox 2003, Fox & Weisberg 2018) packages.

Results

Foraging preferences

From the 1,471 individual trees examined, 798 (54.24%) had some type of foraging marks upon them. In the study areas, woodpeckers foraged mainly upon Turkey oaks and sessile oaks (*Figure 2*). The order of frequency of the tree species was the following: Turkey oak (51%), sessile oak (42%), pedunculate oak (5%). Other species had less than 1% of frequency: black locust (*Robinia pseudoacacia*), hawthorn (*Crataegus* sp.), hornbeam, common ash (*Fraxinus excelsior*), manna ash (*Fraxinus ornus*), red oak (*Quercus rubra*), downy oak (*Quercus pubescens*) and field maple (*Acer campestre*). The most preferred tree species in terms of both trunk and limb use was the pedunculate oak. When just trunk usage was examined, the most preferred species was the red oak, and when only limbs were considered, mainly downy oak was used. However, it must be mentioned that both red and downy oaks were hardly present in the study areas, thus, these data are biased to 1–2 individual trees (*Figure 3*). The Turkey oak can also be mentioned for trunk use and sessile oak and hawthorn for limb use as tree species utilized at a moderate level. As reflected in the negative Jacobs' index values, woodpeckers avoided common ash, manna ash, hornbeam, and field maple.

The percentage of coverage of foraging signs was the highest on trees falling in the middle DBH category. At the same time, on trees with a DBH under 20 cm, woodpecker foraging marks were scarcely present (*Figure 4*), as is also reflected in the preference index (*Figure 5*).

In the case of tree height (*Figure 6*), the 15.01–25 m category was the most frequent, followed by the category of >25 m. The least utilized trees belonged to the lowest height category (below 15 m). Regarding both trunks and limbs, woodpeckers preferred the highest trees and avoided the medium-height category (*Figure 7*).

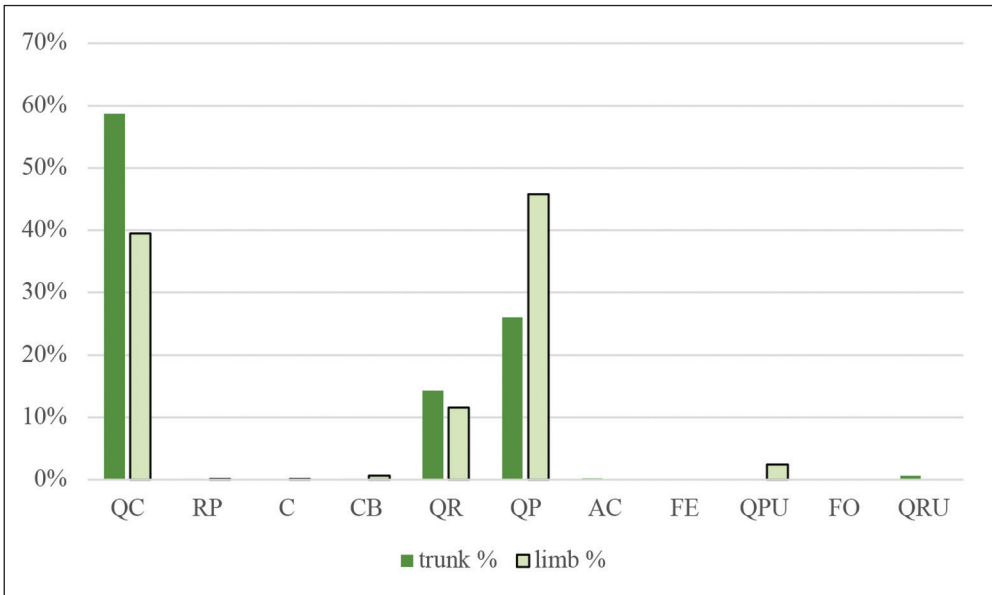


Figure 2. Percentage distribution of woodpecker foraging signs on the trunks and limbs on each tree species. (For abbreviations of tree species see the legend of Table 1)

2. ábra A felmért harkály táplálkozási nyomok százalékos megoszlása a törzseken és az ágakon fajok szerint. (A fajok rövidítését lásd az 1. táblázat jelmagyarázatánál)

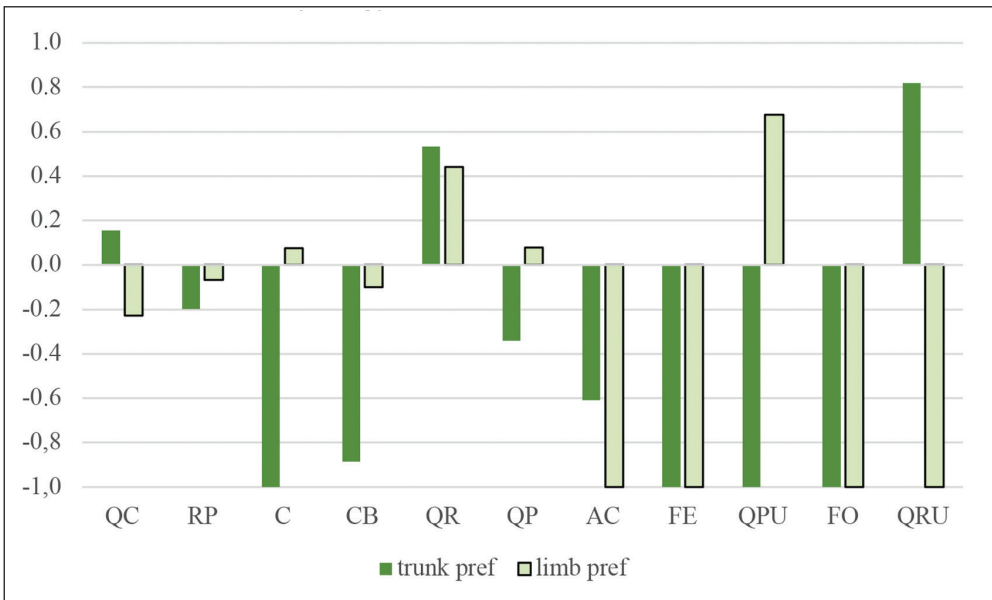


Figure 3. Jacobs' preference index of woodpecker foraging signs on trunks and limbs on each tree species. (For abbreviations of tree species see the legend of Table 1)

3. ábra Jacobs preferencia értékek a törzseken és az ágakon fajok szerint. (A fajok rövidítését lásd az 1. táblázat jelmagyarázatánál)

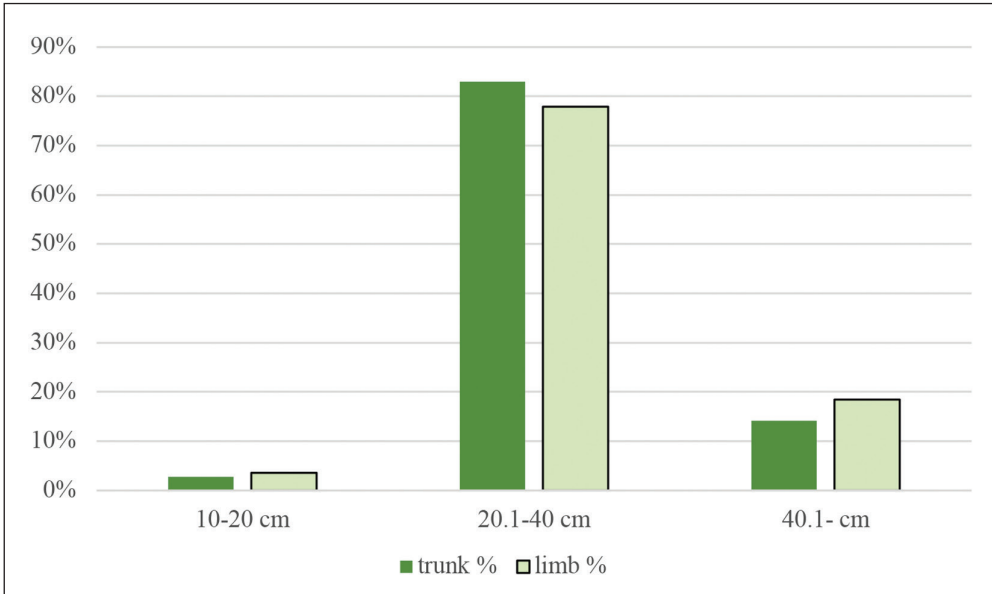


Figure 4. Percentage distribution of woodpecker foraging signs on trunks and limbs according to breast height categories

4. ábra A felmért harkály táplálkozási nyomok százalékos megoszlása a törzseken és az ágakon a megadott átmérőkategóriák szerint

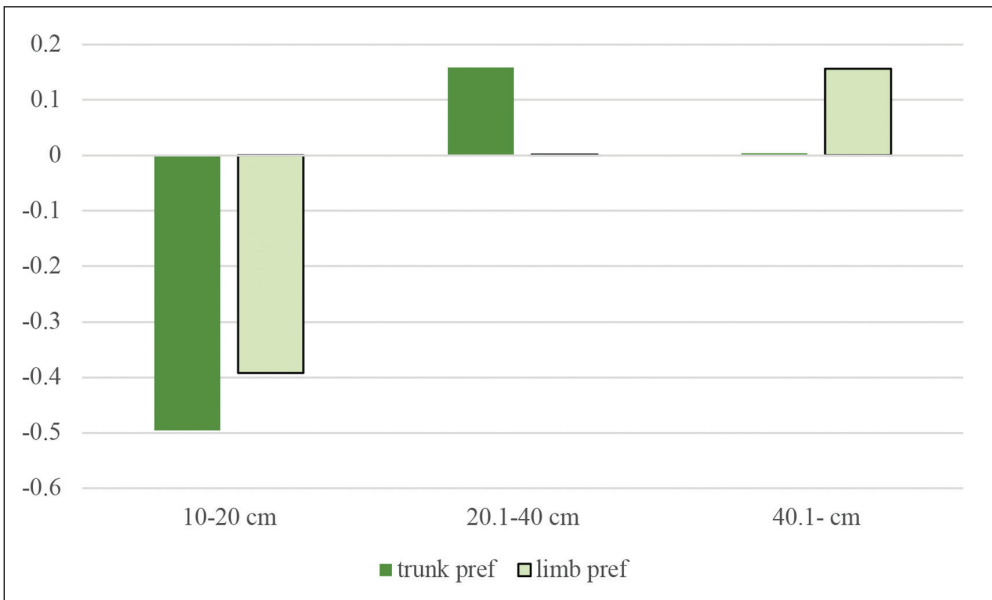


Figure 5. Jacobs' preference index of woodpecker foraging signs on trunks and limbs according to diameter at breast height categories

5. ábra Jacobs preferencia értékek a törzseken és az ágakon a megadott átmérőkategóriák szerint

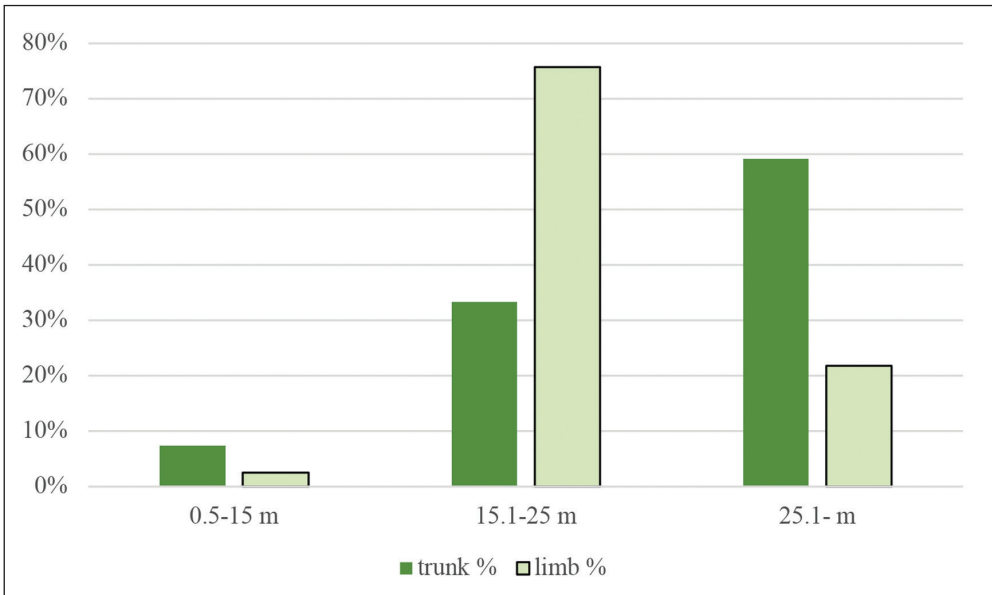


Figure 6. Percentage distribution of woodpecker foraging signs on trunks and limbs according to height categories

6. ábra A felmért harkály táplálkozási nyomok százalékos megoszlása a törzseken és az ágakon a megadott magassági kategóriák szerint

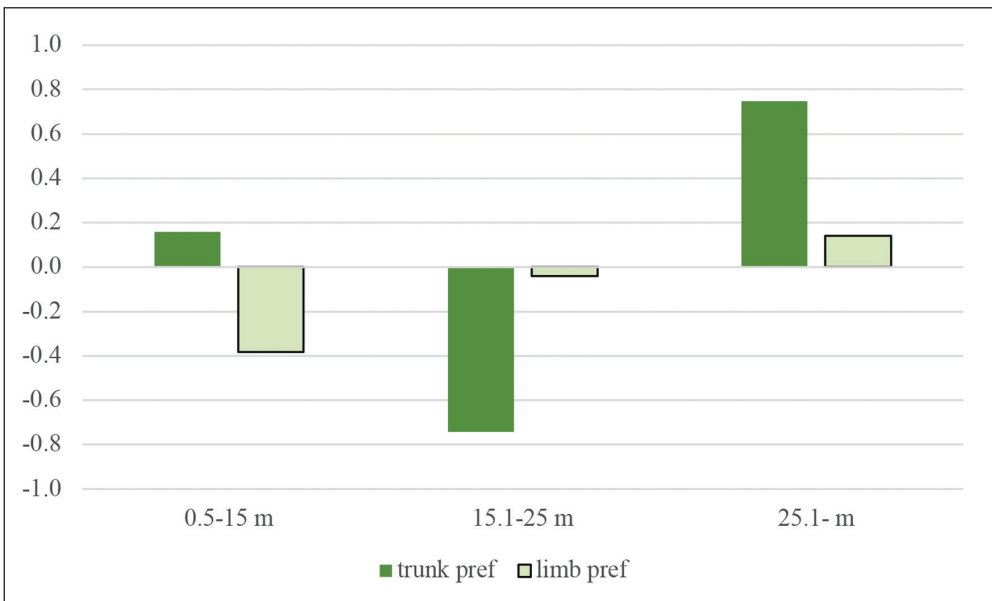


Figure 7. Jacobs' preference index of woodpecker foraging signs on trunks and limbs according to defined height categories

7. ábra Jacobs preferencia értékek a törzseken és az ágakon a megadott magassági kategóriákban

Foraging sign distributions (glmmTMB)

Regarding trunks, tree species significantly affected the occurrence of foraging signs. At the same time, interaction effects of the variables DBH and height also proved to be significant. On limbs, the effects of both tree species, DBH, and height were significant ($p < 0.01$). The correlation here was stronger for limbs than for trunks (*Table 2*).

Table 2. Effects of tree species, diameter and height on the presence of foraging signs on trees. Numbers in bold represent significant differences

2. táblázat A faj, az átmérő és a magasság hatása a táplálkozási nyomok előfordulására. A szignifikáns értékek félkövérrel szedettek

ANOVA Type=II, component=zi		Chisq	Df	Pr(>Chisq)
trunk	tree species	12.08	2	0.0024
	DBH	1.89	1	0.1696
	Height	3.50	1	0.0615
	species:DBH	0.85	2	0.6536
	species:Height	1.57	2	0.4565
	DBH:Height	11.13	1	0.0009
limbs	tree species	28.844	3	<0.0001
	DBH	19.92	1	<0.0001
	Height	9.92	1	0.0016
	species:DBH	5.47	2	0.0648
	species:Height	5.38	2	0.0677

Table 3. Effects of tree species, diameter, and height of trees on the amount of foraging signs present. Numbers in bold represent significant differences

3. táblázat A faj, az átmérő és a magasság hatása az előforduló táplálkozási nyomok mennyiségére. A szignifikáns értékek félkövérrel szedettek

ANOVA Type=II, component=cond		Chisq	Df	Pr(>Chisq)
trunk	tree species	0.57	2	0.7505
	DBH	0.37	1	0.5439
	Height	0.001	1	0.9702
	species:DBH	0.64	2	0.7251
	species:Height	2.96	2	0.2280
	DBH:Height	0.48	1	0.4883
limbs	tree species	28.50	2	<0.0001
	DBH_cm	0.001	1	0.9767
	Height_m	1.25	1	0.2643
	species:DBH	5.95	2	0.0511
	species:Height	2.76	2	0.2512

Table 4. Estimated probability of the presence of foraging signs and their relative amount when present on the different tree species. (For abbreviations of tree species see the legend of *Table 1*)

4. táblázat A táplálkozási nyomok előfordulásának és relatív kiterjedésének becsült valószínűségi értéke, amennyiben előfordul a vizsgált nyom, különböző fafajokra vizsgálva. (A fafajok rövidítését lásd az 1. táblázat jelmagyarázatánál)

Species	Trunk (presence of sign, %)	Limb (presence of sign, %)	Limb (relative area of sign, when present, %)
QC	9.31 (2.18–32.1) ^b	37.3 (31.5–43.5) ^a	6.94 (6.18–7.78) ^a
QR	4.23 (0.85–18.6) ^a	55.8 (40.8–69.8) ^b	12.11 (9.28–15.65) ^b
QP	16.92 (4.25–48.3) ^c	55.1 (48.4–61.6) ^b	7.90 (7.12–8.76) ^a

When a foraging sign occurred on a trunk, its area was not related to any of the studied predictors (tree species, DBH, height), while on limbs, only the tree species used had a significant effect on the area of signs (*Table 3*). On trunks, the presence of foraging signs was most frequent on sessile oak, while on limbs, both sessile oak and pedunculate oak shared almost the same probability of presence. Regarding the relative area of signs, their extent, when present, was the highest on the limbs of pedunculate oak (*Table 4*).

From the four different height categories, the following conclusions were drawn. The lower the tree, the greater the effect of diameter on the occurrence of signs. In greater height categories, the impact of diameter was moderate (*Figure 8*). The results also showed that signs were more frequent on trunks with greater diameters and heights (*Figure 9–10*).

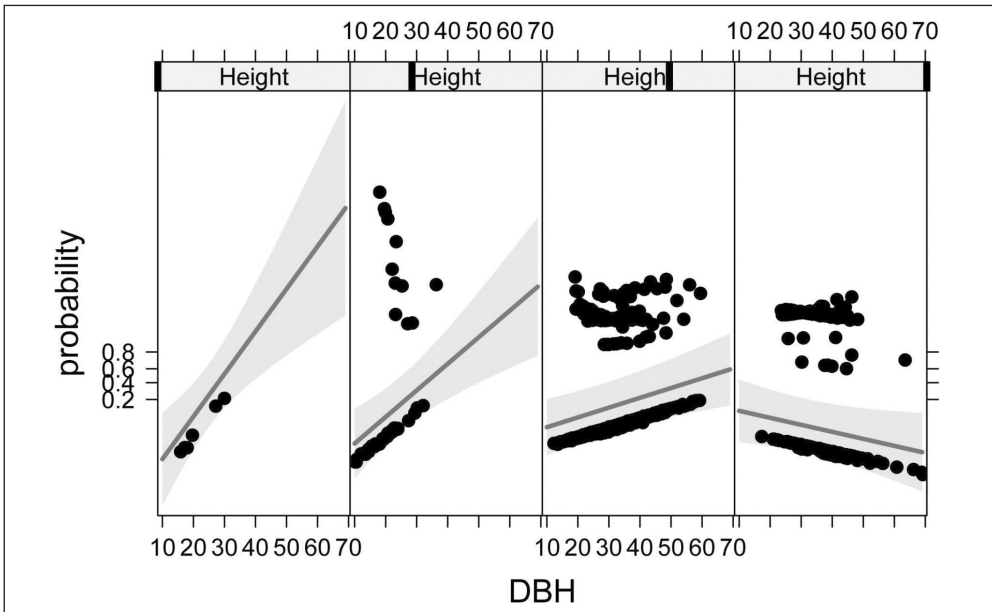


Figure 8. Interaction of the variables DBH and height with regards to the presence of foraging data on trunks

8. ábra A mellmagassági átmérő és a magasság interakciója a törzseken előforduló táplálkozási nyomok tekintetében

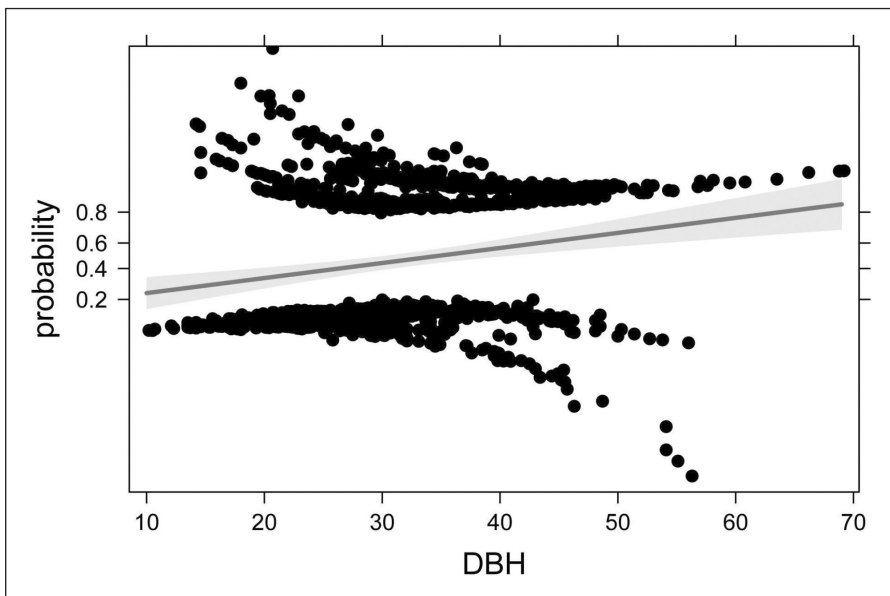


Figure 9. Linear correspondence (logit distribution) of DBH and the probability of presence of foraging signs on limbs

9. ábra A mellmagassági átmérő és a táplálkozási nyomok előfordulásának lineáris korrespondencia vizsgálata a vizsgált ágak vonatkozásában

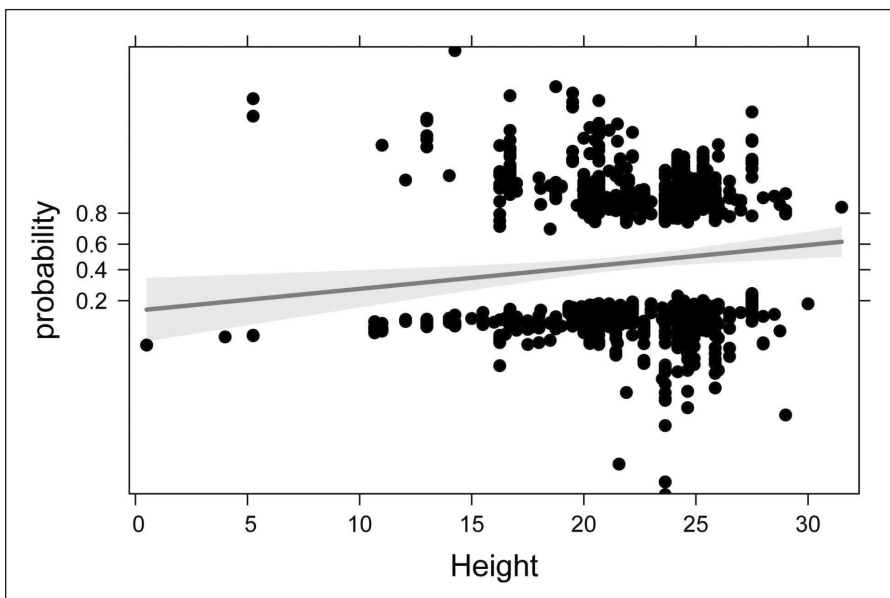


Figure 10. Linear correspondence (logit distribution) of height and the probability of presence of foraging signs on limbs

10. ábra A magasság és a táplálkozási nyomok előfordulásának lineáris korrespondencia vizsgálata a vizsgált ágak vonatkozásában

Discussion

In the present study, we assessed managed, commercial forests, which are generally considered to be of little importance for nature conservation and biodiversity. Neither the structure nor the species composition is as rich in such forests as it is in natural ones (Tomiałojć *et al.* 1984, Kraigher *et al.* 2003, Bobiec *et al.* 2005, Christensen *et al.* 2005). Data from Central European managed deciduous forests are scarce (Mazgajski 1998, Kosinski 2006, Kosinski & Kempa 2007), compared to the number of similar research projects that have been carried out in so-called primeval forests such as Białowieża in Poland (Wesołowski *et al.* 2010, Walankiewicz *et al.* 2011, Czeszczewik *et al.* 2015). Possibilities for comparison were, and are, therefore limited. Nevertheless, it is worth comparing our results with those that are available from unmanaged forests.

Similar to the observations by Kosinski (2006) and Pasinelli (2007), our results confirm that in mixed forests in Europe, woodpeckers mainly prefer oak species. This is due to the less diverse nature of the studied managed forests, primarily composed of oak species with a lower proportion of secondary tree species. However, woodpeckers, especially Great and Middle Spotted Woodpeckers, forage mainly on oak trees that have a fissured bark rich in arthropod fauna, providing an important food source even in forests where oaks are less dominant (Török 1990, Pasinelli & Hegelbach 1997, Kruszyk 2003, Kosinski 2006). Our results showed a relatively high preference for red oak. Red oak is an adventive species in Hungary, and thus, few insect ‘pest’ species (bark and wood-boring insects) use it (Rédei *et al.* 2011, Keserű *et al.* 2017), thus this phenomenon is noteworthy. In this study, woodpeckers utilized hornbeam only moderately. Studies in Białowieża showed that woodpeckers prefer to nest and forage on hornbeam, while other researchers stated they avoid this species (Hardersen 2004). The reason for this deviation could be that in primeval forests, the hornbeam trees used are older, more decayed, sizable, and hence often have substantial amounts of deadwood (Kosinski & Kempa 2007).

According to Roberge *et al.* (2008), the basal area/ha is one of the determining factors for foraging Middle Spotted and Great Spotted Woodpeckers, since they prefer older and wider trees.

In the framework of this baseline survey, we studied foraging on living trees, a subject which is generally uncommon in woodpecker-related research. Nonetheless, some previous studies have indicated that Great Spotted Woodpeckers are often associated with living trees (Török 1990, Farris & Zack 2005, Pasinelli 2007, Ónodi & Csörgő 2014, Ónodi & Winkler 2016, Kosiński *et al.* 2017).

Many papers discuss the relationship between snags and woodpeckers and the importance of deadwood to them (Angelstam *et al.* 2003, Farris & Zack 2005, Löhmus *et al.* 2010, Kosinski *et al.* 2017). Deadwood is usually scarce in managed forests, so our results might highlight some of the traits on trees that woodpeckers prefer if no deadwood material is available. We found stronger correlations for the canopy than for trunks, which may have been related to dead limbs being available in higher amounts in the canopy through the decaying processes initiated by wood-rotting fungi via mechanical damage e.g., windbreak (Gibbons & Lindenmayer 2002). Dead branches are crucial for, among other species, the Lesser Spotted Woodpecker (Roberge *et al.* 2008, Charman *et al.* 2010).

Nowadays, the vast majority of forests worldwide are managed in some way. To have diverse and stable ecosystems, it is often necessary to improve their natural characteristics through nature conservation management. To achieve this aim, it is important to diversify forests both structurally and compositionally. Conservationists can use various methods to create deadwood, new microhabitats and open canopy gaps, which can all help increase the diversity and abundance of a wide range of taxa: plants, fungi, saproxylic beetles, birds and mammals. Currently, such management activities are mostly employed in North America (Swallow *et al.* 1988, Hallett *et al.* 2001, Arnett *et al.* 2010, Kilgo & Vukovich 2014, Weiss *et al.* 2017, Sandström *et al.* 2019), although they are on the increase in Europe (Aulén 1991, Aszalós *et al.* 2020).

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References

- Angelstam, P. K., Bütler, R., Lazdinis, M., Mikusiński, G. & Roberge, J. M. 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation. – Dead wood as an example. – *Annales Zoologici Fennici* 40(6): 473–482.
- Arnett, E. B., Kroll, A. J. & Duke, S. D. 2010. Avian foraging and nesting use of created snags in intensively-managed forests of western Oregon, USA. – *Forest Ecology and Management* 260(10): 1773–1779. DOI: 10.1016/j.foreco.2010.08.021
- Aszalós, R., Szigeti, V., Harnos, K., Csernák, S., Frank, T. & Ónodi, G. 2020. Foraging activity of woodpeckers on various forms of artificially created deadwood. – *Acta Ornithologica* 55(1): 63–76. DOI: 10.3161/00016454AO2020.55.1.007
- Aulén, G. 1991. Increasing insect abundance by killing deciduous trees: A method of improving the food situation for endangered woodpeckers. – *Holarctic Ecology* 14(1): 68–80. DOI: 10.1111/j.1600-0587.1991.tb00635.x
- Barry, A. M., Hagar, J. C. & Rivers, J. W. 2018. Use of created snags by cavity-nesting birds across 25 years. – *Journal of Wildlife Management* 82(7): 1376–1384. DOI: 10.1002/jwmg.21489
- Bobiec, A., Gutowski, J. M., Laudenslayer, W. F., Pawlaczyk, P. & Zub, K. 2005. The afterlife of a tree. – WWF Poland, Warszawa-Hajnówka
- Bocca, M., Carisio, L. & Rolando, A. 2007. Habitat use, home ranges and census techniques in the Black Woodpecker *Dryocopus martius* in the Alps. – *Ardea* 95: 17–29. DOI: 10.5253/078.095.0103
- Brandeis, T. J., Newton, M., Filip, G. M. & Cole, E. C. 2002. Cavity-nester habitat development in artificially made Douglas-Fir Snags. – *Journal of Wildlife Management* 66(3): 625–633. DOI: 10.2307/3803129
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. & Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – *The R Journal* 9(2): 378–400. DOI: 10.3929/ethz-b-000240890

- Campion, D., Pardo, I., Elósegui, M. & Villanua, D. 2020. Gps Telemetry and Home Range of the White-Backed Woodpecker *Dendrocopos leucotos*: Results of the First Experience. – *Acta Ornithologica* 55(1): 77–87. DOI: 10.3161/00016454AO2020.55.1.008
- Charman, E. C., Smith, K. W., Guar, D. J., Dodd, S. & Grice, P. V. 2010. Characteristics of woods used recently and historically by Lesser Spotted Woodpeckers *Dendrocopos minor* in England. – *Ibis* 152(3): 543–555. DOI: 10.1111/j.1474-919X.2010.01020.x
- Christensen, M., Hanh, K., Mountford, E. P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S. & Vrska, T. 2005. Dead wood in European beech (*Fagus sylvatica*) forest reserves. – *Forest Ecology and Management* 210: 267–282. DOI: 10.1016/j.foreco.2005.02.032
- Czeszczewik, D. 2009. Foraging behaviour of White-backed Woodpeckers *Dendrocopos leucotos* in a primeval forest (Białowieża National Park, NE Poland): Dependence on habitat resources and season. – *Acta Ornithologica* 44(2): 109–118. DOI: 10.3161/000164509X482687
- Czeszczewik, D., Zub, K., Stanski, T., Sahel, M., Kapusta, A. & Walankiewicz, W. 2015. Effects of forest management on bird assemblages in the Białowieża Forest, Poland. – *iForest* 8: 377–385. DOI: 10.3832/ifer1212-007
- Drever, M. C., Aitken, K. E. H., Norris, A. R. & Martin, K. 2008. Woodpeckers as reliable indicators of bird richness, forest health and harvest. – *Biological Conservation* 141: 624–634. DOI: 10.1016/j.biocon.2007.12.004
- Farris, K. L. & Zack, S. 2005. Woodpecker-snag interactions: an overview of current knowledge in ponderosa pine systems. – USDA Forest Service General Technical Report 198: 183–195.
- Fox, J. & Weisberg, S. 2018. Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. – *Journal of Statistical Software* 87(9): 1–27. <https://www.jstatsoft.org/article/view/v087i09>.
- Fox, J. 2003. Effect Displays in R for Generalised Linear Models. – *Journal of Statistical Software* 8(15): 1–27. <https://www.jstatsoft.org/article/view/v008i15>.
- Garmendia, A., Cárcamo, S. & Schwendtner, O. 2006. Forest management considerations for conservation of Black Woodpecker *Dryocopus martius* and White-backed Woodpecker *Dendrocopos leucotos* populations in Quinto Real (Spanish Western Pyrenees). – *Biodiversity and Conservation* 15(4): 1399–1415. DOI: 10.1007/s10531-005-5410-0
- Gibbons, P. & Lindenmayer, D. 2002. Tree hollows and wildlife conservation in Australia. – CSIRO Publishing
- Gorman, G. 2004. Woodpeckers of Europe. A study of the European Picidae. – Bruce Coleman
- Gorman, G. 2011. The Black Woodpecker. A monograph on *Dryocopus martius*. – Lynx Edicions
- Gorman, G. 2015. Foraging signs and cavities of some European woodpeckers (Picidae): Identifying the clues that lead to establishing the presence of species. – *Denisia* 36: 87–97.
- Grubb, T. C. Jr. 1975. Weather dependent foraging behaviour of some birds wintering in a deciduous woodland. – *Condor* 77: 175–182.
- Hallett, J. G., Lopez, T., O'Connell, M. A. & Borysewicz, M. A. 2001. Decay dynamics and avian use of artificially created snags. – *Northwest Science* 75(4): 378–386.
- Hardersen, S. 2004. Habitat usage of Woodpeckers and Nuthatch. – *Ricerche Naturalistiche a Bosco Della Fontana – Quaderni Conservazione Habitat* 3: 49–59. (in Italian with English Summary)
- Hothorn, T., Bretz, F. & Westfall, P. 2008. Simultaneous inference in general parametric models. – *Biometrical Journal* 50(3): 346–363. DOI: 10.1002/bimj.200810425
- Jacobs, J. 1974. Quantitative measurement of food selection. – *Oecologia* 14: 413–417. DOI: 10.1007/BF00384581
- Jusino, M. A., Lindner, D. L., Banik, M. T. & Walters, J. R. 2015. Heart rot hotel: fungal communities in Red-cokaded Woodpecker excavations. – *Fungal Ecology* 14: 33–43. DOI: 10.1016/j.funeco.2014.11.002
- Keserű, Zs., Csiha, I., Kovács, Cs., Rásó, J. & Rédei, K. 2017. Vörös tölgyesek természetes felújítása és erdőnevelése: Esettanulmányok [Natural regeneration of red oak (*Quercus rubra*) stands: case studies]. – *Erdészettudományi Közlemények* 7(2): 115–125. DOI: 10.17164/EK.2017.008 (in Hungarian)
- Kilgo, J. C. & Vukovich, M. A. 2014. Can snag creation benefit a primary cavity nester: Response to an experimental pulse in snag abundance. – *Biological Conservation* 171: 21–28. DOI: 10.1016/j.biocon.2014.01.003
- Kosiński, Z. 2006. Factors affecting the occurrence of Middle Spotted and Great Spotted Woodpeckers in deciduous forests – a case study from Poland. – *Annales Zoologici Fennici* 43(2): 198–210.
- Kosiński, Z. & Kempa, M. 2007. Density, distribution and nest-sites of woodpeckers *Picidae*, in a managed forest of Western Poland. – *Polish Journal of Ecology* 55(3): 519–533.

- Kosiński, Z., Pluta, M., Ulanowska, A., Walczak, L., Winiecki, A. & Zarębski, M. 2017. Do increases in the availability of standing dead trees affect the abundance, nest-site use, and niche partitioning of Great Spotted and Middle Spotted Woodpeckers in riverine forests? – *Biodiversity and Conservation* 27(1): 123–145. DOI: 10.1007/s10531-017-1425-6
- Kraigher, H., Jurc, D., Kalan, P., Kutnar, L., Levanic, T., Rupel, M. & Smolej, I. 2002. Beech coarse woody debris characteristics in two virgin forest reserves in southern Slovenia. – *Zbornik Gozdarstva in Lesarstva* 69: 91–134.
- Kruszyk, R. 2003. Population density and foraging habits of the Middle Spotted Woodpecker *Dendrocopos medius* and Great Spotted Woodpecker *D. major* in the Odra valley woods near Wrocław. – *Notatki Ornitologiczne* 44: 75–88.
- Lenth, R. V. 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.4. – <https://CRAN.R-project.org/package=emmeans>
- Lõhmus, A., Kinks, R. & Soon, M. 2010. The importance of dead-wood supply for woodpeckers in Estonia. – *Baltic Forestry* 16(1): 76–86.
- Mazgajski, T. D. 1998. Nest-site characteristic of Great Spotted Woodpecker *Dendrocopos major* in central Poland. – *Polish Journal of Ecology* 46(1): 33–41.
- Melletti, M. & Penteriani, V. 2003. Nesting and feeding tree selection in the endangered White-backed Woodpecker, *Dendrocopos leucotos lilfordi*. – *Wilson Bulletin* 115(3): 299–306. DOI: 10.1676/03-022
- Mikusinski, G. 2006. Woodpeckers: distribution, conservation, and research in a global perspective. – *Annales Zoologici Fennici* 43: 86–95.
- Mikusinski, G., Gromadzki, M. & Chylarecki, P. 2001. Woodpeckers as indicators of forest bird diversity. – *Conservation Biology* 15(1): 208–217. DOI: 10.1046/j.1523-1739.2001.99236.x
- Ónodi, G. & Csörgő, T. 2014. Habitat preference of Great-spotted Woodpecker (*Dendrocopos major linnaeus*, 1758) and Lesser-spotted Woodpecker (*Dendrocopos minor Linnaeus*, 1758) in the presence of invasive plant species – Preliminary study. – *Ornis Hungarica* 22(2): 50–64. DOI: 10.2478/orhu-2014-0018
- Ónodi, G. & Winkler, D. 2016. Nest site characteristics of the Great-spotted Woodpecker in a bottomland riparian forest in the presence of invasive tree species. – *Ornis Hungarica* 24(1): 81–95. DOI: 10.1515/orhu-2016-0005
- Pasinelli, G. & Hegelbach, J. 1997. Characteristics of trees preferred by foraging Middle Spotted Woodpecker *Dendrocopos medius* in Northern Switzerland. – *Ardea* 85: 203–209.
- Pasinelli, G. 2007. Nest site selection in Middle and Great Spotted Woodpeckers *Dendrocopos medius* & *Dendrocopos major*: implications for forest management and conservation. – *Biodiversity Conservation* 16: 1283–1298. DOI: 10.1007/s10531-007-9162-x
- Puverel, C., Abourachid, A., Böhrner, C., Leban, J. M., Svoboda, M. & Paillet, Y. 2019. This is my spot: What are the characteristics of the trees excavated by the Black Woodpecker? A case study in two managed French forests. – *Forest Ecology and Management* 453: 117621. DOI: 10.1016/j.foreco.2019.117621
- R Core Team 2018. R: A Language and environment for statistical computing. – <https://www.r-project.org/>
- Rédei, K., Csiha, I. & Keserű, Zs. 2011. Vöröstölgyesek nevelése [Silvicultural treatment of red oak stands]. – *Erdészeti Lapok* 146(11): 333–334. (in Hungarian)
- Roberge, J. M., Angelstam, P. & Villard, M. A. 2008. Specialised woodpeckers and naturalness in hemiboreal forests – Deriving quantitative targets for conservation planning. – *Biological Conservation* 141(4): 997–1012. DOI: 10.1016/j.biocon.2008.01.010
- Sandström, J., Bernes, C., Junninen, K., Lõhmus, A., Macdonald, E., Müller, J. & Jonsson, B. G. 2019. Impacts of dead wood manipulation on the biodiversity of temperate and boreal forests. A systematic review. – *Journal of Applied Ecology* 56(7): 1770–1781. DOI: 10.1111/1365-2664.13395
- St-Amand, J., Tremblay, J. A. & Martin, K. 2018. Foraging ecology of the Williamson's Sapsucker: Implications for forest management. – *Condor* 120(3): 680–702. DOI: 10.1650/CONDOR-17-238.1
- Swallow, S. K., Howard, R. A. & Gutierrez, R. J. 1988. Snag preferences of woodpeckers in a northeastern hardwood foraging. – *Wilson Bulletin* 100(2): 236–246.
- Thompson, I. D., Baker, J. A. & Ter-Mikaelian, M. 2003. A review of the long-term effects of post-harvest silviculture on vertebrate wildlife, and predictive models, with an emphasis on boreal forests in Ontario, Canada. – *Forest Ecology and Management* 177: 441–469. DOI: 10.1016/S0378-1127(02)00453-X
- Tomiałojć, L., Wesolowski, T. & Walankiewicz, W. 1984. Breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland). – *Acta Ornithologica* 20(8): 241–308.
- Török, J. 1990. Resource partitioning among three woodpecker species *Dendrocopos* spp. during the breeding season. – *Holarctic Ecology* 13: 257–264. DOI: 10.1111/j.1600-0587.1990.tb00617.x

- Virkkala, R. 2006. Why study woodpeckers? The significance of woodpeckers in forest ecosystems. – *Annales Zoologici Fennici* 43(2): 82–85.
- Walankiewicz, W., Czeszczewik, D., Tumieli, T. & Stański, T. 2011. Woodpecker abundance in the Białowieża Forest – a comparison between deciduous, strictly protected and managed stands. – *Ornis Polonica* 52: 161–168.
- Weiss, S. A., Corace, R. G., Toman, E. L., Herms, D. A. & Goebel, P. C. 2018. Wildlife implications across snag treatment types in jack pine stands of Upper Michigan. – *Forest Ecology and Management* 409: 407–416. DOI: 10.1016/j.foreco.2017.10.013
- Wesołowski, T. 2007. Lessons from long-term hole-nester studies in a primeval temperate forest. – *Journal of Ornithology* 148: 395–405. DOI: 10.1007/s10336-007-0198-1
- Wesołowski, T., Mitrus, C., Czeszczewik, D. & Rowiński, P. 2010. Breeding bird dynamics in a primeval temperate forest over thirty-five years: Variation and stability in the changing world. – *Acta Ornithologica* 45(2): 209–232. DOI: 10.3161/000164510x551354
- Wesołowski, T. & Tomialojc, L. 1986. The breeding ecology of woodpeckers in a temperate primeval forest – preliminary data. – *Acta Ornithologica* 22(1): 1–21.

