

Space Use of the White-Backed Woodpecker in a Heterogeneous Landscape: Implications for Forest Management

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Table of contents

Summary	1
General introduction	4
Chapter 1	17
<i>Seasonal variation in home range size of white-backed woodpeckers</i>	
Chapter 2	38
<i>Home range size of the white-backed woodpecker in relation to resource distribution, habitat availability, and intraspecific competition</i>	
Chapter 3	67
<i>Multi-level habitat selection of a forest specialist in a spatially heterogeneous landscape</i>	
Chapter 4	104
<i>Landscape context plays an important role for the occurrence of the white-backed woodpecker</i>	
General discussion.....	132
Acknowledgements	143
Curriculum vitae	145

Summary

Deforestation and forest management have resulted in massive habitat loss and habitat degradation for forest-dependent species, particularly for those associated with late successional stages. Whether integrative conservation measures, e.g., retaining deadwood and habitat trees in managed forests, are sufficient for the conservation of such species is unclear. In heterogeneous forest landscapes, habitat specialists with large area requirements may use a variety of forest stands to compensate for the lack of high-quality habitat or to meet different biological requirements. Investigating the space use of old-growth forest species in landscapes comprising stands of different management intensity may thus help to provide key insights into the potential of managed forests as habitat for such species and to better incorporate their requirements into forest management planning.

In this thesis, I examined the space use of the white-backed woodpecker *Dendrocopos leucotos*, a habitat specialist associated with old deciduous and mixed forests with high amounts of deadwood and a species of high conservation concern in Europe. I used data of adult white-backed woodpeckers radio-tracked in a region with high heterogeneity in landscape composition and forest management intensity combined with data on forest structure characteristics to examine variation in home range size and habitat selection in different seasons and at various spatial scales. The aims of this thesis were to close knowledge gaps in this species' ecology and to find out how the occurrence of an old-growth forest specialist can be reconciled with forest management.

In Chapter 1, I computed seasonal and yearly home range sizes based on three home range estimators and examined variation in home range size in relation to season, year, sex, and body weight. Home range size varied depending on the used home range estimator and between seasons, with minimum convex polygons and autocorrelated kernel density estimation producing 1.6 – 1.8 and 2 – 3.3 times larger seasonal home ranges than traditional kernel density estimation, and summer, fall and winter home ranges being 1.6 to 3.3 times larger than those during the breeding season in spring. These results highlight the usefulness of using multiple methods for home range estimation and the importance of considering the full annual cycle for assessing home range sizes.

In Chapter 2, I evaluated three hypotheses proposed to explain variation in breeding and post-breeding home range sizes: the resource distribution hypothesis, the restricted habitat availability hypothesis, and the intraspecific competition hypothesis. I found support for the resource distribution and intraspecific competition hypotheses in the breeding season, whereas none of the hypotheses

explained post-breeding home range size. In the breeding season, home range size decreased with increasing proportion of resource-rich habitat, particularly when forest cover was low. Moreover, breeding home range size decreased with increasing population density when the proportion of resource-rich habitat was high. These results suggest that the mechanisms determining breeding home range size varied with habitat quality. In regions with low forest cover and presumably low habitat quality, home range size appeared to be mainly determined by the distribution of resources. By contrast, home range size in regions with high habitat quality seemed to be restricted by intraspecific competition. I concluded that deadwood and old trees should ideally be clumped within stands with little or no forest management, and that these resource-rich forests should constitute a high proportion of areas at least the size of a breeding home range to improve the habitat quality for the white-backed woodpecker.

In Chapter 3, I analyzed seasonal habitat selection at three hierarchical levels. White-backed woodpeckers selected old deciduous and mixed stands for establishing seasonal home ranges within the annual home range in both the pre-breeding and breeding seasons, and deadwood and large-diameter trees at the level of foraging tree selection throughout the year and in all habitat types. By contrast, the proportions of all measured habitat types within post-breeding, summer/fall and winter home ranges corresponded to their availability in an area representing the annual home range, and within the seasonal home range, the habitat types were used according to their availability during all seasons. These findings suggest that coniferous and young deciduous forests can generally serve as non-breeding habitat for white-backed woodpeckers as long as suitable foraging trees and close-by (largely) unmanaged old deciduous or mixed stands are available as breeding habitat.

In Chapter 4, I investigated the occurrence of the white-backed woodpecker in 60 study sites in relation to local habitat (forest structure characteristics within the sites, i.e., at the spatial scale of the breeding home range) and landscape context (habitat amount, habitat fragmentation, and matrix quality at spatial scales ranging from 1 to 25 times the annual home range size). Habitat amount, habitat fragmentation and matrix quality at the landscape scale explained 2.5 times more of the variance in occurrence probability than local habitat (however, the amount of deadwood was high also in absence sites), showing that conservation measures for the white-backed woodpecker might be ineffective in areas with low forest cover at the landscape scale, even if enough high-quality habitat at the local scale is available. I concluded that conservation measures should focus on the conservation of and habitat improvements in areas with enough forest to sustain multiple breeding pairs, and that these areas should ideally be connected via dispersed patches of old deciduous forest.

In summary, the results of the four chapters show that addressing multiple seasons, spatial scales, and levels of habitat selection might be necessary to gain a comprehensive understanding of a species' space use. In accordance with previous studies on the white-backed woodpecker's habitat requirements, the results of the thesis generally confirm the high importance of old deciduous or mixed forest with abundant deadwood as breeding habitat for this habitat specialist, underpinning its dependence on old forest stands with low management intensity and supporting the idea of land-sparing as useful conservation approach for a deadwood-dependent species. Complementing this existing knowledge, I found that white-backed woodpeckers appeared to be more flexible in their space use and less bound to old deciduous forests in the non-breeding season; as they selected deadwood and large-diameter trees in all forest types throughout the year, integrative measures such as the retention of deadwood and habitat trees in more intensively managed stands (including coniferous and young deciduous or mixed stands) may thus be a useful supplement in areas close to old (almost) unmanaged stands. Lastly, the high importance of the landscape context for the occurrence of the white-backed woodpecker showed that conservation measures might only be effective if the surrounding landscape is taken into account.

General introduction

Forests support the majority of terrestrial biodiversity (FAO, 2022), and forest loss and degradation are among the main drivers of global biodiversity decline (Betts et al., 2017; Watson et al., 2018). In Europe, where forests are the natural vegetation across most of the continent, the impact of deforestation and forest degradation has been particularly strong. Today, only 35% of Europe's total land area is covered by forest due to human land use (Forest Europe, 2020), and thereof only 0.7% can still be considered primary forest (Sabatini et al., 2018). The remaining forests have been altered by forest management of varying intensities and are often characterized by a homogeneous tree species composition, canopy structure and age structure, as well as by low amounts of large old trees and deadwood (Gibb et al., 2005; Kuuluvainen et al., 1996; Thorn et al., 2020).

While many species are able to cope with or even benefit from forest management (Brunet et al., 1996; Nordén et al., 2013), some species, typically those associated with late-successional stages, require habitat characteristics that are incompatible with timber production (Bässler and Müller, 2010; Moning and Müller, 2009; Sillett et al., 2000). Accordingly, old-growth forest specialists are most affected by habitat loss due to intensive forest management (Betts et al., 2022; Fraixedas et al., 2015), and the occurrence of many of these species across various taxa, including insects, fungi, lichens, mollusks, and birds, is restricted to old forests with low management intensity or unmanaged stands (Juutilainen et al., 2014; Martikainen et al., 2000; Moning and Müller, 2009; Penttilä et al., 2004). Today, many forest species which were once widespread across Europe are threatened or regionally extinct (Grove, 2002; Tomiałojć, 2000).

Reconciling the conservation of forest biodiversity with the high demands for timber as well as with other pressures on forests is a challenging task in conservation and forest management planning. Generally, there are two approaches to preserve forest biodiversity: the creation of protection area networks and the adjustment of management practices (i.e., land-sparing or segregative vs. land-sharing or integrative approaches). Strictly protected areas provide high conservation value but are insufficient for preserving biodiversity due to their limited area (Lindenmayer and Franklin, 2002). By contrast, integrating biodiversity conservation into forest management, e.g., by retaining or creating deadwood or old-growth patches in production forests (Bauhus et al., 2009; Bollmann and Braunisch, 2013; Lindenmayer et al., 2012), is feasible over large areas; however, whether and under which conditions old-growth forest specialists can use or persist in such stands is unclear. While many habitat specialists benefit from integrative measures (e.g., saproxylic beetles from the availability of artificially created deadwood, Jonsell et al., 2004; Lindhe et al., 2004), others are found in managed stands only

when old-growth forests are nearby (Brunet and Isacson, 2009), or not at all (Bässler and Müller, 2010; Siitonen and Saaristo, 2000).

Understanding the space use of habitat specialists to improve conservation and forest management planning

Mobile old-growth forest species with large area requirements may use a variety of forest stands differing in management intensity and forest structure. First, they might be able to compensate for the lack or low availability of old-growth forests by increasing their home ranges and using larger areas of younger forest with presumably lower resource abundance. For instance, home range size of spotted owls (*Strix occidentalis caurina*) increased with decreasing proportion of old coniferous forest (Glenn et al., 2004), indicating that this species is to some extent able to adapt its space use to suboptimal conditions. Moreover, habitat specialists might be able to use different habitat types to meet different biological requirements such as foraging, breeding, or shelter (Orians and Wittenberger, 1991). For example, Crampton and Barclay (1998) found that little brown bats (*Myotis lucifugus*) and silver-haired bats (*Lasionycteris noctivagans*) roosted exclusively in old forests but foraged also in younger stands. Investigating the space use of old-growth forest species in landscapes comprising stands of different management intensity may help to provide further insight into the potential of managed forests as habitat for such species and to better incorporate their requirements into forest management planning. In this thesis, I focused on two aspects of space use – home range size and habitat selection – which I briefly describe below.

Home range size

Home range is typically defined as the area used by an animal to carry out the activities of food gathering, mating, and caring for young (Burt, 1943). Home range size generally increases with the body size of a species (McNab, 1963) but can also considerably vary between populations of a species, between individuals of a population, or within an individual (McLoughlin and Ferguson, 2000). This variation can be a result of different intrinsic and extrinsic factors. Intrinsic factors include reproductive status (van Beest et al., 2011), age (Börger et al., 2006), or body mass (Kowalczyk et al., 2003); three of the most important extrinsic factors are population density and the abundance and distribution of resources (Krebs, 1971; Myers et al., 1979). As both intrinsic and extrinsic factors may underlie substantial temporal variation, the considered time frame plays an important role in home range studies and should cover biologically meaningful time periods (Fieberg and Börger, 2012).

Habitat selection

Habitat selection, that is, the disproportionate use of habitat types, resources, or conditions by animals, is considered to be a hierarchical process which can take place at different orders or levels and at different spatial and temporal scales (Mayor et al., 2009). Johnson (1980) suggested four orders of habitat selection (note that I generally use the term “level” instead of “order” in this thesis following Mayor et al., 2009, and McGarigal et al., 2016; both terms refer to the same concept), where first-order selection refers to the selection of a geographical range of a species, second-order selection determines the home range of an individual within the landscape, third-order selection describes the selection of habitat types within the home range, and fourth-order refers to the selection of fine-scale resources such as food items. This concept assumes that habitat selection at a given level determines availability at subsequent levels. By contrast, “scale” refers to the extent (spatial scale) or the duration (temporal scale) of an analysis, pattern, or process (Mayor et al., 2009). Within a given level of habitat selection, organisms may select different environmental conditions at different scales. As these scales are often not known a priori, habitat selection analyses should ideally include the evaluation of multiple scales per predictor and level of habitat selection (McGarigal et al., 2016). Similar to home range size, habitat selection may vary temporally. For instance, seasonal variation in food availability or different habitat requirements in the course of the annual cycle can result in seasonal differences in habitat selection.

Study system

The white-backed woodpecker

In this thesis, I investigated the space use of the white-backed woodpecker (*Dendrocopos leucotos*). The white-backed woodpecker is a resident forest bird widely distributed over large parts of the Palearctic. Its range reaches from Western Europe to Japan and encompasses 11 subspecies, two of which occur in Europe (Winkler and Christie, 2002): the nominate subspecies *D. l. leucotos* (addressed in this PhD thesis) in North, East and Central Europe and *D. l. lilfordi* in South and Southeast Europe (Winkler and Christie, 2002). The white-backed woodpecker breeds in deciduous or mixed forests throughout its range, using a variety of forest types and tree species (Glutz von Blotzheim and Bauer, 1994). Its diet largely consists of wood-boring and bark-living beetle larvae (Aulén, 1988; Hogstad and Stenberg, 1997); this specialization restricts it to old deciduous or mixed stands with high amounts of deadwood and thus low forest management intensity (Czeszczewik and Walankiewicz, 2006; Hogstad and Stenberg, 1994; Scherzinger, 1982).

Because of its large range and worldwide population size, the white-backed woodpecker is classified as Least Concern (LC) in the IUCN Red List of Threatened Species (Birdlife International, 2023). In Europe,

the overall population is today considered stable (Keller et al., 2020). However, the species has experienced massive declines in Europe in the past because of intensive forest management. Such declines are well documented for Sweden (Aulén, 1988; Carlson, 2000) and Finland (Lehikoinen et al., 2011; Virkkala et al., 1993), where the species was close to extinction by the end of the 20th century as a result of habitat loss, and the Białowieża forest in Poland (Czeszczewik and Walankiewicz, 2006). As a result, the species is considered threatened in various national red lists and listed in the Annex 1 of the European Union's Birds Directive. As it is also considered as an umbrella species for other organisms associated with old-growth forests, including threatened saproxylic beetles (Angeleri, 2023; Bell et al., 2015), threatened cryptogams (Roberge et al., 2008), and forest birds of conservation concern (Roberge et al., 2008), the white-backed woodpecker has become a species of high conservation concern in Europe.

However, the implementation of conservation measures may be hampered by knowledge gaps regarding the species' ecology, in particular its space use. First, the knowledge about the species' area requirements is limited, as to my knowledge no studies using telemetry have been published so far (a telemetry study by Campion et al. (2020) on the *lilfordi* subspecies, which has slightly different habitat preferences than the nominate subspecies, being the exception). Current estimates of the white-backed woodpecker's home range size are based on the mapping of territorial individuals during the mating and breeding seasons, foraging marks, or color-banded individuals (Scherzinger, 1982; Stenberg, 1990; Wesołowski, 1995), and the factors driving variation in home range size are unknown. Second, knowledge about the white-backed woodpecker's habitat preferences is mainly limited to the mating and breeding seasons. White-backed woodpeckers behave inconspicuously after fledging of the chicks and data on habitat use and selection in summer, fall, and early winter are thus difficult to record without the use of telemetry techniques. Third, while previous studies addressing the habitat preferences of the white-backed woodpecker have consistently concluded that old unmanaged deciduous-dominated forests are the ideal breeding habitat for this species (Czeszczewik and Walankiewicz, 2006; Hogstad and Stenberg, 1994; Kajtoch et al., 2013; Scherzinger, 1982), the extent to which managed stands can serve as habitat is unclear. Anecdotal observations suggest that white-backed woodpeckers use intensively managed stands at least occasionally (Bühler, 2009; Scherzinger, 1982; personal observation). However, systematically collected data are missing, and how this old-growth forest specialist uses landscapes with a high heterogeneity in management intensity and forest structure is unknown.

Study area

I conducted the study in the Eastern Alps in Western Austria (State of Vorarlberg), Eastern Switzerland (Cantons of Grisons and St Gallen), and the Principality of Liechtenstein (46.8 - 47.5°N, 9.3 - 10°E, Fig. 1), a region with high heterogeneity in landscape composition and forest management intensity. This region constitutes the western edge of the white-backed woodpecker's distribution in Central Europe and was colonized by this species between the 1970s and 1990s (Kilzer, 1976; Knaus, 1997; Mollet et al., 2009), probably as a result of an increase in deadwood amount at the landscape scale (Mollet et al., 2009). In contrast to other studies addressing the white-backed woodpecker's habitat requirements, which were mostly conducted either in declining populations (Aulén, 1988; Virkkala et al., 1993) or in regions with relicts of primeval forests (Czeszczewik, 2009; Frank, 2002; Scherzinger, 1982), my thesis focuses on a population which has extended its range into a region with a long history of human land use, including forest management. Today, there are no relicts of primeval forest or large forest reserves in the study area; however, forest management intensity is generally rather low.

The region is characterized by mountainous terrain (Fig. 2a-b) with elevations between 400 and 3000 m a.s.l. Forest cover is naturally limited by the partly high elevations (the tree line being at 1600 – 1800 m) and has been additionally reduced by deforestation, particularly in the bottoms of larger valleys. Today, about 40% of the study area is covered by forest. The occurrence of the white-backed woodpecker in the study area is mostly restricted to deciduous forests dominated by European beech (*Fagus sylvatica*) in the submontane belt and mixed forests dominated by European beech, Norway spruce (*Picea abies*) and silver fir (*Abies alba*) in the montane belt at elevations ranging from 600 to 1300 m a.s.l. Forest management intensity in the study area varies depending on the accessibility of the terrain and the landowner; it ranges from intensive management for timber production in easily accessible stands to the occasional logging of single trees in steep protection forests or some privately owned stands. Clearcuts are prohibited by law in Switzerland and Liechtenstein and do not play an important role in the Austrian part of the study area. However, even-aged spruce monocultures are still found in the study area as a result of past forest management. These differences in current and past forest management have led to a mosaic of forest stands differing in forest structure (see examples in Fig. 2c-f) in many parts of the study area. Large contiguous forests with low management intensity are mainly found in a few remote or inaccessible valleys (Fig. 2b).

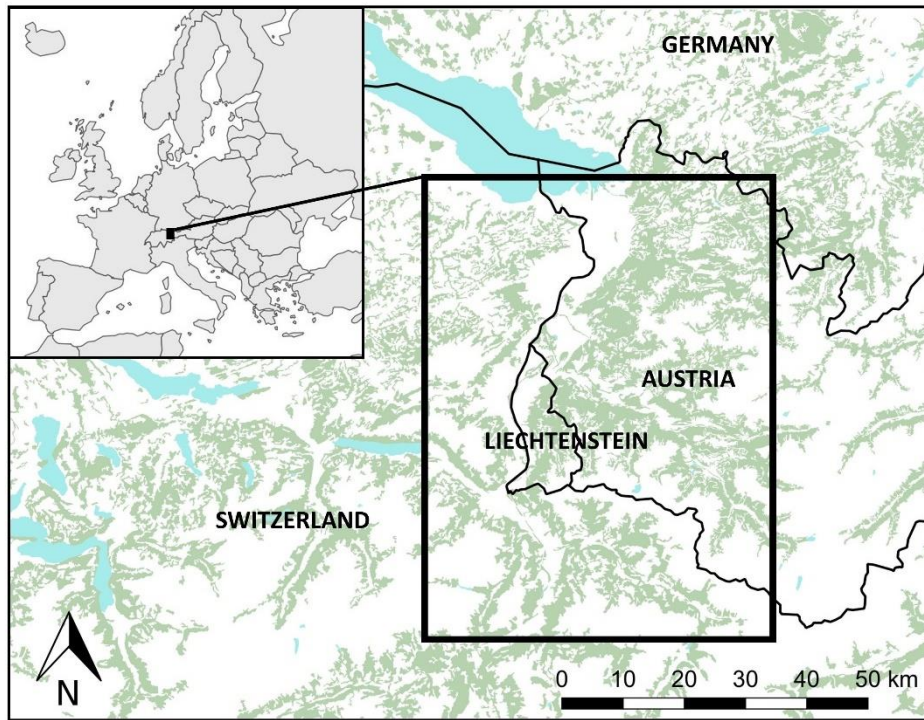


Figure 1 Study area. ©EuroGeographics (borders) and European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (forest cover)

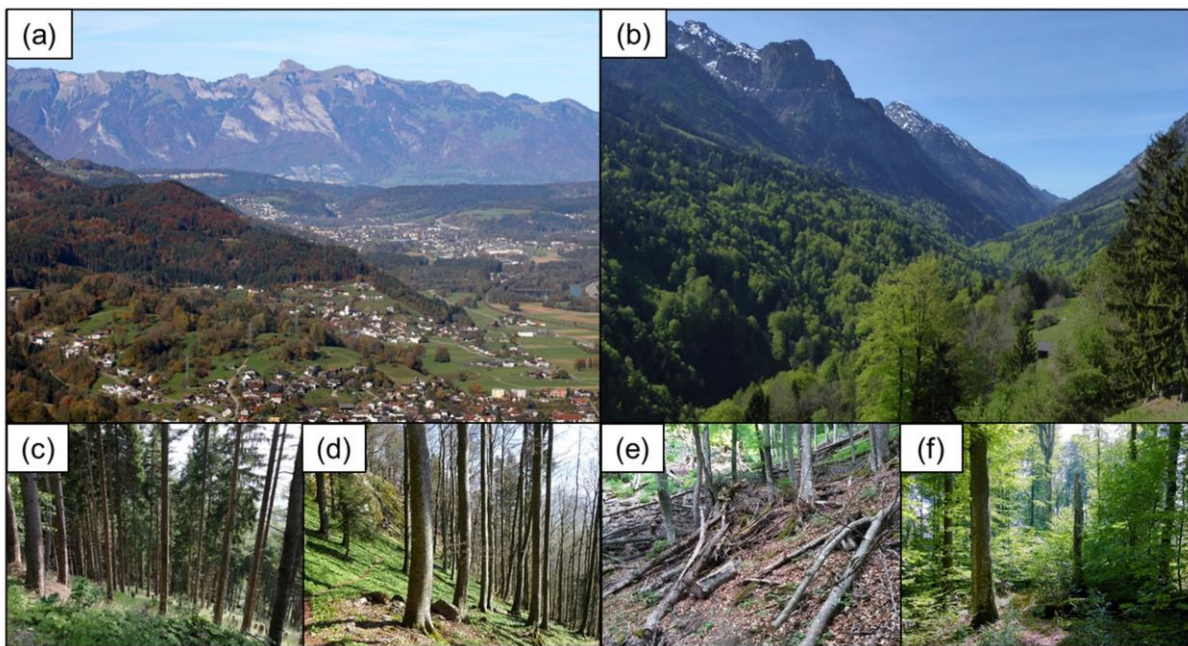


Figure 2 Typical landscapes (a) and (b) and forest stands (c-f) in the study area in Western Austria, Liechtenstein, and Eastern Switzerland. All displayed forest stands were used by the white-backed woodpecker at least occasionally. ©Antonia Ettwein

Aims of the thesis

The range expansion of the white-backed woodpecker into a region with a long history of forest management provided the opportunity to study aspects of an old-growth forest specialist's ecology outside of its ideal habitat. In this thesis, I used data of radio-tracked adult white-backed woodpeckers and data on forest structure (recorded in the field and derived from remote sensing data) to analyze this species' space use in forests differing in management intensity and forest structure. The two main objectives of the thesis were to close knowledge gaps regarding the white-backed woodpecker's space use and to find out how the occurrence of the white-backed woodpecker and forest management can be reconciled. More specifically, my aims were (1) to estimate seasonal and yearly home range sizes (Chapter 1); to understand the factors driving variation in breeding and post-breeding home range size (Chapter 2); to find out which habitat types and foraging trees are selected within the home ranges and whether and how habitat selection differs between seasons (Chapter 3); and to assess the role of the surrounding landscape for the occurrence of this species in occupied and unoccupied sites (Chapter 4).

References

- Angeleri, R., 2023. Communities of saproxylic beetles associated with the White-backed Woodpecker (*Dendrocopos leucotos*) in temperate forests of central Europe (Dissertation). Universität Bern, Bern.
- Aulén, G., 1988. Ecology and distribution of the white-backed woodpecker *Dendrocopos leucotos* in Sweden (Dissertation). Swedish University of Agricultural Sciences, Uppsala.
- Bässler, C., Müller, J., 2010. Importance of natural disturbance for recovery of the rare polypore *Antrodiella citrinella* Niemelä & Ryvarde. Fungal Biol. 114, 129–133. <https://doi.org/10.1016/j.funbio.2009.11.001>
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For. Ecol. Manag. 258, 525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>
- Bell, D., Hjältén, J., Nilsson, C., Jørgensen, D., Johansson, T., 2015. Forest restoration to attract a putative umbrella species, the white-backed woodpecker, benefited saproxylic beetles. Ecosphere 6, 1–14. <https://doi.org/10.1890/ES14-00551.1>
- Betts, M.G., Wolf, C., Ripple, W.J., Phalan, B., Millers, K.A., Duarte, A., Butchart, S.H.M., Levi, T., 2017. Global forest loss disproportionately erodes biodiversity in intact landscapes. Nature 547, 441–444. <https://doi.org/10.1038/nature23285>

Betts, M.G., Yang, Z., Hadley, A.S., Smith, A.C., Rousseau, J.S., Northrup, J.M., Nocera, J.J., Gorelick, N., Gerber, B.D., 2022. Forest degradation drives widespread avian habitat and population declines. *Nat. Ecol. Evol.* 6, 709–719. <https://doi.org/10.1038/s41559-022-01737-8>

Birdlife International, 2023. *Dendrocopos leucotos*. The IUCN Red List of Threatened Species 2023.

Bollmann, K., Braunisch, V., 2013. To integrate or to segregate: balancing commodity production and biodiversity conservation in European forests. In Integrative approaches as an opportunity for the conservation of forest biodiversity. Kraus D., Krumm F. (eds). European Forest Institute, Freiburg, p. 284.

Börger, L., Franconi, N., Ferretti, F., Meschi, F., Michele, G.D., Gantz, A., Coulson, T., 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *Am. Nat.* 168, 471–485. <https://doi.org/10.1086/507883>

Brunet, J., Falkengren-Grerup, U., Tyler, G., 1996. Herb layer vegetation of south Swedish beech and oak forests—effects of management and soil acidity during one decade. *For. Ecol. Manag.* 88, 259–272. [https://doi.org/10.1016/S0378-1127\(96\)03845-5](https://doi.org/10.1016/S0378-1127(96)03845-5)

Brunet, J., Isacson, G., 2009. Restoration of beech forest for saproxylic beetles—effects of habitat fragmentation and substrate density on species diversity and distribution. *Biodivers. Conserv.* 18, 2387. <https://doi.org/10.1007/s10531-009-9595-5>

Bühler, U., 2009. Totholz – existenziell für den Weissrückenspecht in Nordbünden | Dead wood – a vital necessity for the white-backed woodpecker in the Grisons. *Schweiz. Z. Forstwes.* 160, 210–217. <https://doi.org/10.3188/szf.2009.0210>

Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24, 346–352. <https://doi.org/10.2307/1374834>

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 Ornithol.* 55, 77–87. <https://doi.org/10.3161/00016454AO2020.55.1.008>

Carlson, A., 2000. The effect of habitat loss on a deciduous forest specialist species: the white-backed woodpecker (*Dendrocopos leucotos*). *For. Ecol. Manag.* 131, 215–221. [https://doi.org/10.1016/S0378-1127\(99\)00215-7](https://doi.org/10.1016/S0378-1127(99)00215-7)

Crampton, L.H., Barclay, R.M.R., 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conserv. Biol.* 12, 1347–1358. <https://doi.org/10.1111/j.1523-1739.1998.97209.x>

Czeszczewik, D., 2009. Marginal differences between random plots and plots used by foraging white-backed woodpeckers demonstrates supreme primeval quality of the Białowieża National Park, Poland. *Ornis Fenn.* 86, 30–37.

Czeszczewik, D., Walankiewicz, W., 2006. Logging affects the white-backed woodpecker *Dendrocopos leucotos* distribution in the Białowieża Forest. *Ann. Zool. Fenn.* 43, 221–227.

FAO, 2022. The state of the world's forests 2022. Forest pathways for green recovery and building inclusive, resilient and sustainable economies. FAO, Rome.

Fieberg, J., Börger, L., 2012. Could you please phrase “home range” as a question? *J. Mammal.* 93, 890–902. <https://doi.org/10.1644/11-MAMM-S-172.1>

Forest Europe, 2020. State of Europe's forests 2020.

Fraixedas, S., Lindén, A., Lehtikainen, A., 2015. Population trends of common breeding forest birds in southern Finland are consistent with trends in forest management and climate change. *Ornis Fenn.* 92, 187–203.

Frank, G., 2002. Brutzeitliche Einnischung des Weissrückenspechtes *Dendrocopos leucotos* im Vergleich zum Buntspecht *Dendrocopos major* in montanen Mischwäldern der nördlichen Kalkalpen. *Vogelwelt* 123, 225–239.

Gibb, H., Ball, J.P., Johansson, T., Atlegrim, O., Hjältén, J., Danell, K., 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scand. J. For. Res.* 20, 213–222. <https://doi.org/10.1080/02827580510008392>

Glenn, E.M., Hansen, M.C., Anthony, R.G., 2004. Spotted owl home-range and habitat use in young forests of Western Oregon. *J. Wildl. Manag.* 68, 33–50. [https://doi.org/10.2193/0022-541X\(2004\)068\[0033:SOHAHU\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2004)068[0033:SOHAHU]2.0.CO;2)

Glutz von Blotzheim, U.N., Bauer, K., 1994. Handbuch der Vögel Mitteleuropas. Band 9: Columbiformes - Piciformes, 2nd ed. Aula-Verlag, Wiesbaden.

Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. *Annu. Rev. Ecol. Syst.* 33, 1–23. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150507>

Hogstad, O., Stenberg, I., 1997. Breeding success, nestling diet and parental care in the white-backed woodpecker *Dendrocopos leucotos*. *J. Für Ornithol.* 138, 25–38. <https://doi.org/10.1007/BF01651649>

Hogstad, O., Stenberg, I., 1994. Habitat selection of a viable population of white-backed woodpeckers *Dendrocopos leucotos*. *Fauna Nor. Ser. C Cinclus* 17, 75–94.

Johnson, D., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.

Jonsell, M., Nittérus, K., Stighäll, K., 2004. Saproxyllic beetles in natural and man-made deciduous high stumps retained for conservation. *Biol. Conserv.* 118, 163–173. <https://doi.org/10.1016/j.biocon.2003.08.017>

Juutilainen, K., Mönkkönen, M., Kotiranta, H., Halme, P., 2014. The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. *For. Ecol. Manag.* 313, 283–291. <https://doi.org/10.1016/j.foreco.2013.11.019>

Kajtoch, L., Figarski, T., Pelka, J., 2013. The role of forest structural elements in determining the occurrence of two specialist woodpecker species in the Carpathians, Poland. *Ornis Fenn.* 90, 23–40.

Keller, V., Herrando, S., Voríšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvanová, A., Kalyakin, M.V., 2020. European breeding bird atlas 2: distribution, abundance and change. European Bird Census Council & Lynx Edicions, Barcelona.

Kilzer, R., 1976. Erste Beobachtung eines Weißrückenspechtes (*Dendrocopos leucotos*) in Vorarlberg. *Egretta* 19, 62–63.

Knaus, P., 1997. Erstnachweis des Weissrückenspechts *Dendrocopos leucotos* in der Schweiz. *Ornithol Beob* 94, 185–190.

Kowalczyk, R., Zalewski, A., Jedrzejewska, B., Jedrzejewski, W., 2003. Spatial organization and demography of badgers (*Meles meles*) in Białowieża Primeval Forest, Poland, and the influence of earthworms on badger densities in Europe. *Can. J. Zool.* 81, 74–87. <https://doi.org/10.1139/z02-233>

Krebs, J.R., 1971. Territory and breeding density in the great tit, *Parus major* L. *Ecology* 52, 2–22. <https://doi.org/10.2307/1934734>

Kuuluvainen, T., Penttinen, A., Leinonen, K., Nygren, M., 1996. Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: an example from boreal spruce forest in southern Finland. *Silva Fenn.* 30, 315–328.

Lehikoinen, A., Lehikoinen, P., Lindén, A., Laine, T., 2011. Population trend and status of the endangered white-backed woodpecker *Dendrocopos leucotos* in Finland. *Ornis Fenn.* 8, 195–207.

Lindenmayer, D. b., Franklin, J. f., Löhmus, A., Baker, S. c., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., Gustafsson, L., 2012. A major shift to the retention approach for forestry can help resolve some global

forest sustainability issues. *Conserv. Lett.* 5, 421–431. <https://doi.org/10.1111/j.1755-263X.2012.00257.x>

Lindenmayer, D.B., Franklin, J.F., 2002. *Conserving forest biodiversity: a comprehensive multiscaled approach*. Island Press.

Lindhe, A., Åsenblad, N., Toresson, H.-G., 2004. Cut logs and high stumps of spruce, birch, aspen and oak – nine years of saproxylic fungi succession. *Biol. Conserv.* 119, 443–454. <https://doi.org/10.1016/j.biocon.2004.01.005>

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., Rauh, J., 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biol. Conserv.* 94, 199–209. [https://doi.org/10.1016/S0006-3207\(99\)00175-5](https://doi.org/10.1016/S0006-3207(99)00175-5)

Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat selection at multiple scales. *Ecoscience* 16, 238–247. <https://doi.org/10.2980/16-2-3238>

McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. *Landsc. Ecol.* 31, 1161–1175. <https://doi.org/10.1007/s10980-016-0374-x>

McLoughlin, P.D., Ferguson, S.H., 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Écoscience* 7, 123–130.

McNab, B.K., 1963. Bioenergetics and the determination of home range size. *Am. Nat.* 97, 133–140. <https://doi.org/10.1086/282264>

Mollet, P., Zbinden, N., Schmid, H., 2009. Steigende Bestandszahlen bei Spechten und anderen Vogelwarten dank Zunahme von Totholz? *Schweiz. Z. Forstwes.* 160, 334–340.

Moning, C., Müller, J., 2009. Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. *Ecol. Indic.* 9, 922–932. <https://doi.org/10.1016/j.ecolind.2008.11.002>

Myers, J.P., Connors, P.G., Pitelka, F.A., 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. *The Auk* 96, 551–561. <https://doi.org/10.1093/auk/96.3.551>

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *J. Ecol.* 101, 701–712. <https://doi.org/10.1111/1365-2745.12085>

Orians, G.H., Wittenberger, J.F., 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* 137, S29–S49. <https://doi.org/10.1086/285138>

Penttilä, R., Siitonen, J., Kuusinen, M., 2004. Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biol. Conserv.* 117, 271–283. <https://doi.org/10.1016/j.biocon.2003.12.007>

Roberge, J.-M., Mikusiński, G., Svensson, S., 2008. The white-backed woodpecker: umbrella species for forest conservation planning? *Biodivers. Conserv.* 17, 2479–2494. <https://doi.org/10.1007/s10531-008-9394-4>

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Marques Duarte, I., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.-P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. Where are Europe's last primary forests? *Divers. Distrib.* 24, 1426–1439. <https://doi.org/10.1111/ddi.12778>

Scherzinger, W., 1982. Die Spechte im Nationalpark Bayerischer Wald. Nationalparkverwaltung Bayerischer Wald, Grafenau.

Siitonen, J., Saaristo, L., 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biol. Conserv.* 94, 211–220. [https://doi.org/10.1016/S0006-3207\(99\)00174-3](https://doi.org/10.1016/S0006-3207(99)00174-3)

Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R., Ruchty, A., 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* 10, 789–799. [https://doi.org/10.1890/1051-0761\(2000\)010\[0789:DLOELR\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0789:DLOELR]2.0.CO;2)

Stenberg, I., 1990. Preliminary results of a study on woodpeckers in More and Romsdal Country, western Norway, in: Carlson, A, Aulén, G. (Eds): Conservation and Management of Woodpecker Populations. Report 17, Uppsala. Departement of Wildlife Ecology, Swedish University of Agricultural Sciences, Uppsala, pp. 67–79.

Thorn, S., Seibold, S., Leverkus, A.B., Michler, T., Müller, J., Noss, R.F., Stork, N., Vogel, S., Lindenmayer, D.B., 2020. The living dead: acknowledging life after tree death to stop forest degradation. *Front. Ecol. Environ.* 18, 505–512. <https://doi.org/10.1002/fee.2252>

Tomiałojć, L., 2000. An East-West gradient in the breeding distribution and species richness of the European woodland avifauna. *Acta Ornithol.* 35, 3–17.

van Beest, F., Rivrud, I.M., Loe, L.E., Milner, J., Mysterud, A., 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *J. Anim. Ecol.* 80, 771–785. <https://doi.org/10.1111/j.1365-2656.2011.01829.x>

Virkkala, R., Alanko, T., Laine, T., Tiainen, J., 1993. Population contraction of the white-backed woodpecker *Dendrocopos leucotos* in Finland as a consequence of habitat alteration. *Biol. Conserv.* 66, 47–53. [https://doi.org/10.1016/0006-3207\(93\)90133-L](https://doi.org/10.1016/0006-3207(93)90133-L)

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J.G., Painter, M., Wilkie, D., Filardi, C., Laurance, W.F., Houghton, R.A., Maxwell, S., Grantham, H., Samper, C., Wang, S., Laestadius, L., Runting, R.K., Silva-Chávez, G.A., Ervin, J., Lindenmayer, D., 2018. The exceptional value of intact forest ecosystems. *Nat. Ecol. Evol.* 2, 599–610. <https://doi.org/10.1038/s41559-018-0490-x>

Wesołowski, T., 1995. Ecology and behaviour of white-backed woodpecker (*Dendrocopos leucotos*) in a primeval temperate forest (Białowieża National Park, Poland). *Vogelwarte* 38, 61–75.

Winkler, H., Christie, D., 2002. Family Picidae (woodpeckers), in: Del Hoyo, J., Elliott, A. & Sargatal, J. (Eds): *Handbook of the Birds of the World*. Lynx Edicions, Barcelona, pp. 296–555.

Chapter 1

Seasonal variation in home range size of white-backed woodpeckers

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Abstract

Knowing a species' area requirements is fundamental for species conservation. For the nominate subspecies of the white-backed woodpecker *Dendrocopos leucotos*, a species of high conservation concern in Europe, estimates of the seasonal and year-round area requirements based on telemetry are missing. In the present study, we radio-tracked adult white-backed woodpeckers in Western Austria, Eastern Switzerland and Liechtenstein and investigated bi-monthly home range sizes based on three home range estimators in relation to season, sex, body weight, and year. Home range size of 49 radio-tracked individuals greatly varied depending on the used home range estimator, with minimum convex polygons (MCP) and autocorrelated kernel density estimation (AKDE) producing 1.6 – 1.8 and 2 – 3.3 times larger seasonal home ranges than traditional kernel density estimation (KDE). Regardless of the home range estimator, however, bi-monthly home range size was best explained by season. Home ranges were smallest in February/March (predicted median home range sizes ranged from 35 ha with KDE to 88 ha with AKDE) and April/May (KDE: 30 ha, AKDE: 55 ha) and larger during the rest of the year (KDE: 48 – 67, AKDE: 136 – 184 ha). The mean home range size of six individuals tracked for at least one year (calculated with all locations per individual) was 116 ha with KDE, 304 ha with MCP and 350 ha with AKDE. Our results highlight the importance of considering the full annual cycle when addressing area requirements of white-backed woodpeckers and likely of other species as well. Furthermore, our study shows that using multiple methods for home range estimation may be useful to obtain results that are both comparable with those of other studies and capture the range in which the true home range size is likely to be. For the conservation of the white-backed woodpecker, we conclude that at least 116 to 350 ha of forest should be present for a pair.

Introduction

Knowing the area requirements of a species is fundamental for its effective conservation. For instance, one of the most basic questions for species conservation is how much habitat has to be available to sustain an individual, pair, or group of individuals. Moreover, knowledge about a species' area requirements is often used for estimating population sizes or densities (Furnas et al., 2017; Ramsey et al., 2015) or assessing the adequate size of protected areas (Chundawat et al., 2016). Area requirements of animals are usually described by their home ranges, the area "traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt, 1943), and can vary considerably among individuals of a species. Many studies addressing variation in home range size have highlighted the importance of resource availability (Grigione et al., 2002; Herfindal et al., 2005), inter- and intraspecific competition (Marneweck et al., 2019; Schoepf et al., 2015), or the presence of predators (Desy et al., 1990) as factors determining home range size. However, species-specific patterns of space use may also underlie substantial within-individual and temporal variation, an aspect which has received less attention (Fieberg and Börger, 2012). For example, a species may be a central place forager with small home ranges when raising offspring and shift to a nomadic movement strategy in the non-breeding season (Lenz et al., 2015). In addition, fluctuating environmental conditions such as seasonal changes in food availability may cause temporal variation in home range size (Morellet et al., 2013; Shannon et al., 2010). Thus, the considered time frame plays an important role in home range studies and should cover well-defined and biologically meaningful time periods (Fieberg and Börger, 2012).

Here, we investigated seasonal variation in home range size of the white-backed woodpecker (*Dendrocopos leucotos leucotos*) in Central Europe. This species typically breeds in old-growth deciduous or mixed forests with abundant deadwood (Aulén, 1988; Czeszczewik and Walankiewicz, 2006; Scherzinger, 1982). A long history of deforestation and forest management have has caused massive habitat loss for the white-backed woodpecker in large parts of Europe, and the species is today considered threatened in many countries (Gärdenfors, 2010; Knaus et al., 2021; Ryslavý et al., 2020). Although the white-backed woodpecker is a species of high conservation concern and has already been a target species of various conservation projects (Bell et al., 2015; Kreiner et al., 2012), little is known about its spatial ecology. Observations of color-banded individuals of the nominate subspecies suggest high site fidelity and the use of a common territory by a pair throughout the year, although mates may be changed between years (Stenberg, 1990; Stenberg and Hogstad, 2004). Based on the mapping of territorial individuals during the mating and breeding seasons, foraging marks, or color-banded individuals, territory size of a breeding pair has been estimated at approximately 100 ha in Germany,

Norway, and Poland (Scherzinger, 1982; Stenberg, 1990; Wesolowski, 1995). The only published study investigating space use of the species by means of telemetry addressed the subspecies *lilfordi* and revealed mean home range sizes of 300 ha in the breeding and post-breeding seasons and differences between the sexes (Campion et al., 2020). Home range sizes in fall and winter are completely unknown.

Complementing Chapter 2, which addresses variation in seasonal home range size in relation to resource distribution, habitat availability, and intraspecific competition, we here focused on home range sizes per se. The aim of the present study was to estimate seasonal and, for individuals that were tracked for at least one year, total home range sizes. We expected home range size to differ between seasons, being smallest in spring, when movements are expected to occur in a relatively small area around the nest, and largest in winter, when food availability is usually lowest. As home range size is related to sex and body weight in many species (McLoughlin and Ferguson, 2000) and might differ between years, we also investigated the effects of these three factors.

Methods

Study area

Our study area was located in the Alps in western Austria, eastern Switzerland, and the Principality of Liechtenstein in an area of approximately 2000 km² (46.8 - 47.5°N, 9.3 - 10°E). Elevations range from 400 to 3000 m a.s.l., with white-backed woodpeckers occurring mainly in the montane forests dominated by European beech *Fagus sylvatica*, Norway spruce *Picea abies*, and silver fir *Abies alba* at elevations between 600 and 1300 a.s.l. Forest management intensity in these mountain forests is generally low but can vary considerably at a small scale.

Capture, radio tagging, and radio telemetry

Between 2016 and 2019, 62 adult white-backed woodpeckers (40 males, 22 females) were captured during the pre-breeding and breeding seasons and in fall by luring them into a mist net with a playback tape. Eight of the 62 individuals were caught and tracked in two years, one individual in three years. The woodpeckers were fitted with very high frequency (VHF) transmitters (PIP3, Biotrack/Lotek Ltd., Wareham, UK; weight = 3 g), which were either glued onto the base of the two central tail feathers or fixed on the back with a leg-loop harness. Moreover, each woodpecker was weighed with a spring scale and marked with two color rings and an official aluminum ring of the country in which the bird was caught.

Each tagged woodpecker was tracked with a portable receiver (R-1000, Communications Specialists, Orange, California) and a hand-held yagi antenna (Advanced Telemetry Systems ATS, Isanti, Minnesota)

twice a week during a two- and a four-hours session. The start time of the tracking sessions was varied to cover the whole activity period of each individual (sunrise to sunset). Within a tracking session, the woodpecker's locations and their accuracies (estimated as the radius of the circle in which the woodpecker was assumed to be) were recorded every 15 minutes. The average estimated accuracy of the locations (\pm standard deviation SD) was 107 ± 69 m ($n = 15047$). It was also noted when a woodpecker could not be located after 15 minutes. While the birds were mostly located by triangulation in the two-hours sessions, the four-hours sessions were used to approach the bird as closely as possible in the often inaccessible terrain to improve the accuracy of the locations. The woodpeckers were usually tracked until the battery of the transmitters was dead after nine months or until they lost the transmitter, which mostly happened during the molt in July or August. As most birds were caught between March and May and fitted with a tail-mount transmitter, most data were collected between April and July (Fig. 1).

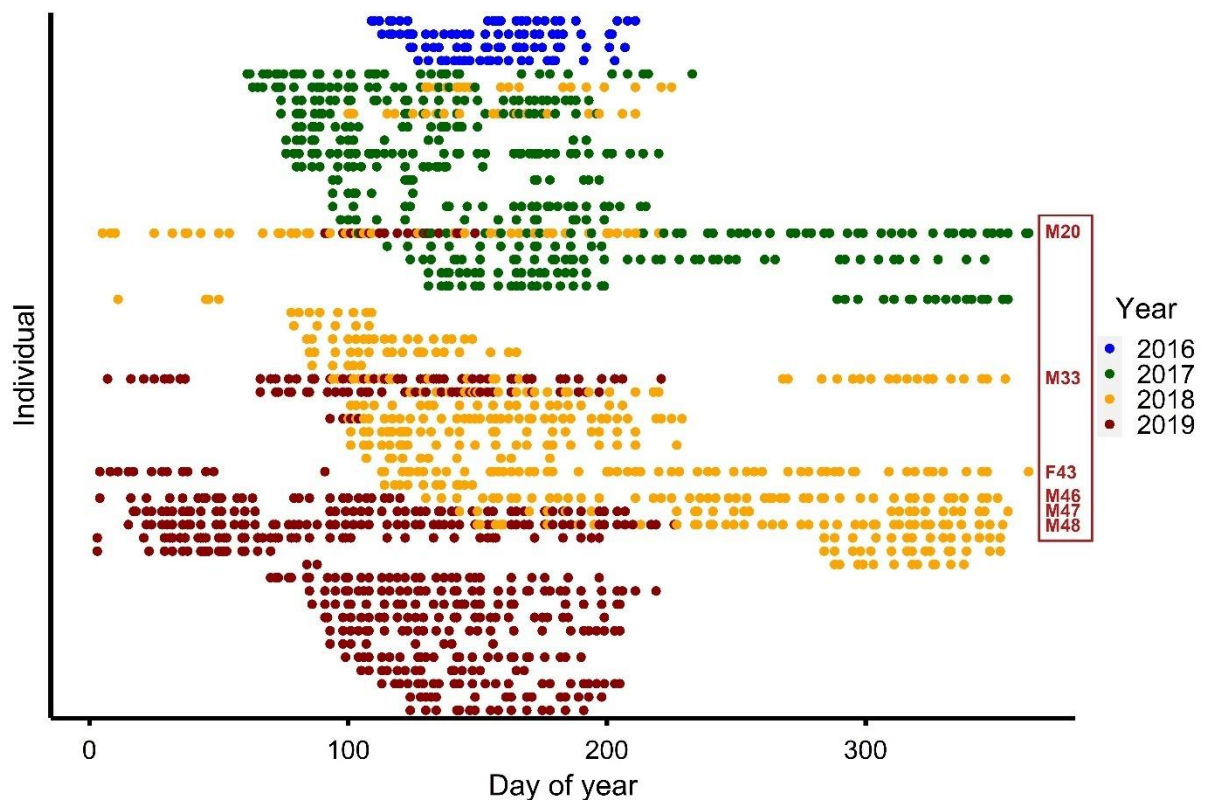


Figure 1 Days on which radio-tagged white-backed woodpeckers were tracked from 2016 to 2019. Each horizontal line represents one individual. The six labelled individuals (one female F, five males M) were used for estimating the total home range size (all locations included) of an individual.

Home range estimation

We first divided the year into bi-monthly time intervals (seasons), where February/March overlaps with the mating season, April/May with the breeding season, June/July with the post-breeding season (fledging until full independence of the chicks), and August/September, October/November, and December/January represent late summer, fall, and winter, respectively. We then computed home ranges for each individual-season combination in R (R Core Team, 2020) using three methods. To facilitate comparing the results with those of other studies, we used kernel density estimation (KDE) based on the 95% utilization distribution and the plug-in method for bandwidth selection, and 100% minimum convex polygons (MCPs). As the importance of accounting for autocorrelation between successive locations in home range analyses has been increasingly recognized (Fleming et al., 2015; Noonan et al., 2019; Silva et al., 2022) and new methods have been developed (Calabrese et al., 2016; Fleming et al., 2015), we used 95% autocorrelated kernel density estimation (AKDE) as third method. AKDE computes home ranges based on movement models that account for autocorrelation between the locations and has been shown to provide more reliable home range estimates than KDE and MCP (Silva et al., 2022). We performed AKDE following the guidelines described by Silva et al. (2022) using the R package *ctmm* (Calabrese et al., 2016). To mitigate the bias in the autocorrelation model parameter estimates caused by small sample size, we used pHREML (perturbative Hybrid Residual Maximum Likelihood estimation) and, for seasonal home ranges with an expected order of pHREML bias > 5% ($n = 2$), parametric bootstrapping. To correct for irregular sampling, we applied weighted AKDE, which upweights observations recorded in under-sampled times.

Prior to all home range analyses, we discarded locations with accuracy >200 m and locations recorded when a woodpecker was known to be in the breeding cavity. To avoid unreliable results due to poor data quality, we only used home ranges reliably representing the respective season. To test the sensitivity of home range size to the number of locations, we used area-location plots (based on the KDE home ranges) and visually assessed whether an asymptote was reached (Kenward, 2001). We retained all home ranges with an asymptotic relationship ($n = 99$). Next, we used these retained home ranges to assess the number of locations at which home range sizes stabilized for each season. We also retained all home ranges which did not show a clear asymptote, but which had more locations than this threshold ($n = 16$). Home ranges with a clear linear area-location relationship ($n=29$) were not used for the analyses, regardless of the number of locations used for their calculation.

Lastly, we computed total home range size by including all locations of six individuals that were tracked for at least one year to obtain an estimate of the annual home range size of an individual.

Statistical analyses

We modeled home range size using linear mixed effects models with *season*, *sex*, and (body) *weight* as fixed effects (see Table 1 for a list of all models). As home range size might differ between males and females in the pre-breeding, breeding, and post-breeding seasons due to potential differences in efforts put into territory defense, incubation, and raising nestlings, we also considered the interaction between *season* and *sex*. We built models including one to four of the variables *season*, *sex*, *weight*, and *season:sex* using all possible combinations, with the restriction that we included the interaction between *season* and *sex* only in models with the respective main effects. To account for potential differences in home range size between years, we fitted a random intercept for *year* in each model. To evaluate if this potential year effect differed between seasons, we ran all models once using only the random intercept and once also including a random slope for *season* per *year*. Furthermore, we included a random intercept for individual ID (*ind*) to account for repeated observations (> 1 seasonal home range) of most individuals. As home range size has been shown to be sensitive to the number of days on which an individual was tracked (Börger et al., 2006), we included the number of tracking days (*trackdays*) as fixed (linear and quadratic) effect in each model. In addition, we included the proportion of unsuccessful location attempts (*signal*) as fixed effect to account for data gaps during the tracking sessions. Lastly, to see if the home range estimator affects model selection results, we ran each model twice, once using KDE home range size and once using AKDE home range sizes as response variable.

All analyses were performed in a Bayesian framework using the software Stan via R (R Core Team 2020; package *rstanarm*, Goodrich et al. 2020). We centered and scaled all linear predictors prior to the analyses and log-transformed home range size as dependent variable. We used the default prior settings in the *rstanarm* package and four Markov chains with 4000 iterations each. For presenting effect sizes of the model parameters, we computed the median and 2.5% and 97.5% quantiles as credible interval (CrI) from the corresponding marginal posterior distributions. We used the leave-one-out-cross-validation information criterion LOOIC (package *loo*, Vehtari et al., 2019) for model comparison, where models with lower LOOIC values are expected to have higher predictive accuracy.

Results

We obtained a total of 115 bi-monthly home ranges of 49 individuals with enough locations to reliably represent home range size (120 ± 44 locations per individual; depending on the season, up to 70-100 locations were necessary until bi-monthly home range size stabilized). Six individuals were tracked for at least one year, which resulted in 836 ± 193 locations per individual.

The home range estimator had little effect on the model ranking, with Δ LOOIC values comparing models using AKDE home range size differing only marginally from those with KDE home range sizes (Table 1). After controlling for year, individual ID, and number of tracking days, both bi-monthly KDE and AKDE home range sizes were best explained by a model including season as fixed effect (Table 1). Home range size increased in the course of the year as indicated by the well-supported linear component of the factor season (CrI 'season linear' did not include zero, Table 2). Moreover, predicted home range sizes tended to be largest in 2017 and smallest in 2016 and 2018; a model including a random slope for season per year ranking similarly high as the top-ranked one (Δ LOOIC = 0.32 and 0.18 for KDE and AKDE home ranges, respectively; Table 1) showed that this trend was consistent across seasons (Fig. 2). However, the sample sizes per season were small (on average, only 4.6 home ranges per season-year combination were available), the variability between individuals high, and the credible intervals for the predicted seasonal home range sizes per year thus very large (Fig. 2).

Table 1 Fixed and random effects used for modeling bi-monthly white-backed woodpecker home range sizes. Home range sizes were calculated using 95% kernel density estimation (KDE) and 95% autocorrelated kernel density estimation (AKDE) based on radio-tracking data collected in Central Europe between 2016 and 2019. Model selection was performed based on the leave-one-out-cross-validation information criterion LOOIC. Δ LOOIC = difference between a model's LOOIC and the top-ranked model's LOOIC. Trackdays/trackdays² = number of days an individual was tracked/quadratic term, signal = proportion of unsuccessful location attempts, weight = body weight, day_captured = day on which the individual was captured and weighed.

Model	LOOIC	Δ LOOIC	LOOIC	Δ LOOIC
season + trackdays + (1 year) + (1 ind_id)	195.06	0.00	286.44	0.01
season + trackdays + (season year) + (1 ind_id)	195.61	0.32	286.60	0.18
season + trackdays + signal + (1 year) + (1 ind_id)	195.68	0.39	286.42	0.00
season + trackdays + signal + (season year) + (1 ind_id)	196.36	1.08	287.17	0.74
season + trackdays + trackdays ² + (1 year) + (1 ind_id)	196.70	1.41	288.18	1.76
season + weight + day_captured + sex + trackdays + signal + (1 year) + (1 ind_id)	197.49	2.20	289.03	2.61
season + sex + trackdays + signal + (1 year) + (1 ind_id)	197.55	2.26	287.70	1.26
season + weight + day_captured + trackdays + signal + (1 year) + (1 ind_id)	197.86	2.58	288.50	2.08
season + sex + trackdays + signal + (season year) + (1 ind_id)	198.01	2.73	289.27	2.84
season + weight + day_captured + sex + trackdays + signal + (season year) + (1 ind_id)	198.21	2.93	289.86	3.44
season + weight + day_captured + trackdays + signal + (season year) + (1 ind_id)	198.65	3.37	289.36	2.94
season + trackdays + trackdays ² + (season year) + (1 ind_id)	198.77	3.49	289.01	2.58
season + sex + season:sex + trackdays + signal + (season year) + (1 ind_id)	200.99	5.70	292.71	6.28
season + sex + season:sex + trackdays + signal + (1 year) + (1 ind_id)	201.02	5.74	291.99	5.57
season + weight + day_captured + sex + season:sex + trackdays + signal + (1 year) + (1 ind_id)	201.93	6.65	293.92	7.50
season + weight + day_captured + sex + season:sex + trackdays + signal + (season year) + (1 ind_id)	202.87	7.58	295.17	8.74
trackdays + signal + (1 year) + (1 ind_id)	217.74	22.46	314.91	28.49

According to the highest-ranked model including body weight and sex (Δ LOOIC to the top-ranked model = 2.2 and 2.61 for KDE and AKDE home ranges, respectively, Table 1), home range size tended to decrease with increasing body weight (with credible intervals including zero) and to be larger in males than females (Table 2, see Table 4 for predicted bi-monthly home range sizes of males and females). All trends were similar for both home range estimators (Table 3, Fig. 2). However, home range sizes per se substantially differed depending on the used home range estimator in all seasons. Predicted AKDE home ranges were 2 – 3.3 times larger than KDE home ranges and increased from 55 ha in April/May to 184 ha in October/November, while KDE home ranges increased from 30 to 67 ha in the same time period (Table 3). MCP home ranges were 1.6 – 1.8 times larger than those computed with KDE and ranged from 61 ha in April/May to 128 ha in July/August (Table 3).

Lastly, the mean home range size of six individuals tracked for at least one year (see Fig. 1 for tracking durations) was 116 ± 28 (range: 75 – 155) ha when using 95% KDE, 304 ± 125 (range: 160 – 465) ha when using 100% MCPs and 350 ± 126 (range: 190 – 513) ha when using 95% AKDE. All 6 individuals showed marked site fidelity, with large overlaps between the bi-monthly home ranges and distances < 1 km between the nests of consecutive years (Fig. 3).

Table 2 Estimates and credible intervals [CrI] of the fixed and random effects included in four models explaining variation in the logarithm of bi-monthly white-backed woodpecker home range size (calculated with 95% kernel density estimation) in Central Europe. Values are based on the top-ranked models with home range size based on a) 95% kernel density estimation (KDE) and b) autocorrelated kernel density estimation (AKDE); and on the highest-ranked models including body weight and sex with home range size based on c) KDE and d) AKDE, respectively. Season was used as an ordered factor; hence the intercept is an estimate for the mean of the season-means, and the polynomials represent corresponding trends. Trackdays = number of days on which the individual was tracked, weight = body weight, day_captured = day of the year on which the individual was captured, signal = proportion of unsuccessful location attempts. $n = 115$.

Variable	Estimate [CrI]			
	a) KDE	b) AKDE	c) KDE	d) AKDE
Fixed effects				
Intercept	3.86 [3.44;4.25]	4.81 [4.35;5.24]	3.77 [3.33;4.19]	4.7 [4.18;5.21]
season linear	0.65 [0.30;1.03]	0.86 [0.33;1.39]	0.78 [0.40;1.18]	1.02 [0.46;1.61]
season^2	-0.10 [-0.44;0.24]	-0.18 [-0.7;0.34]	-0.08 [-0.43;0.28]	-0.14 [-0.67;0.38]
season^3	-0.26 [-0.55;0.02]	-0.46 [-0.91;-0.02]	-0.29 [-0.60;0.00]	-0.52 [-0.98;-0.08]
season^4	0.13 [-0.16;0.41]	0.37 [-0.04;0.8]	0.11 [-0.18;0.39]	0.35 [-0.08;0.78]
season^5	-0.13 [-0.45;0.21]	-0.19 [-0.68;0.3]	-0.08 [-0.42;0.25]	-0.13 [-0.63;0.38]
trackdays	0.13 [0.02;0.23]	0.07 [-0.09;0.23]	0.14 [0.03;0.25]	0.09 [-0.07;0.25]
weight	-	-	-0.11 [-0.23;0.01]	-0.14 [-0.3;0.03]
day_captured	-	-	-0.04 [-0.17;0.10]	-0.05 [-0.24;0.14]
sex (male)	-	-	0.18 [-0.11;0.48]	0.23 [-0.17;0.64]
signal	-	-	0.08 [-0.04;0.19]	0.12 [-0.05;0.29]
Random effects				
Variance ind	0.04 [0.00;0.14]	0.04 [0;0.21]	0.04 [0;0.15]	0.04 [0;0.22]
Variance year	0.06 [0.00;0.59]	0.07 [0;0.9]	0.07 [0.01;0.66]	0.07 [0;0.87]
Residual variance	0.25 [0.18;0.35]	0.59 [0.44;0.79]	0.25 [0.18;0.35]	0.59 [0.44;0.79]

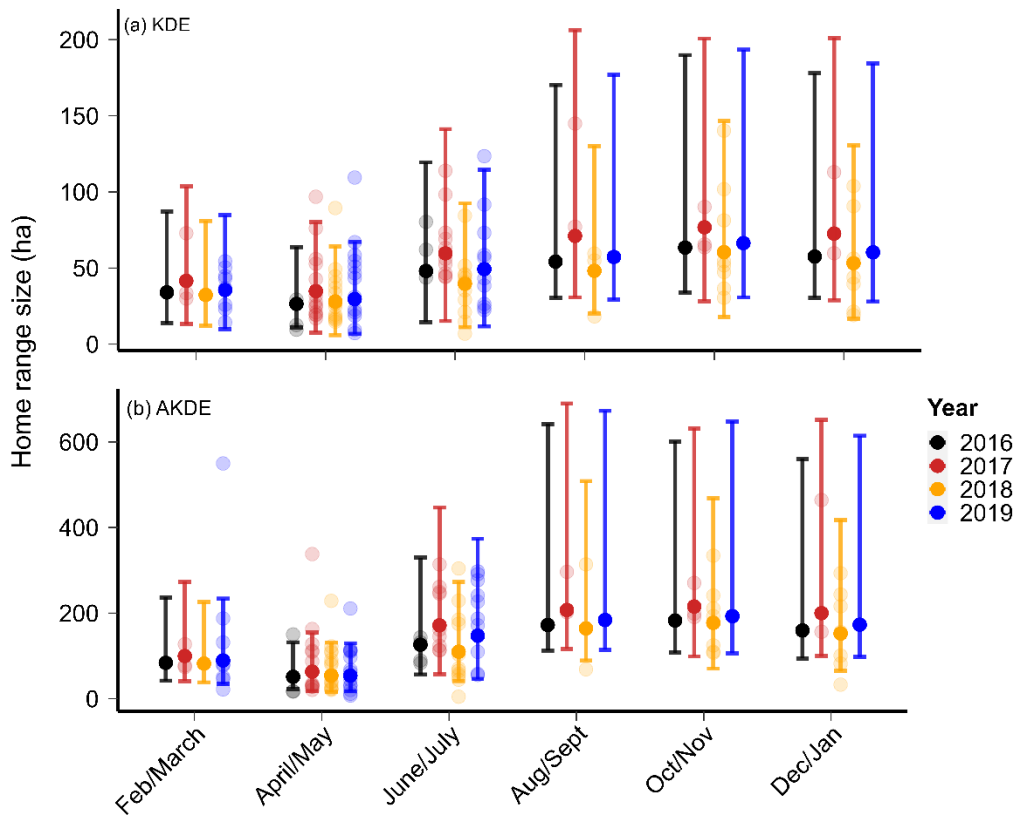


Figure 2 Predicted median bi-monthly home range sizes (with 95% credible intervals) of radio-tracked white-backed woodpeckers per year after accounting for number of tracking days and individual ID ($n = 115$). Home ranges were estimated with (a) kernel density estimation (KDE) and (b) autocorrelated kernel density estimation (AKDE) based on data collected in Central Europe between 2016 and 2019.

Table 3 Bi-monthly home range sizes (ha) of radio-tracked white-backed woodpeckers in Central Europe. Shown are predicted median home range sizes and 95% credible intervals after accounting for individual ID, sampling intensity, and year; mean home range sizes (\pm standard deviation) calculated from the raw data; and sample sizes (n). Home range sizes were calculated based on 95% kernel density estimation (KDE), 95% autocorrelated kernel density estimation (AKDE), and 100% minimum convex polygons (MCP).

Season	Predicted KDE	Raw data KDE	Predicted AKDE	Raw data AKDE	Raw data MCP	n
Feb/March	35.1 [21.7;55.6]	39 \pm 16.5	87.9 [46.2;158.1]	129.4 \pm 146.8	65.6 \pm 22.6	11
April/May	29.6 [20.0;43.2]	36.1 \pm 23.6	55.0 [33.2;86.2]	78.3 \pm 66.5	61.4 \pm 40.4	44
June/July	48.2 [32.9;70.4]	53.5 \pm 26.7	135.7 [81.9;215.5]	194.1 \pm 228.9	95.5 \pm 48.8	35
Aug/Sept	55.4 [30.7;98.7]	70.9 \pm 46.6	169.5 [72.9;378.8]	208.9 \pm 100.6	127.9 \pm 57.2	5
Oct/Nov	66.6 [41.3;106.8]	69.4 \pm 32.1	183.8 [96.4;343.1]	196.4 \pm 69	117.5 \pm 52.7	11
Dec/Jan	60.7 [36.7;99.9]	60.8 \pm 34.5	163.8 [80.4;322.4]	193.8 \pm 130.3	97.8 \pm 45.4	9

Table 4 Bi-monthly home range sizes (ha) of male and female white-backed woodpeckers radio-tracked in Central Europe. Shown are predicted home range sizes and credible intervals based on 95% kernel density estimation (KDE) and 95% autocorrelated kernel density estimation (AKDE) after accounting for body weight, individual ID, year, and sampling quality (number of tracking days and proportion of unsuccessful location attempts); mean 100% Minimum Convex Polygon (MCP) home range sizes (\pm standard deviation) calculated from the raw data; and sample sizes (n) for males (m) and females (f).

Season	m (KDE)	f (KDE)	m (AKDE)	f (AKDE)	m (MCP)	f (MCP)	n (m/f)
Feb/March	36.7 [21.9;58.3]	30.7 [17.3;51.4]	92.6 [48.1;173.5]	74.1 [35.2;151.7]	64.8 \pm 23.7	73.7	10/1
April/May	31.1 [20.6;45.1]	26 [16.6;39.2]	58.3 [35.1;93.9]	46.6 [27.1;78.6]	63.2 \pm 41.5	57 \pm 39	31/13
June/July	49 [32.5;71.6]	40.9 [25.7;62.5]	137.6 [83;221.7]	109.9 [62.2;189]	92.8 \pm 52.5	103.3 \pm 37.5	26/9
Aug/Sept	62.4 [34.6;111.7]	52.2 [28.3;95.2]	200.3 [87;449.7]	160.1 [67.2;375.2]	113.9 \pm 55.2	184.1	4/1
Oct/Nov	76.9 [45.3;128.7]	64.3 [36.7;108.8]	224 [113.2;438.8]	179.1 [87.4;363.7]	103 \pm 38.9	156.4 \pm 74.1	8/3
Dec/Jan	70.7 [41.3;121.2]	59.1 [33.7;102.5]	203.1 [101.2;411]	162.4 [76.7;344.1]	109.8 \pm 41.8	55.9 \pm 38.9	7/2

Discussion

Based on data of 49 radio-tracked individuals, we provide the first estimates for seasonal and total home range sizes of the nominate subspecies of the white-backed woodpecker. Home range size varied between seasons, being smallest in February/March (35 ha; to facilitate comparisons with previous studies, we refer to predicted home range sizes based on KDE in this paragraph), when the birds defend their future breeding territories, and in April/May (30 ha), which corresponds to the breeding season. These relatively small home ranges are likely due to the energetic costs of defending a territory and moving far away from the nest tree during the nestling period. Bi-monthly home ranges during the rest of the year were approximately twice the size (48 – 67 ha) of the above mentioned seasons. Contrary to our expectations, winter home ranges were not larger than those in summer and fall, although in our study area, logs (which serve as foraging substrate) are usually covered with snow during winter and the availability of surface-living arthropods is low. One reason for the similar home range sizes despite the presumably reduced food availability in winter could be that white-backed woodpeckers extend their home range in summer and fall to explore the forest; hence, the habitat could be used more efficiently in winter. Moreover, home range size might be constrained by the presence of territoriality also in winter. The seasonal home ranges of neighboring individuals usually did not overlap (we even hardly ever observed overlaps of home ranges between neighboring individuals which were tracked in different seasons or years, unpublished data), which suggests territoriality throughout the year.

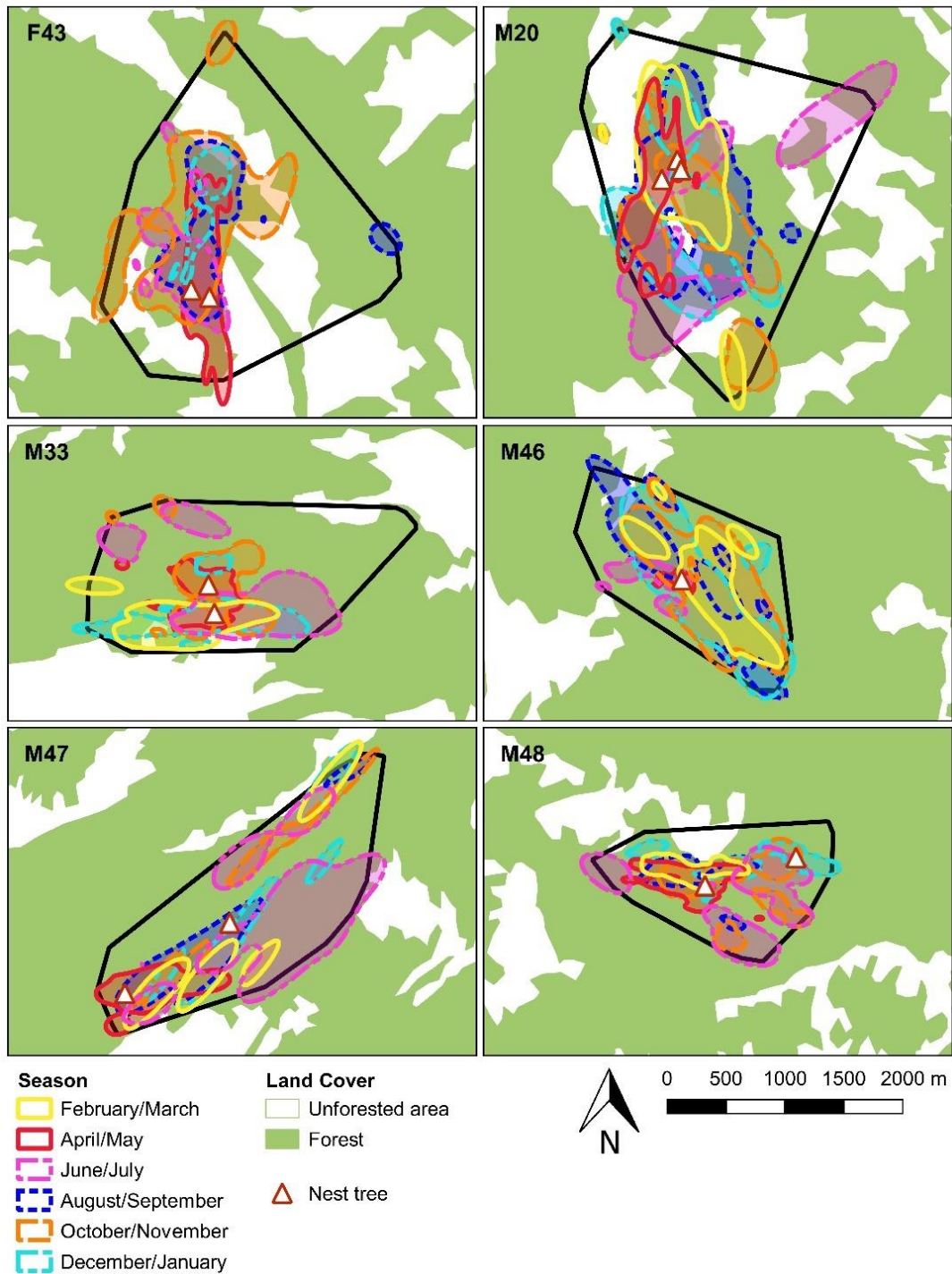


Figure 3 Seasonal home ranges (based on 95% kernel density estimation) of 6 white-backed woodpeckers (1 female, 5 males) that were radio-tracked in Central Europe between 2016 and 2019 for at least one year. For the sake of clarity, only one home range per season was plotted for each individual. For individuals that were tracked during 2 or 3 breeding seasons, all nest trees are shown. Black polygons are the 100% minimum convex polygons calculated with all telemetry locations of each individual. Tracking durations of the individuals are shown in Fig. 1. Data on forest cover: © European Environment Agency 2019, CORINE Land Cover (CLC) 2018.

Our study adds to previous research on seasonal variation in home range size of woodpeckers, all of which that we are aware of also addressed resident insectivorous species (we considered only studies including more than two seasons). The ratios for seasonal differences in pre-breeding, breeding, and post-breeding home range size of three-toed woodpeckers (*Picooides tridactylus*; Pechacek, 2004) and in winter, pre-breeding, and breeding home range size of middle spotted woodpeckers (*Dendrocoptes medius*; Pasinelli et al., 2001) were similar as in our study. By contrast, lesser spotted (*Dendrocopos minor*; Höntschi, 2004; Wiklander et al., 2001) and gray headed woodpeckers (*Picus canus*; Rolstad and Rolstad, 1995) had massively larger home ranges in winter than during breeding. Both middle-spotted and lesser spotted woodpeckers did not appear to be territorial in winter (Pasinelli et al., 2001; Wiklander et al., 2001). Hence, the hypothesis that territorial behavior restricts winter home range size does at least not seem to generally apply to woodpeckers. Another explanation for the species-specific ratios in seasonal home range sizes could be seasonal shifts in some of these species' diet and foraging behavior. However, all three species for which data on winter home range size was available exhibit such seasonal shifts to some degree (Olsson et al., 1999; Pettersson, 1983; Rolstad and Rolstad, 1995), whereas white-backed woodpeckers in our study population were strongly bound to deadwood throughout the year (Chapter 3; however seasonal differences in the white-backed woodpecker's diet have not yet been studied).

Home ranges tended to be largest in 2017 and smallest in 2016 and 2019 in all seasons, but the predicted home ranges sizes per season and year based on our model were associated with high uncertainty due to the small sample sizes. However, our raw data of all individuals that were tracked in the same season of two different years ($n = 8$ seasonal home ranges of 6 individuals) are in accordance with this trend: Individuals that were tracked both in 2017 and 2018 had 1.6 and 3.3 times larger April/May KDE home ranges ($n = 2$) and 2.5 and 8.1 times larger June/July KDE home ranges ($n = 2$) in 2017 than in 2018. Similarly, individuals that were tracked both in 2018 and 2019 had 2.2 to 2.7 times larger April/May KDE home ranges ($n = 3$) and 1.9 times larger June/July KDE home ranges ($n = 1$) in 2018 than in 2019. These relatively large differences in home range size between the years even within individuals show that it can be important to consider multiple years to obtain representative home range estimates. In our study population, these differences were possibly related to differences in food availability. Both 2018 and 2019 (we do not discuss 2016 here because of the very low sample size in this year) were years with hot summers and massive bark beetle (*Ips typographus*) outbreaks (Stroheker et al., 2020). Although white-backed woodpeckers are known to feed mainly on large insect larvae such as those of Cerambycidae or Buprestidae (Glutz von Blotzheim and Bauer, 1994), the comparatively small larvae of bark beetles could provide additional food and allow white-backed

woodpeckers to find enough food in smaller areas. Moreover, the warm temperatures in these two years might have also benefited other saproxylic beetles.

Total annual home ranges were much larger than those during the bi-monthly time periods, because the bi-monthly home ranges of an individual overlapped only partly (see Fig. 3 for examples). The mean total home range size of six individuals tracked in all seasons was 116 ha, which is consistent with previous territory mapping-based estimates of the species' area requirements in Central Europe (Frank and Hochebner, 2001; Scherzinger, 1982; Wesołowski, 1995). In contrast, the home ranges in our study area were much smaller than in Norway, where Stenberg (1990) estimated breeding territory size at 70 – 150 ha (based on observations of color-banded individuals) and movements over 2 – 4 km prior to breeding appeared normal, and in Spain, where breeding and post-breeding KDE home ranges of the subspecies *lilfordi* had a size of 300 ha (Campion et al., 2020). That breeding home ranges of *D. l. lilfordi* were 10 times larger than those of the nominate subspecies in our study area might at least partly be due to the lower availability of deadwood in the Spanish Pyrenees (Campion et al., 2020). Moreover, the two subspecies have been shown to strongly differ in their genetics (Pons et al., 2021) and morphology (Glutz von Blotzheim and Bauer, 1994) and also appear to exhibit different habitat preferences (Grangé, 2015). Differences in the home range sizes of the subspecies might be a result of these morphological and ecological differences.

Our seasonal and total home range sizes mentioned above probably underestimate the true home range sizes as shown by markedly larger home range sizes when accounting for autocorrelation between the locations. AKDE has been shown to provide larger but more reliable home range estimates than conventional KDE or MCPs. For instance, Noonan et al. (2019) demonstrated by using cross validation that KDE failed to predict future space use, whereas vacant areas of the larger AKDE home ranges became occupied over time. This underestimation of home range size with traditional KDE appears to be particularly pronounced when effective sample sizes (which can be interpreted as the number of home range crossings that occurred during the observation period) are low; in the study by Noonan et al. (2019), AKDE performed substantially better than KDE when effective sample sizes were lower than 32 (mean effective sample size \pm SD in our study was 16 ± 8). Indeed, our KDE home ranges conformed very closely to the recorded locations, and movements outside the boundary of the KDE home range and underestimated home range sizes using this method are therefore likely. By contrast, we believe that AKDE overestimated home range size in our study area. For instance, the AKDE home ranges of some individuals included unforested areas or overlapped with those of neighboring individuals, although we hardly ever recorded locations outside forested areas or within the MCP or KDE home range of another white-backed woodpecker. Although this positive bias is assumed to be

less influential than the negative bias caused by unmodelled autocorrelation (Silva et al., 2022), we suggest that ranges (30 - 55 ha to 67 – 184 ha for bi-monthly and 116 to 350 ha for total home range sizes) instead of single values should be considered as the mean area requirements of the white-backed woodpecker in our study area.

Sex was not included in the top-ranked model, and according to a marginally lower-ranked model including sex, home ranges of males were only slightly larger than those of females (Table 2 and Table 4). By contrast, breeding home range sizes of *D. l. lilfordi* were almost twice as large for males as for females (Campion et al., 2020; differences were less pronounced in the post-breeding season and for both seasons combined). However, our finding is in accordance with results from studies on other woodpecker species with comparable mating systems, i.e., in which both sexes defend a common breeding territory, incubate the eggs, and feed the nestlings. For example, no or only small differences in seasonal home range sizes between the sexes have been reported for the three-toed woodpecker (Pechacek, 2004), middle spotted woodpecker (Pasinelli et al., 2001), white-headed woodpecker *Picoides albolarvatus* (Lorenz et al., 2015), black-backed woodpecker *Picoides arcticus* (Tingley et al., 2014), northern flicker *Colaptes auratus* (Elchuk and Wiebe, 2003) and lesser spotted woodpecker (Höntschi, 2004; Wiklander et al., 2001).

Conclusions

The marked differences across seasonal home range sizes and between seasonal and total home range sizes highlight the importance of considering the full annual cycle when addressing the area requirements of white-backed woodpeckers and probably also other species. Importantly, the calculated home range sizes also greatly depended on the used home range estimator, which shows that using multiple methods may be useful to obtain results that are both comparable with those of other studies and capture the range in which the true home range size is likely to be. For the conservation of the white-backed woodpecker, we conclude that at least 116 to 350 ha of forest should be present for one breeding pair.

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References

Aulén, G., 1988. Ecology and distribution of the white-backed woodpecker *Dendrocopos leucotos* in Sweden (Dissertation). Swedish University of Agricultural Sciences, Uppsala.

Bell, D., Hjältén, J., Nilsson, C., Jørgensen, D., Johansson, T., 2015. Forest restoration to attract a putative umbrella species, the white-backed woodpecker, benefited saproxylic beetles. *Ecosphere* 6, 1–14. <https://doi.org/10.1890/ES14-00551.1>

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., Coulson, T., 2006. Effects of sampling regime on the mean and variance of home range size estimates. *J. Anim. Ecol.* 75, 1393–1405. <https://doi.org/10.1111/j.1365-2656.2006.01164.x>

Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24, 346–352. <https://doi.org/10.2307/1374834>

Calabrese, J.M., Fleming, C.H., Gurarie, E., 2016. ctm: an r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol. Evol.* 7, 1124–1132. <https://doi.org/10.1111/2041-210X.12559>

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 Ornithol.* 55, 77–87. <https://doi.org/10.3161/00016454AO2020.55.1.008>

Chundawat, R.S., Sharma, K., Gogate, N., Malik, P.K., Vanak, A.T., 2016. Size matters: scale mismatch between space use patterns of tigers and protected area size in a tropical dry forest. *Biol. Conserv.* 197, 146–153. <https://doi.org/10.1016/j.biocon.2016.03.004>

Czeszczewik, D., Walankiewicz, W., 2006. Logging affects the white-backed woodpecker *Dendrocopos leucotos* distribution in the Białowieza Forest. *Ann. Zool. Fenn.* 43, 221–227.

Desy, E.A., Batzli, G.O., Liu, J., 1990. Effects of food and predation on behaviour of prairie voles: a field experiment. *Oikos* 58, 159–168. <https://doi.org/10.2307/3545423>

Elchuk, C.L., Wiebe, K.L., 2003. Home-range size of northern flickers (*Colaptes auratus*) in relation to habitat and parental attributes. *Can. J. Zool.* 81, 954–961. <https://doi.org/10.1139/z03-077>

Fieberg, J., Börger, L., 2012. Could you please phrase “home range” as a question? *J. Mammal.* 93, 890–902. <https://doi.org/10.1644/11-MAMM-S-172.1>

- Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., Calabrese, J.M., 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* 96, 1182–1188. <https://doi.org/10.1890/14-2010.1>
- Frank, G., Hochebner, T., 2001. Erfassung der Spechte - insbesondere des Weißrückenspechtes *Picoides leucotos* - im Rhmen des LIFE-Projektes Wildnisgebiet Dürrenstein. in: LIFE- Projekt Wildnisgebiet Dürrenstein. Amt der Niederösterreichischen Landesregierung (Ed.). Amt der Niederösterreichischen Landesregierung, St. Pölten.
- Furnas, B.J., Landers, R.H., Callas, R.L., Matthews, S.M., 2017. Estimating population size of fishers (*Pekania pennanti*) using camera stations and auxiliary data on home range size. *Ecosphere* 8, e01747. <https://doi.org/10.1002/ecs2.1747>
- Gärdenfors, U., 2010. Rödlistade arter i Sverige 2010 - The 2010 Red List of Swedish Species. ArtDatabanken, SLU, Uppsala.
- Glutz von Blotzheim, U.N., Bauer, K., 1994. Handbuch der Vögel Mitteleuropas. Band 9: *Columbiformes* - *Piciformes*, 2nd ed. Aula-Verlag, Wiesbaden.
- Goodrich, B., Gabry, J., Ali, I., Brilleman, S., 2020. "rstanarm: Bayesian applied regression modeling via Stan." R package version 2.19.3, <https://mc-stan.org/rstanarm>.
- Grangé, J.-L., 2015. Breeding biology of the Lilford woodpecker *Dendrocopos leucotos lilfordi* in the Western Pyrenees (SW France). *Denisia* 36, 99–111.
- Grigione, M.M., Beier, P., Hopkins, R.A., Neal, D., Padley, W.D., Schonewald, C.M., Johnson, M.L., 2002. Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). *Anim. Conserv.* 5, 317–324. <https://doi.org/10.1017/S1367943002004079>
- Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B., Andersen, R., 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *J. Zool.* 265, 63–71. <https://doi.org/10.1017/S0952836904006053>
- Höntschi, K., 2004. Der Kleinspecht (*Picoides minor*): Autökologie einer bestandsbedrohten Vogelart im hessischen Vordertaunus (Dissertation). Johann Wolfgang Goethe-Universität, Frankfurt am Main.
- Kenward, R.E., 2001. A manual for wildlife radio tagging, 2nd ed. Academic Press, New York.
- Knaus, P., Antoniazza, S., Keller, V., Sattler, T., Schmid, H., Strebel, N., 2021. Rote Liste der Brutvögel. Gefährdete Arten der Schweiz. Bundesamt für Umwelt (BAFU); Schweizerische Vogelwarte. Umwelt-Vollzug Nr. 2124.

Kreiner, D., Maringer, A., Zechner, L., 2012. ECONNECT - Improving connectivity in the Alps: implementation in the pilot region Northern Limestone Alps. *Ecomont J. Prot. Mt. Areas Res.* 4, 41–46. <https://doi.org/10.1553/eco.mont-4-1s41>

Lenz, J., Böhning-Gaese, K., Fiedler, W., Mueller, T., 2015. Nomadism and seasonal range expansion in a large frugivorous bird. *Ecography* 38, 54–62. <https://doi.org/10.1111/ecog.00522>

Lorenz, T.J., Vierling, K.T., Kozma, J.M., Millard, J.E., Raphael, M.G., 2015. Space use by white-headed woodpeckers and selection for recent forest disturbances. *J. Wildl. Manag.* 79, 1286–1297. <https://doi.org/10.1002/jwmg.957>

Marneweck, C., Marneweck, D.G., Schalkwyk, O.L. van, Beverley, G., Davies-Mostert, H.T., Parker, D.M., 2019. Spatial partitioning by a subordinate carnivore is mediated by conspecific overlap. *Oecologia* 191, 531–540. <https://doi.org/10.1007/s00442-019-04512-y>

McLoughlin, P.D., Ferguson, S.H., 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Écoscience* 7, 123–130.

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J.D.C., Nicoloso, S., Sustr, P., Urbano, F., Mysterud, A., 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *J. Anim. Ecol.* 82, 1326–1339. <https://doi.org/10.1111/1365-2656.12105>

Noonan, M.J., Tucker, M.A., Fleming, C.H., Akre, T.S., Alberts, S.C., Ali, A.H., Altmann, J., Antunes, P.C., Belant, J.L., Beyer, D., Blaum, N., Böhning-Gaese, K., Cullen Jr., L., de Paula, R.C., Dekker, J., Drescher-Lehman, J., Farwig, N., Fichtel, C., Fischer, C., Ford, A.T., Goheen, J.R., Janssen, R., Jeltsch, F., Kauffman, M., Kappeler, P.M., Koch, F., LaPoint, S., Markham, A.C., Medici, E.P., Morato, R.G., Nathan, R., Oliveira-Santos, L.G.R., Olson, K.A., Patterson, B.D., Paviolo, A., Ramalho, E.E., Rösner, S., Schabo, D.G., Selva, N., Sergiel, A., Xavier da Silva, M., Spiegel, O., Thompson, P., Ullmann, W., Zięba, F., Zwijacz-Kozica, T., Fagan, W.F., Mueller, T., Calabrese, J.M., 2019. A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecol. Monogr.* 89, e01344. <https://doi.org/10.1002/ecm.1344>

Olsson, O., Wiktander, U., Holmgren, N.M.A., Nilsson, S.G., 1999. Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. *Oikos* 87, 264–276. <https://doi.org/10.2307/3546741>

Pasinelli, G., Hegelbach, J., Reyer, H.-U., 2001. Spacing behavior of the middle spotted woodpecker in central Europe. *J. Wildl. Manag.* 65, 432–441. <https://doi.org/10.2307/3803095>

- Pechacek, P., 2004. Spacing behavior of Eurasian three-toed woodpeckers (*Picoides tridactylus*) during the breeding season in Germany. *The Auk* 121, 58–67. <https://doi.org/10.1093/auk/121.1.58>
- Pettersson, B., 1983. Foraging behaviour of the middle spotted woodpecker *Dendrocopos medius* in Sweden. *Ecography* 6, 263–269. <https://doi.org/10.1111/j.1600-0587.1983.tb01090.x>
- Pons, J.-M., Campión, D., Chiozzi, G., Ettwein, A., Grangé, J.-L., Kajtoch, Ł., Mazgajski, T.D., Rakovic, M., Winkler, H., Fuchs, J., 2021. Phylogeography of a widespread Palaearctic forest bird species: The white-backed woodpecker (Aves, Picidae). *Zool. Scr.* 50, 155–172. <https://doi.org/10.1111/zsc.12466>
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ramsey, D.S.L., Caley, P.A., Robley, A., 2015. Estimating population density from presence–absence data using a spatially explicit model. *J. Wildl. Manag.* 79, 491–499. <https://doi.org/10.1002/jwmg.851>
- Rolstad, J., Rolstad, E., 1995. Seasonal patterns in home range and habitat use of the greyheaded woodpecker *Picus canus* as influenced by the availability of food. *Ornis Fenn.* 72, 1–13.
- Ryslavy, T., Bauer, H.-G., Gerlach, B., Hüppop, O., Stahmer, J., Südbeck, P., Sudfeldt, C., 2020. Rote Liste der Brutvögel Deutschlands, 6. Fassung. *Ber Vogelschutz* 57, 13–112.
- Scherzinger, W., 1982. Die Spechte im Nationalpark Bayerischer Wald. Nationalparkverwaltung Bayerischer Wald, Grafenau.
- Schoepf, I., Schmohl, G., König, B., Pillay, N., Schradin, C., 2015. Manipulation of population density and food availability affects home range sizes of African striped mouse females. *Anim. Behav.* 99, 53–60. <https://doi.org/10.1016/j.anbehav.2014.10.002>
- Shannon, G., Page, B.R., Duffy, K.J., Slotow, R., 2010. The ranging behaviour of a large sexually dimorphic herbivore in response to seasonal and annual environmental variation. *Austral Ecol.* 35, 731–742. <https://doi.org/10.1111/j.1442-9993.2009.02080.x>
- Silva, I., Fleming, C.H., Noonan, M.J., Alston, J., Folta, C., Fagan, W.F., Calabrese, J.M., 2022. Autocorrelation-informed home range estimation: A review and practical guide. *Methods Ecol. Evol.* 13, 534–544. <https://doi.org/10.1111/2041-210X.13786>
- Stenberg, I., 1990. Preliminary results of a study on woodpeckers in More and Romsdal Country, western Norway, in: Carlson, A, Aulén, G. (Eds): Conservation and Management of Woodpecker Populations. Report 17, Uppsala. Departement of Wildlife Ecology, Swedish University of Agricultural Sciences, Uppsala, pp. 67–79.

Stenberg, I., Hogstad, O., 2004. Sexual dimorphism in relation to winter foraging in the white-backed woodpecker (*Dendrocopos leucotos*). J. Ornithol. 145, 321–326. <https://doi.org/10.1007/s10336-004-0045-6>

Stroheker, S., Forster, B., Queloz, V., 2020. Zweithöchster je registrierter Buchdruckbefall (*Ips typographus*) in der Schweiz. Waldschutz Aktuell 1/2020.

Tingley, M.W., Wilkerson, R.L., Bond, M.L., Howell, C.A., Siegel, R.B., 2014. Variation in home-range size of black-backed woodpeckers. Condor 116, 325–340. <https://doi.org/10.1650/CONDOR-13-140.1>

Vehtari, A., Gabry, J., Yao, Y., Gelman, A., 2019. loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models." R package version 2.1.0, <https://CRAN.R-project.org/package=loo>.

Wesołowski, T., 1995. Ecology and behaviour of white-backed woodpecker (*Dendrocopos leucotos*) in a primeval temperate forest (Białowieża National Park, Poland). Vogelwarte 38, 61–75.

Wiktander, U., Olsson, O., Nilsson, S.G., 2001. Seasonal variation in home-range size, and habitat area requirement of the lesser spotted woodpecker (*Dendrocopos minor*) in southern Sweden. Biol. Conserv. 100, 387–395. [https://doi.org/10.1016/S0006-3207\(01\)00045-3](https://doi.org/10.1016/S0006-3207(01)00045-3)

Chapter 2

Home range size of the white-backed woodpecker in relation to resource distribution, habitat availability, and intraspecific competition

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Abstract

Understanding the factors driving variation in home range size is fundamental for understanding the distribution and abundance of animals and ultimately for their conservation. We investigated variation in home range size of the white-backed woodpecker (*Dendrocopos leucotos*), a species dependent on old-growth structures, in Central European forests varying in management intensity. Specifically, we used data from woodpeckers radio-tracked between 2016 and 2019 to test predictions of three hypotheses proposed to explain variation in home range size. We found support for the resource distribution and intraspecific competition hypotheses in the breeding season, whereas none of the hypotheses explained post-breeding home range size. In the breeding season, home range size decreased with increasing proportion of resource-rich habitat, particularly when forest cover was low. Moreover, breeding home range size decreased with increasing population density when the proportion of resource-rich habitat was high. These results suggest that the mechanisms determining breeding home range size varied with habitat quality in the landscape. In regions with low forest cover and presumably generally low habitat quality, home range size appeared to be influenced by the distribution of resources. By contrast, in areas with high resource abundance and thus high population density, home range size seemed to be regulated by intraspecific competition. To improve habitat quality for the white-backed woodpecker, deadwood and old trees should ideally be clumped within stands with little or no forest management. These resource-rich forests should constitute a high proportion of areas at least the size of a breeding home range and are particularly important in regions with low forest cover.

Introduction

Many animals restrict their movements to fairly well-defined areas, their home ranges, instead of wandering randomly (Powell, 2000). Knowing the factors driving variation in home range size is fundamental for understanding the distribution and abundance of animals and ultimately for their conservation. The home range size of individuals of a species can vary substantially within a population; this variation can be related to both intrinsic factors, e.g., reproductive status (van Beest et al., 2011) or age (Börger et al., 2006), and extrinsic factors.

Several hypotheses have been proposed to explain the relationships between home range size and extrinsic factors. According to the *resource distribution hypothesis*, the spatial distribution of food and other resources shapes an individual's movement patterns (Marable et al., 2012; McClintic et al., 2014). As individuals attempt to maximize energy efficiency by using small areas in habitats with high food abundance, home ranges are expected to be small in areas with aggregated resources and large in areas with spatially dispersed resources. Habitat loss and fragmentation typically lead to a reduction and break-up of habitat and thus to an increasingly discontinuous resource distribution, which may lead to increased home range sizes in landscapes with low forest cover. However, according to the *restricted habitat availability hypothesis*, the opposite effect may also be possible, e.g., when a landscape contains so little habitat that the distance between patches exceeds a species' gap-crossing tolerance (Desrochers and Hannon, 1997), and movements are therefore restricted by the surrounding matrix (Hinam and St. Clair, 2008). Hence, low habitat availability in the landscape would result in large home ranges according to the resource distribution hypothesis and in small home ranges according to the restricted habitat availability hypothesis. Moreover, the *intraspecific competition hypothesis* suggests that home range sizes of territorial species are restricted by the energetic costs of defending a territory, resulting in small territories at high population densities (Krebs, 1971; Sillett et al., 2004).

In the present study, we investigated variation in home range size in the white-backed woodpecker (*Dendrocopos leucotos*) in Central European forests varying in management intensity. The species is a food specialist that mainly feeds on larvae of wood-boring insects. Hence, it requires high amounts of deadwood and is usually found in old forest stands with low management intensity or in primeval forests (e.g., Aulén, 1988; Czeszczewik and Walankiewicz, 2006; Scherzinger, 1982). The species is distributed over the entire Palearctic (BirdLife International, 2022), with two subspecies occurring in Europe: the nominate subspecies *D. l. leucotos* (addressed in the present study) in North, East and Central Europe and *D. l. lilfordi* in South and Southeast Europe (Winkler and Christie, 2002). Because of its large range and population size, the white-backed woodpecker is globally categorized as Least Concern according to the IUCN Red List of Threatened Species (BirdLife International, 2022). However,

the species has suffered a massive range contraction due to deforestation and forest management in the last centuries (Glutz von Blotzheim and Bauer, 1994; Tomiałoć, 2000) and is of high conservation concern in Europe (listed in Annex 1 of the European Union's Birds Directive and considered threatened in various national red lists). The knowledge about the white-backed woodpecker's home range size is still incomplete as it is mainly based on territory mapping and observations of color-banded individuals (Stenberg, 1990; Wesołowski, 1995) or on the subspecies *D.l.lilfordi* (Campion et al., 2020). In Chapter 1, we found that home range sizes of radio-tracked white-backed woodpeckers in the study area varied seasonally and ranged, depending on the used home range estimator, from on average 30 – 55 ha in spring to 67 – 184 ha in fall. Moreover, seasonal home range sizes did not differ between the sexes. However, the factors driving variation in seasonal home range size are unknown.

Given that the white-backed woodpecker is dependent on deadwood, a scarce resource in most landscapes with human impact, an obligate forest species, and territorial at least in parts of the year (Glutz von Blotzheim and Bauer, 1994), the white-backed woodpecker is a well-suited model species for testing the hypotheses mentioned above aiming to explain variation in home range size. The aims of the present study were 1) to evaluate which hypotheses describing effects of extrinsic factors best explain home range size during the breeding and post-breeding seasons and 2) to suggest conservation measures based on the results of the study. For evaluating the hypotheses, we examined the following predictions. According to the *resource distribution hypothesis*, home range sizes would increase with increasing resource dispersion, i.e., with decreasing proportion of high-quality habitat, increasing distances between high-quality patches, and decreasing abundance of resources in close vicinity to the nest tree, whereas the mean density of resources would have little effect. Moreover, home range size would increase with decreasing amount of habitat in the landscape, i.e., with decreasing forest area and increasing forest edge length. By contrast, the *restricted habitat availability hypothesis* proposes that if movements were restricted by the surrounding inhospitable area, home range sizes would decrease with decreasing forest area. Lastly, the *intraspecific competition hypothesis* suggests that home range size would decrease with increasing population density.

Methods

Study area

We conducted the study in western Austria (state Vorarlberg), eastern Switzerland (St. Galler Rheintal and Prättigau) and the Principality of Liechtenstein in an area of approximately 2000 km². The region is characterized by mountainous terrain (elevation 400 – 3000 m above sea level), which leads to large variation in mean annual temperature (0 - 10° Celsius) and precipitation (1200 – 2700 mm; Auer et al. 2001). The study region has a temperate continental climate with 4 distinct seasons: spring (March –

May), summer (June – August), fall (September – November), and winter (December – February). Human settlements and agricultural land are mostly restricted to the valley bottoms, while steeper slopes are typically covered with forest. The occurrence of white-backed woodpeckers in the study area is strongly linked to European beech (*Fagus sylvatica*), the dominating deciduous tree species, which was mainly found in mixed stands dominated by Norway spruce (*Picea abies*), European beech, and silver fir (*Abies alba*) up to approximately 1300 m above sea level. Due to the heterogeneous terrain and many private landowners, the study region comprises forests of different structures and management intensities. Easily accessible stands are often managed intensively, as opposed to stands at remote or steep locations. Similarly, the proportion of forest cover varies, ranging from completely deforested areas in the bottoms of larger valleys to large continuous forests along steep slopes.

Radio telemetry

Between 2016 and 2019, 62 adult white-backed woodpeckers (40 males, 22 females) were captured and fitted with very high frequency (VHF) transmitters as described in Chapter 1. Each tagged woodpecker was tracked twice a week during a two- and a four-hours session, in which the woodpecker's location and its accuracy (estimated as the radius of the circle in which the woodpecker was assumed to be) was recorded every 15 minutes (see Chapter 1 for details). The woodpeckers were tracked until the battery of the transmitter died after nine months or until the transmitter was lost. As only few individuals were tracked in fall and winter, we restricted our analyses to the breeding season in April and May and the post-breeding season in June and July.

Home range estimation

We computed seasonal (breeding season/post-breeding season) home ranges for each individual in R 3.4.0 (R Core Team, 2019). We defined 'breeding season' as time between egg laying and fledging and 'post-breeding season' as the 39 days after fledging because 39 days was the mean time we observed the fledglings following the adults before becoming fully independent. For breeding home ranges, we only used data from individuals that successfully raised chicks until fledging. We computed home ranges using fixed kernel density estimation (KDE) with a 95% isopleth and the plug-in method for bandwidth selection. Prior to all home range analyses, we discarded locations with accuracy >200 m and locations recorded when a woodpecker was known to be in the breeding cavity.

To select home ranges reliably representing the respective season, we plotted the relationship between home range size and the number of locations per home range (Kenward, 2001) to define a threshold at which home range size stabilized for each season as described in Chapter 1. We then selected all home ranges which either showed an asymptotic area-location relation ($n = 19$ breeding and 15 post-

breeding home ranges) or which did not show a clear asymptote but were calculated with more locations than the threshold ($n = 14$ breeding and 14 post-breeding home ranges). We did not use home ranges with a clear linear area-location relationship for further analyses, regardless of the number of locations used for their calculation, to avoid biased home range sizes. For four individuals, breeding home ranges from two years were available, and we excluded the home range with fewer locations. As we additionally removed three home ranges with unknown population density estimates (see “Local population density”), 27 breeding and 28 post-breeding home ranges were retained for the analyses. Lastly, we computed 100% minimum convex polygons (MCPs) for all retained individual-season combinations as MCPs were necessary to obtain a habitat variable based on remote sensing data (see “Forest structure characteristics”).

Habitat data

Forest structure characteristics

Between 2017 and 2019,, we mapped forest structure characteristics in the field within circular sample plots (radius = 12.6 m, 0.05 ha) situated within the breeding home ranges. The centers of the plots were situated at the intersections of a 200 x 200 m grid within the 95% KDE home ranges (Fig. 1). On average (\pm SD) we mapped 7.4 ± 3.4 plots per home range ($n = 29$ home ranges). Additionally, we mapped five sample plots per nest tree, with the center of one plot being the nest tree and the centers of the four other plots being 100 m from the nest tree in the cardinal directions (Fig. 1). Within the plots, we recorded diameter at breast height (DBH), tree species, and whether dead branches with a diameter ≥ 10 cm were present or not for all live trees with a DBH ≥ 30 cm. Furthermore, we recorded DBH and height of all snags (standing deadwood ≥ 1.3 m height) with a DBH ≥ 5 cm as well as diameter (in the middle) and height and length of all stumps (standing deadwood < 1.3 m height) and logs (lying deadwood > 50 cm length), respectively, with a diameter (in the middle) ≥ 7 cm. We used the formula of a cylinder to calculate the volume of individual snags, logs, and stumps and then calculated their volumes per hectare for each plot. We used the following variables for further analysis (variable names are given in italic): number of live trees and live beech trees with a DBH ≥ 50 cm ha^{-1} (*tree50* and *beech50*), number of trees with dead branches ha^{-1} (*deadbr*), basal area of live trees ha^{-1} (*blive*), basal area of snags ha^{-1} (*bsnag*), number of snags and logs with a DBH ≥ 30 cm ha^{-1} (*snag30* and *log30*), volume of snags and logs in $\text{m}^3 \text{ha}^{-1}$ (*vsnag* and *vlog*) and total deadwood volume in $\text{m}^3 \text{ha}^{-1}$ (including snags, logs, and stumps; *vdw*).

As the effort to map habitat characteristics in the field would have been too high for the large post-breeding home ranges, we also used light detection and ranging (LiDAR) data to characterize forest

structure. First and last return LiDAR data were available as classified point clouds from three datasets, which were all based on flights conducted under leaf-off conditions: one for Vorarlberg (data were from 2017 and had a mean (\pm SD) point density of 59.8 ± 14.4 points m^{-2} within our study sites), one for Liechtenstein and the Canton of St. Gallen (2017; 36.7 ± 15.4 points m^{-2}), and one for the Canton of Grisons (2003; 1.4 ± 0.3 points m^{-2}). 52 of the 55 retained breeding and post-breeding home ranges were located in Vorarlberg, Liechtenstein, and St. Gallen; hence, high-resolution LiDAR data collected during our study period were available for almost all home ranges. We used the lascanopy tool in LAStools (Isenburg, 2019) to compute forest structure characteristics describing vegetation height and vegetation height distribution. These proxies for stand age and within-stand structural complexity, respectively, are likely to be relevant to the white-backed woodpecker, given its preference for old, natural stands (Hogstad and Stenberg, 1994; Scherzinger, 1982). We only considered vegetation points > 1.37 m above the ground and calculated maximum (*max*), mean (*avg*), standard deviation (*std*), mean square (*qav*), and 95% percentile (*p95*) of the height above the ground, the percentage of points in the vegetation layer >30 m above the ground (*vp30*), and skewness (*ske*) and kurtosis (*kur*) of the height distribution within 50x50 m pixels within all 95% KDE and 100% MCP breeding and post-breeding home ranges.

To obtain sets of variables describing different types of resource distribution at the home range level, we processed the field and LiDAR habitat variables (for the sake of simplicity henceforward referred to as 'resources') at the plot (field data) and pixel (LiDAR data) level, respectively, by applying five approaches (Fig. 1). First, we calculated the mean from all sample plots/pixels within the home range for each resource; these means describe the average amount of a resource, but not its spatial distribution. Second, we calculated the proportion of plots/pixels with a high abundance of the resource within the home range for each resource. This type of resource distribution describes whether resources are mainly clumped within high-quality patches (high proportion of plots/pixels with high resource abundance) or occur in low densities across the home range (low proportion of plots/pixels with high resource abundance). We defined the threshold for high abundance as the median calculated from all sample plots/pixels within all home ranges (see Table A.1, Appendix, for all thresholds) and considered all plots/pixels with a resource variable exceeding this threshold to have a high abundance of the respective resource. Two exceptions were the skewness and kurtosis of the LiDAR point height distribution, for which we expected lower values in combination with a large mean vegetation height to be associated with higher habitat quality. Here, we considered a pixel to have a high resource abundance when the mean vegetation height was higher and the skewness/kurtosis lower than the median from all pixels. As third and fourth approaches, we calculated metrics describing the

distribution of plots/pixels with high resource abundance. For field variables, we calculated the mean distance between plots with high resource abundance because the low number of plots per home range did not allow for more sophisticated analyses. For LiDAR variables, we calculated an aggregation index per home range by dividing the number of adjacent pixel pairs with a high abundance of a given resource ('like adjacencies') by the maximum possible number of like adjacencies using FRAGSTATS (McGarigal et al., 2012). Fifth, we calculated the sum of each resource at and around the nest tree from the five nest sample plots as metric describing resource abundance in close vicinity to the nest tree. All sets of variables except for the aggregation index were calculated for 95% KDE home ranges. For the aggregation index, we used 100% MCPs because the index could not be computed when KDE home ranges consisted of two or more polygons. We obtained seven sets of habitat variables for breeding home ranges (four from field data, three from lidar data), and three sets for post-breeding home ranges (only from lidar variables, no field data available). Because of the large number of variables, we performed a principal component analysis (PCA) for each set of variables and used the first two principal components (PCs) for further analyses (Fig. 1). Results of the PCAs are shown in the Appendix (Table A.2 and Table A.3).

Local population density

Local population density (popdens) was represented by the number of territory centers per 100 ha forest in a 2-km buffer around the home range centroid in a given year. The buffer of 2 km was chosen because it encompassed the centers of all territories adjacent to a home range. Territory centers were defined based on our telemetry data ($n = 37$) and on white-backed woodpecker observations made while searching for individuals for capturing ($n = 22$). For radio-tracked individuals, we defined the territory center as the centroid of the breeding ($n = 31$) or, if not available, pre-breeding home range ($n = 6$). When no individual was tagged within a territory, we defined the territory center as the centroid of all observations (five territory centers were based on one observation, 16 on more than two observations) or by the location of the nest tree when the breeding cavity had been found ($n = 1$). We considered only observations between February and June, when white-backed woodpeckers are territorial (Glutz von Blotzheim and Bauer, 1994). If a territory known from other years was not visited in a given year, we considered it occupied for the population density estimation. 13 of the 16 territories with unknown occupancy in a year relevant for further analyses were in the Austrian or Northern Liechtenstein part of the study area, where at least 86% of the territories were occupied in all years we visited the sites (as the species is difficult to detect and our search effort was partly low, the proportion of continuously occupied territories was probably even higher). Hence, it is unlikely that false positives had a large influence on our population density estimates in this part of the study area.

Field data (available for breeding season HRs)				LiDAR data (available for breeding and post-breeding season HRs)			
Var. at plot level	Plots used for calculation	Original Var. at HR level	Final Var. at HR level	Var. at pixel level	Pixels used for calculation	Original Var. at HR level	Final Var. at HR level
tree50 beech50 deadbr blive bsnag snag30 log30 vsnag vlog vdw		mean.tree50 mean.beech50 mean.deadbr mean.blive mean.bsnag mean.snag30 mean.log30 mean.vsnag mean.vlog mean.vdw	PCA pc1.mean pc2.mean	max avg qav std ske kur p95 vp30		mean.max mean.avg mean.qav mean.std mean.ske mean.kur mean.p95 mean.vp30	PCA pc1.l.mean pc2.l.mean
		prop.tree50 prop.beech50 prop.deadbr prop.blive prop.bsnag prop.snag30 prop.log30 prop.vsnag prop.vlog prop.vdw	PCA pc1.prop pc2.prop			prop.max prop.avg prop.qav prop.std prop.ske prop.kur prop.p95 prop.vp30	PCA pc1.l.prop pc2.l.prop
		dist.tree50 dist.beech50 dist.deadbr dist.blive dist.bsnag dist.snag30 dist.log30 dist.vsnag dist.vlog dist.vdw	PCA pc1.dist pc2.dist			ai.max ai.avg ai.qav ai.std ai.ske ai.kur ai.p95 ai.vp30	PCA pc1.l.ai pc2.l.ai
		nest.tree50 nest.beech50 nest.deadbr nest.blive nest.bsnag nest.snag30 nest.log30 nest.vsnag nest.vlog nest.vdw	PCA pc1.nest pc2.nest				

●/○ plot used/plot not used for calculation X nesting tree ■/□ pixel used/pixel not used for calculation

Figure 1 Sampling design for recording habitat data within white-backed woodpecker home ranges (HR) in Central Europe and methods used for producing variables (var.) describing 4 types of resource distribution. Data were collected in the field and with light detection and ranging (LiDAR) data for breeding HRs and with LiDAR data for post-breeding HRs. Field data were mapped within 0.05 ha plots and used to produce variables on deadwood and live trees (tree50/beech50 = number of live trees/live beech trees with diameter at breast height > 50 cm ha⁻¹, deadbr = number of trees with dead branches ha⁻¹, blive/bsnag = basal area (m² ha⁻¹) of live trees/snags, snag30/log30 = number of snags/logs with diameter > 30 cm ha⁻¹, vsnag/vlog/vdw = volume (m³ ha⁻¹) of snags/logs/total deadwood). LiDAR data were processed within 50 x 50 m pixels and used to produce variables describing vegetation height (max/avg/qav/std/p95 = maximum/average/mean square/standard deviation/ 95% percentile of the height above the ground) and vegetation height distribution (ske/kur = skewness/kurtosis). Variables at the plot/pixel level were then used to calculate 7 sets of variables at the HR level and each set of original variables at the HR level was summarized in a principal component analysis (PCA). The first two principal components (PC) of each PCA were used for modeling relationships between HR size and habitat.

In the Swiss part of the study area, which constitutes the subspecies' range edge in Central Europe, only 45% of the territories were occupied in all years we visited the sites. Hence, we did not use home

ranges with uncertain population density estimates located in Switzerland (n = 2 breeding and 1 post-breeding home range) for further analyses.

Forest cover

We extracted the classes 'Broad-leaved forest', 'Coniferous forest', and 'Mixed forest' from CORINE Land Cover data (European Environment Agency 2019, CORINE Land Cover (CLC) 2018, Version 20, Copenhagen, Denmark) and defined the area falling into one of the three classes as forest. We calculated the forested area (*forest*) within a buffer with 750 m radius around each home range centroid. The buffer of 750 m was chosen because it was large enough to include each home range.

Statistical analyses

We modeled home range size using linear mixed effects models in a Bayesian framework with the software Stan via R (R Core Team 2020; package *rstanarm*, Goodrich et al. 2020). We built seven candidate models representing the hypotheses described in the introduction (Table 1). Six of these models included resource variables. To evaluate which type of resource distribution is most relevant for variation in home range size, we ran these six candidate models multiple times, each time with the first two PCs from one of the PCAs summarizing variables describing a specific type of resource distribution (Table 2; see also Table A.4 and Table A.5 in the Appendix).

We analyzed breeding and post-breeding home range size separately by building models and performing model selection for each season. As we tested the same hypotheses for both seasons, we generally used the same model structures for breeding and post-breeding models; however, as habitat data collected in the field were available only for breeding home ranges and resources around the nest tree were assumed to be irrelevant during the post-breeding season, some of the models were only used for breeding season model selection (Table 1). We ran breeding season models representing the resource distribution hypothesis once including only field variables and once including only LiDAR variables. This allowed us to compare the importance of LiDAR variables in explaining breeding home range size versus post-breeding home range size. In total, we ran 46 breeding season models (six models including resource variables multiplied by the seven different resource types from Fig. 1, one model including only *popdens*, one model including only *forest*, one model including *popdens* and *forest*, and a null model including only *year* and *trackdays*, see below) and 22 post-breeding season models (six models including resource variables multiplied by the three LiDAR resource distribution types from Fig. 1, one model including only *popdens*, one model including only *forest*, one model including *popdens* and *forest*, and a null model; Table 1).

To enhance the interpretability of the results, we also fitted models in which we replaced the PCs used in the top-ranked model of each season with their original variables. For this step, we ran models with all possible combinations of the respective original variables with high loadings instead of the PCs (using each original variable either instead of PC1 or PC2, depending on where it had the higher loading; Table A.6, Appendix).

We included a random intercept for *year* in all models. Furthermore, to account for potential effects of data quality on home range size, we included the number of tracking days (*trackdays*) as fixed effects in each candidate model. We centered and scaled all linear predictors prior to the analyses and log-transformed home range size as dependent variable. We used default uninformative priors generated by Stan and four Markovian chains with 3000 iterations after 3000 warm-up iterations for each model, which allowed all chains to converge as indicated by rhat values of 1 and effective sample sizes of > 400 for all coefficients (Vehtari et al., 2021). Finally, we compared all models per season via the leave-one-out-cross-validation information criterion LOOIC (package *loo*, Vehtari et al., 2019), where models with lower LOOIC values are expected to have higher predictive accuracy. For presenting effect sizes of the model parameters, we computed the median and 2.5% and 97.5% quantiles as credible interval (CrI) of the corresponding marginal posterior distribution of the top-ranked model.

Results

Mean (\pm SD) 95% KDE home range size was 22 ± 11 ha in the breeding season ($n = 27$) and 47 ± 27 ha in the post-breeding season ($n = 28$). Home ranges of neighboring individuals overlapped neither in the breeding season nor in the post-breeding season, suggesting territoriality in both seasons.

Home range size in the breeding season was best explained by a model including two PCs representing the proportion of plots with high resource abundance, population density, available forest area, and the interaction terms between the PCs and forest area and between the PCs and population density (Δ LOOIC to the null model = 10.3; Table 2). The credible intervals of the effect of available forest area, of the interactions between both PCs and population density, and of the interaction between the first PC and available forest area, did not include zero (Table 2). The relationships between home range size and these variables are plotted and described in Fig. A1 in the Appendix; we used the model described below for a more detailed description and discussion of the results as the original variables instead of the PCs are easier to interpret.

Chapter 2

Table 1 Models explaining the logarithm of breeding and post-breeding home range sizes of white-backed woodpeckers in Central Europe. Data were collected between 2016 and 2019. Each model structure was used in 7 models, in which the first two principal components (pc1, pc2) of a principal component analysis summarizing habitat variables representing a specific type of resource distribution were used (a-g). All models also include the number of tracking days as fixed effect and year as random effect. Each model represents at least one hypothesis (RD = resource distribution hypothesis, RH = restricted habitat availability hypothesis, IC = intraspecific competition hypothesis; hypotheses and their predictions are described in the introduction). Model selection was performed based on the leave-one-out-cross-validation information criterion LOOIC. Δ LOOIC = difference between a model's LOOIC and the top-ranked model's LOOIC; the top-ranked model per season is printed in bold. LOOIC values are shown in Table A.4 and Table A.5.

Hypothesis	Model structure	Δ LOOIC to the top-ranked model						
		(a) mean	(b) prop	(c) dist	(d) nest	(e) l.mean	(f) l.prop	(g) l.ai
Breeding season								
null model	-	10.3						
RD, RH*	forest	15.5						
RD, RH*	pc1 + pc2 + forest	10.2	12.6	15.0	11.5	10.3	8.9	10.6
RD, RH*	pc1 + pc2 + forest + forest:pc1+ forest:pc	5.2	11.3	18.8	5.4	14.8	10.8	9.7
IC	popdens	13.3						
RD, RH*, IC	popdens + forest	17.7						
RD, IC	popdens + pc1 + pc2	12.3	18.4	19	16.9	14.5	12.1	13
RD, IC	popdens + pc1 + pc2 + popdens:pc1 + popdens:pc2	14.8	13.6	22.6	23.6	22	18.7	19.2
RD, RH*, IC	forest + popdens + pc1 + pc2	9.7	10.7	15.9	13.2	11	9.1	12.3
RD, RH*, IC	forest + popdens + pc1 + pc2 + forest:pc1 + forest:pc2 + popdens:pc1 + popdens:pc2	7.3	0	20.3	13.6	25.9	20	21.1
Post-breeding season								
null model	-	0						
RD, RH*	forest	1.6						
RD, RH*	pc1 + pc2 + forest					3.6	2	4.2
RD, RH*	pc1 + pc2 + forest + forest:pc1+ forest:pc					4.5	6.1	9.7
IC	popdens	1.6						
RD, RH*, IC	popdens + forest	3.4						
RD, IC	popdens + pc1 + pc2					2.1	1.5	3.3
RD, IC	popdens + pc1 + pc2 + popdens:pc1 + popdens:pc2					10.12	5.5	10.9
RD, RH*, IC	forest + popdens + pc1 + pc2					4.3	3.2	5.5
RD, RH*, IC	forest + popdens + pc1 + pc2 + forest:pc1 + forest:pc2 + popdens:pc1 + popdens:pc2					15.7	13	18.5

*The RH is only supported when the relationship between home range size and forest area is positive; a negative relationship supports the RD.

When we replaced the PCs of the top-ranked candidate model with the original variables, a model with the variables proportion of plots with high snag volume and with a high number of trees with dead branches ranked highest (Table A.6). The credible intervals of proportion of plots with high number of trees with dead branches, available forest area, and all four interaction terms did not include zero (Table 2). Home range size thus decreased with increasing forest area in the landscape (Fig. 2 A) and increasing proportion of plots with a high number of trees with dead branches. The interactions between forest area and the resource variables show that home range size decreased with increasing proportion of resource-rich habitat mainly when forest cover was low (Fig. 2 B and C). For example, for areas with 74% forest cover (25% quantile; other variables were set to their means), our model predicted a decrease in home range size by 61% when the proportion of habitat with high snag volume increased from 0 to 100%. That is, home ranges in areas with low forest cover were up to 3 times larger when they did not contain habitat with high snag volume than when they did. Moreover, home range size decreased with increasing population density when the proportions of plots with high abundance of snags and trees with dead branches were high (Fig. 2 D and E). For instance, our model predicted a 68% decrease in home range size over the range of observed population densities when the proportion of habitat with high snag volume was 66% (75% quantile). That is, home ranges with a high proportion of habitat with high snag volume and low population density were up to 2.5 times larger than those with comparable habitat and high population density.

A model including the proportion of habitat with a high volume of logs and high number of large-diameter logs instead of the PCs ranked only slightly lower than the top-ranked one (Δ LOOIC 1.8, Table A.6). The credible intervals for the parameter estimates of proportion of habitat with high log volume, forest area, and all interaction terms did not include zero (Table 2). The log volume-dependent relationships between home range size and population density and forest area, respectively, were in line with the trends found in the top-ranked models with PCs and original variables. By contrast, the interactions between proportion of habitat with high abundance of large-diameter logs and population density and forest cover, respectively, predicted the opposite trend (negative relationship between home range size and population density at low proportion of habitat with high log volume and between home range size and proportion of habitat with high log volume at high forest cover).

Table 2 Estimates and 95% credible intervals of the fixed and random effects included in models explaining variation in the logarithm of white-backed woodpecker home range size during the breeding season. Home range sizes were calculated using 95% kernel density estimation based on radio-tracking data collected in Central Europe between 2016 and 2019. a) is the top-ranked candidate model in which habitat variables were summarized with principal component analysis. b) and c) are high-ranked models of a separate model selection procedure, in which the principal components of a) were replaced with their original variables (Table A.6). Variables that have a well-supported effect on home range size (credible intervals do not include zero) are printed in bold. Explanations for variables are given in the methods section and Fig. 1.

Variable	a)	b)	c)
(Intercept)	3.08 [2.62; 3.47]	3.07 [2.56; 3.44]	2.96 [2.72;3.16]
popdens	0.04 [-0.13; 0.21]	-0.12 [-0.3; 0.06]	0 [-0.15;0.14]
pc1.prop	0.08 [0; 0.17]	-	-
pc2.prop	-0.05 [-0.18; 0.08]	-	-
popdens:pc1.prop	0.21 [0.06; 0.35]	-	-
popdens:pc2.prop	-0.15 [-0.27; -0.02]	-	-
forest	-0.25 [-0.43; -0.07]	-0.23 [-0.41; -0.04]	-0.36 [-0.49;-0.2]
forest:pc1.prop	-0.21 [-0.32; -0.1]	-	-
forest.pc2.prop	-0.01 [-0.15; 0.13]	-	-
prop.vsnag	-	-0.07 [-0.26; 0.1]	-
prop.deadbr	-	-0.21 [-0.38; -0.02]	-
popdens:prop.vsnag	-	-0.33 [-0.56; -0.11]	-
popdens:prop.deadbr	-	-0.22 [-0.35; -0.08]	-
forest:prop.vsnag	-	0.36 [0.17; 0.57]	-
forest:prop.deadbr	-	0.21 [0; 0.41]	-
popdens:prop.vlog	-	-	-0.23 [-0.45;-0.01]
popdens:prop.log30	-	-	0.5 [0.17;0.81]
forest:prop.vlog	-	-	0.21 [0.03;0.39]
forest:prop.log30	-	-	-0.39 [-0.62;-0.15]
trackdays	0.07 [-0.14;0.25]	-0.01 [-0.21;0.17]	0.15 [-0.01;0.31]
Variance year	0.08 [0; 0.64]	0.08 [0; 0.67]	0.01 [0;0.21]
Variance residuals	0.1 [0.05; 0.23]	0.1 [0.05; 0.21]	0.1 [0.05;0.2]

Lastly, when modeling post-breeding home range size, the null model, which included only the number of tracking days and year, ranked highest (Table 1). Two models including forest area and population density also ranked high ($\Delta\text{LOOIC} = 1.6$ for both models); however, the credible intervals for both variables included zero.

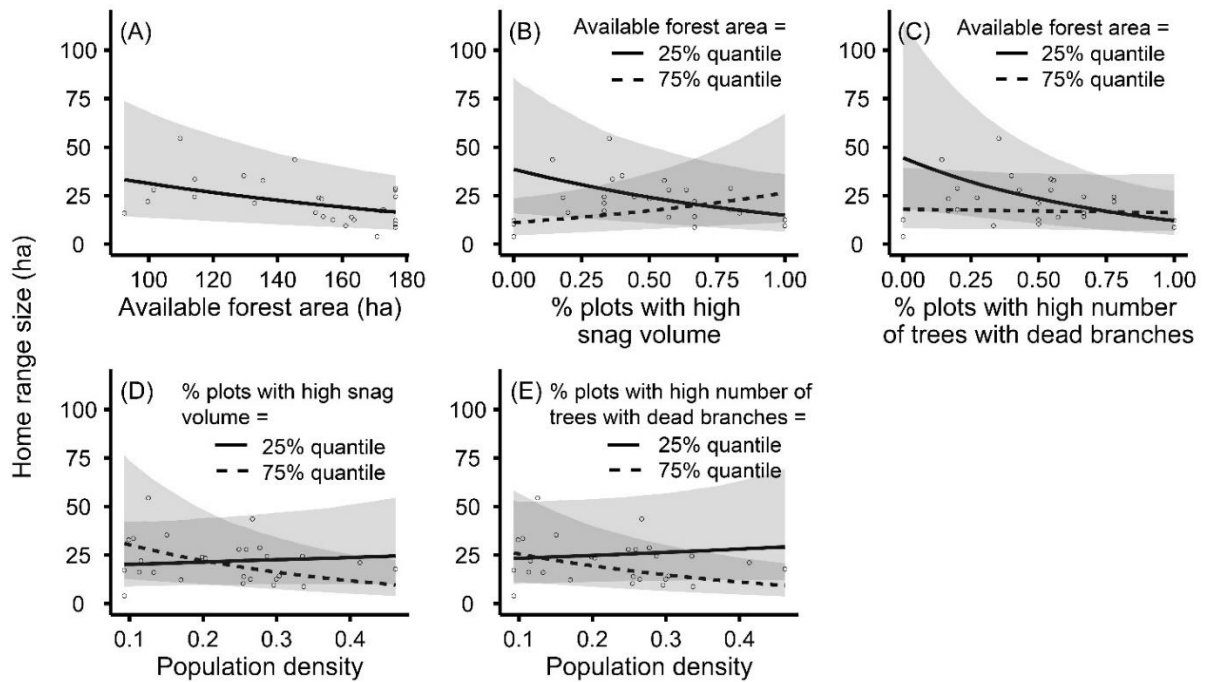


Figure 2 Relationships between white-backed woodpecker breeding home range size and (A) forest area in a buffer of 750 m around the home range centroid, the interactions between forest area and proportion of plots with (B) high volume of snags and (C) high number of trees with dead branches, and the interactions between population density and proportion of plots with (D) high volume of snags and (E) high number of trees with dead branches. Lines and gray areas are means and 95% credible intervals and were calculated with the values for other variables set to their means for (A), with the 25% and 75% quantiles for forest area for (B) and (C), and with the 25% and 75% quantiles for proportion of plots with abundance of snags and trees with dead branches for (D) and (E), respectively. Circles = raw data, $n = 27$. Data for the analyses were collected in Central Europe between 2016 and 2019.

Discussion

We found support for two of the three hypotheses proposed to explain variation in home range size in the breeding season (resource distribution and intraspecific competition hypotheses), whereas none of them was supported in the post-breeding season. As predicted by the resource distribution hypothesis, breeding home range size decreased with increasing proportion of habitat with high resource abundance (snags and trees with dead branches) and increasing forest cover in the landscape. On the one hand, the negative relationship between home range size and proportion of habitat with high abundance of snags and trees with dead branches confirms the importance of deadwood, which has been shown to be vital for white-backed woodpeckers for foraging (Aulén, 1988; Czeszczewik, 2009), nesting (Wesołowski, 1995), and drumming (Scherzinger, 1982). On the other hand, this finding suggests that deadwood should ideally be clumped in resource-rich patches, at least in the breeding habitat, while mean resource abundance across the HR appeared to be less important. That the

distribution of food resources plays an important role in the breeding season is plausible, considering that birds are central place foragers during the nestling period. White-backed woodpeckers can transport only few food items at a time to the nest (e.g., one big beetle larvae, pers. observations); therefore, selecting small home ranges with a high abundance of resources close to the nest reduces travel costs. Interestingly, the negative relationship between home range size and proportion of resource-rich habitat was mainly found when forest cover was relatively low. This could be explained by the generally larger home ranges in areas with low forest cover (Fig. 2 A). As we examined KDE home ranges, which largely exclude unused areas from the home range estimates, these home ranges were not larger because they contained a high proportion of unforested area. Instead, this result suggests a reduced habitat quality of stands in regions with low forest cover, possibly because of a more intensive forest management in the present or past, or because saproxylic beetles are less abundant due to poor habitat connectivity (Sverdrup-Thygeson et al., 2014). For woodpeckers maintaining already large home ranges because of a generally low habitat quality, aggregated resources might be particularly important as the costs of acquiring resources in dispersed high-quality patches (requiring crossing inhospitable habitat types and further enlarging the home range) may be too high. By contrast, a high proportion of habitat with high resource abundance tends to play a less important role when forest cover is high because of a presumably generally better habitat quality.

Likewise, the relationship between home range size and intraspecific competition appeared to vary with habitat quality. As predicted by the intraspecific competition hypothesis, home range size decreased with increasing population density. However, this was only the case when the proportion of resource-rich habitat was high. Although habitat characteristics were recorded only within the breeding home ranges, most habitat variables were positively correlated with local population density (strongest correlations for variables representing stand age, e.g., Pearson correlation coefficient for proportion of plots with high basal area of live trees = 0.56, for mean vegetation height = 0.5). This could indicate that resource abundance determines local population density. Consequently, the small home ranges with a high proportion of resource-rich habitat at high population density are likely a result of high intraspecific competition and the associated high costs of defending large territories rather than of the habitat itself. Such an indirect effect of resource abundance on home range size has been found for sanderlings *Calidris alba* (Myers et al., 1979) and black-shouldered kites *Elanus caeruleus* (Dunk and Cooper, 1994).

Altogether, our results suggest that the mechanisms driving breeding home range size in the studied white-backed woodpecker population varied with habitat quality. In regions with low habitat quality (indicated by low forest cover) and a presumably high anthropogenic impact, home range size appeared

to be mainly determined by the distribution of resources. By contrast, home range size in regions with high habitat quality (indicated by the high proportion of habitat with high resource abundance), probably because of low forest management intensity, seemed to be restricted by intraspecific competition. However, our findings should be interpreted with some caution because sample sizes were low, the relationships relatively weak, and the uncertainty in some parameter estimates high. Moreover, one of the high-ranked models did not support our conclusion above as it partly predicted contradictory trends (e.g., a negative relationship between home range size and population density at low proportion of habitat with high log volume). Nonetheless, habitat-dependent differences in the mechanisms driving home range size are a reasonable explanation for the observed trends and would be in accordance with results for other species. For instance, habitat quality has been proposed as explanation for inter-population differences in the factors determining territory size of coyotes *Canis latrans* (Wilson and Shivik, 2011) and mourning wheatears *Oenanthe lugens* (Khoury and Boulad, 2010). In these studies, territory sizes in study areas with high resource abundance were explained by contender pressure, whereas they seemed to be directly affected by resource abundance in areas with low habitat quality.

Considering that the habitat factors explaining variation in breeding home range size (deadwood, particularly snags, and trees with dead branches) are typically reduced by forest management, our results imply that the habitat alterations caused by forest management and deforestation may have direct (by increasing resource dispersion) and indirect (through the resulting reduced population density) consequences for the spatial behavior of a deadwood-dependent species. White-backed woodpeckers seem to be able to compensate for the lack of large unmanaged forests to some extent by increasing their home ranges. However, large home ranges as a result of dispersed resources may be associated with costs such as lower provisioning rates of the nestlings (Séchaud et al., 2022; Staggborg et al., 2017) and consequently lower fledging success (Pfeiffer and Meyburg, 2015; Séchaud et al., 2022).

Lastly, in contrast to the breeding season, we did not find support for any of the hypotheses in the post-breeding season. One reason for the poor performance of the resource distribution models might be the lack of data on deadwood availability, which was available and important in the breeding season. Another reason for the lacking support for the resource distribution hypothesis could be a higher flexibility in the non-breeding season, when the birds are not restricted by a central place, enabling them to better exploit also dispersed resources.

Conservation implications

Our results suggest that deadwood should ideally be clumped, particularly in areas with low forest cover, and that a high forest cover itself enables white-backed woodpeckers to use small areas in the breeding season. In our study area, white-backed woodpeckers bred in areas with a generally high forest cover ($84 \pm 15\%$, $n = 55$), and considering that the annual home range size was on average 116 - 350 ha (depending on the used home range estimator, Chapter 1), large forested areas have to be considered for implementing conservation measures. Within these large forests, areas at least the size of a breeding home range should include a high proportion of resource-rich habitat. Mean breeding home range size in our study area was 22 ha, about half of which had a high abundance of resources, i.e., $> 51 \text{ m}^3 \text{ ha}^{-1}$ of total deadwood, $>15 \text{ m}^3 \text{ ha}^{-1}$ of snags, $>20 \text{ m}^3 \text{ ha}^{-1}$ of logs, and at least 1 tree with thick dead branches ha^{-1} . Such amounts of deadwood are usually not available in forests managed for timber production, but are rather found in stands with low management intensity or forest reserves (Bouget et al., 2014; Christensen et al., 2005). This indicates that part of the forest should be managed at low intensity (in our study area often by single-tree or group selection) or not at all. However, management measures should not be restricted to habitat improvements in or the protection of areas necessary for breeding. We do not know how the habitat used in the non-breeding season should be composed, but it very likely should not exclusively be production forest, given the overall dependence of this species on dead wood. Thus, as long as detailed knowledge about the composition of the non-breeding habitat and its usage by the species is lacking, areas up to the size of an average yearly home range should provide abundant resources.

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References

- Auer, I., Böhm, R., Dobesch, H., Koch, E., Lipa, W., Mohnl, H., Potzmann, R., Rgette, G., Svabik, O., Heim, H., Werner, R., Groß, G., 2001. Klima von Vorarlberg. Amt der Vorarlberger Landesregierung, Bregenz.
- Aulén, G., 1988. Ecology and distribution of the white-backed woodpecker *Dendrocopos leucotos* in Sweden (Dissertation). Swedish University of Agricultural Sciences, Uppsala.
- BirdLife International, 2022. Species factsheet: *Dendrocopos leucotos*. Downloaded from <http://www.birdlife.org> on 10/01/2022.
- Börger, L., Franconi, N., Ferretti, F., Meschi, F., Michele, G.D., Gantz, A., Coulson, T., 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *Am. Nat.* 168, 471–485. <https://doi.org/10.1086/507883>
- Bouget, C., Parmain, G., Gilg, O., Noblecourt, T., Nusillard, B., Paillet, Y., Pernot, C., Larrieu, L., Gosselin, F., 2014. Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? *Anim. Conserv.* 17, 342–353. <https://doi.org/10.1111/acv.12101>
- 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 Ornithol.* 55, 77–87. <https://doi.org/10.3161/00016454AO2020.55.1.008>
- Christensen, M., Hahn, 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. *For. Ecol. Manag.* 210, 267–282. <https://doi.org/10.1016/j.foreco.2005.02.032>
- Czeczewik, 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 Ornithol.* 44, 109–118. <https://doi.org/10.3161/000164509X482687>
- Czeczewik, D., Walankiewicz, W., 2006. Logging affects the white-backed woodpecker *Dendrocopos leucotos* distribution in the Białowieża Forest. *Ann. Zool. Fenn.* 43, 221–227.
- Desrochers, A., Hannon, S.J., 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conserv. Biol.* 11, 1204–1210.
- Dunk, J.R., Cooper, R.J., 1994. Territory-size regulation in black-shouldered kites. *The Auk* 111, 588–595. <https://doi.org/10.1093/auk/111.3.588>
- Glutz von Blotzheim, U.N., Bauer, K., 1994. Handbuch der Vögel Mitteleuropas. Band 9: Columbiformes - Piciformes, 2nd ed. Aula-Verlag, Wiesbaden.

- Goodrich, B., Gabry, J., Ali, I., Brilleman, S., 2020. "rstanarm: Bayesian applied regression modeling via Stan." R package version 2.19.3, <https://mc-stan.org/rstanarm>.
- Hinam, H., St. Clair, C., 2008. High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of northern saw-whet owls. *Biol. Conserv.* 141, 524–535. <https://doi.org/10.1016/j.biocon.2007.11.011>
- Hogstad, O., Stenberg, I., 1994. Habitat selection of a viable population of white-backed woodpeckers *Dendrocopos leucotos*. *Fauna Nor. Ser. C Cinclus* 17, 75–94.
- Isenburg, M., 2019. LAStools - efficient tools for LiDAR processing, version 111216. <http://lastools.org>.
- Kenward, R.E., 2001. A manual for wildlife radio tagging, 2nd ed. Academic Press, New York.
- Khoury, F., Boulad, N., 2010. Territory size of the mourning wheatear *Oenanthe lugens* along an aridity gradient. *J. Arid Environ.* 74, 1413–1417. <https://doi.org/10.1016/j.jaridenv.2010.05.010>
- Krebs, J.R., 1971. Territory and breeding density in the great tit, *Parus Major* L. *Ecology* 52, 2–22. <https://doi.org/10.2307/1934734>
- Marable, M.K., Belant, J.L., Godwin, D., Wang, G., 2012. Effects of resource dispersion and site familiarity on movements of translocated wild turkeys on fragmented landscapes. *Behav. Processes* 91, 119–124. <https://doi.org/10.1016/j.beproc.2012.06.006>
- McClintic, L.F., Taylor, J.D., Jones, J.C., Singleton, R.D., Wang, G., 2014. Effects of spatiotemporal resource heterogeneity on home range size of American beaver. *J. Zool.* 293, 134–141. <https://doi.org/10.1111/jzo.12128>
- McGarigal, K., Cushman, SA, Ene, E., 2012. FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- Myers, J.P., Connors, P.G., Pitelka, F.A., 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. *The Auk* 96, 551–561. <https://doi.org/10.1093/auk/96.3.551>
- Pfeiffer, T., Meyburg, B.-U., 2015. GPS tracking of Red Kites (*Milvus milvus*) reveals fledgling number is negatively correlated with home range size. *J. Ornithol.* 156, 963–975. <https://doi.org/10.1007/s10336-015-1230-5>

Powell, R.A., 2000. Animal home ranges and territories and home range estimators, in: Boitani, L., Fuller, T. (Eds.), *Research Techniques in Animal Ecology: Controversies and Consequences*. Columbia University Press, New York, p. 476.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Scherzinger, W., 1982. Die Spechte im Nationalpark Bayerischer Wald. Nationalparkverwaltung Bayerischer Wald, Grafenau.

Séchaud, R., Schalcher, K., Almasi, B., Bühler, R., Safi, K., Romano, A., Roulin, A., 2022. Home range size and habitat quality affect breeding success but not parental investment in barn owl males. *Sci. Rep.* 12, 6516. <https://doi.org/10.1038/s41598-022-10324-7>

Sillett, T.S., Rodenhouse, N.L., Holmes, R.T., 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology* 85, 2467–2477. <https://doi.org/10.1890/03-0272>

Staggenborg, J., Schaefer, H.M., Stange, C., Naef-Daenzer, B., Gruebler, M.U., 2017. Time and travelling costs during chick-rearing in relation to habitat quality in Little Owls *Athene noctua*. *Ibis* 159, 519–531. <https://doi.org/10.1111/ibi.12465>

Stenberg, I., 1990. Preliminary results of a study on woodpeckers in More and Romsdal Country, western Norway, in: Carlson, A, Aulén, G. (Eds): *Conservation and Management of Woodpecker Populations*. Report 17, Uppsala. Departement of Wildlife Ecology, Swedish University of Agricultural Sciences, Uppsala, pp. 67–79.

Sverdrup-Thygeson, A., Gustafsson, L., Kouki, J., 2014. Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. *Biodivers. Conserv.* 23, 513–535. <https://doi.org/10.1007/s10531-014-0628-3>

Tomiałojć, L., 2000. An East-West gradient in the breeding distribution and species richness of the European woodland avifauna. *Acta Ornithol.* 35, 3–17.

van Beest, F., Rivrud, I.M., Loe, L.E., Milner, J., Mysterud, A., 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *J. Anim. Ecol.* 80, 771–785. <https://doi.org/10.1111/j.1365-2656.2011.01829.x>

Vehtari, A., Gabry, J., Yao, Y., Gelman, A., 2019. loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models." R package version 2.1.0, <https://CRAN.R-project.org/package=loo>.

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., Bürkner, P.-C., 2021. Rank-normalization, folding, and localization: An improved \hat{R} for assessing convergence of MCMC. *Bayesian Anal.* 16, 667–718. <https://doi.org/10.1214/20-BA1221>

Wesołowski, T., 1995. Ecology and behaviour of white-backed woodpecker (*Dendrocopos leucotos*) in a primeval temperate forest (Białowieża National Park, Poland). *Vogelwarte* 38, 61–75.

Wilson, R.R., Shivik, J.A., 2011. Contender pressure versus resource dispersion as predictors of territory size of coyotes (*Canis latrans*). *Can. J. Zool.* 89, 960–967. <https://doi.org/10.1139/z11-065>

Winkler, H., Christie, D., 2002. Family Picidae (woodpeckers), in: Del Hoyo, J., Elliott, A. & Sargatal, J. (Eds): *Handbook of the Birds of the World*. Lynx Edicions, Barcelona, pp. 296–555.

Appendix

Table A.1 Mean \pm standard deviation of variables used for modeling white-backed woodpecker home range size during the breeding and post-breeding seasons. Data were collected in Central Europe between 2016 and 2019. Variables were recorded in the field in 0.05 ha plots and with light detection and ranging (LiDAR) data per 50 x 50 m pixel. Each variable at the plot/pixel level was used to calculate corresponding variables at the level of white-backed woodpecker home ranges: a) mean abundance, b) proportion of plots/pixels with high abundance, c) mean distance between plots with high abundance and d) aggregation index of pixels with high abundance for field and LiDAR data, respectively, and e) sum from four plots around and one plot including the nest tree. f) Two variables were calculated at the home range level directly and raw data were used in the models. g) Threshold values to define ‘high abundance’ of a resource (variable values > threshold) or “low abundance” (variable values < threshold). Variable names are explained in the methods section and Fig.1.

Variable plot/pixel level	a) mean	b) prop	c) dist	d) ai	e) nest	f) raw	g) threshold
Breeding season							
tree50	52.97	0.39 \pm 0.22	437.47 \pm 171.07	-	264.92 \pm 134.04		58.75
beech50	16.07 \pm 12.43	0.43 \pm 0.24	404.87 \pm 158.06	-	108.41 \pm 82.68		0
log30	27.9 \pm 31.45	0.35 \pm 0.18	467.72 \pm 191.03	-	153.34 \pm 120.33		20
vlog	33.09 \pm 25.47	0.49 \pm 0.19	379.07 \pm 146.88	-	205.25 \pm 125.3		19.64
snag30	12.91 \pm 8.08	0.45 \pm 0.2	390.37 \pm 127.14	-	68.64 \pm 48.04		0
vsnag	29.19 \pm 23.13	0.49 \pm 0.3	372.32 \pm 144.66	-	128.12 \pm 64.32		14.12
vdw	72.5 \pm 43.55	0.51 \pm 0.26	371.66 \pm 109.01	-	374.57 \pm 146.26		50.83
deadbr	19.51 \pm 17	0.47 \pm 0.27	404.59 \pm 132.07	-	165.59 \pm 119.97		0
blive	31.16 \pm 8.63	0.45 \pm 0.19	390.53 \pm 112.71	-	156.89 \pm 49.51		32.06
bsnag	3.38 \pm 2.24	0.53 \pm 0.22	357.68 \pm 114	-	20.35 \pm 10.41		1.98
max	39.25 \pm 2.64	0.53 \pm 0.22	-	73.94 \pm 13.45	-		39.36
avg	19.94 \pm 2	0.55 \pm 0.19	-	75.3 \pm 11.91	-		19.87
qav	492.8 \pm 77.89	0.56 \pm 0.19	-	76.45 \pm 11.33	-		471.27
std	7.69 \pm 0.91	0.46 \pm 0.2	-	67.11 \pm 14.36	-		7.7
ske	-0.38 \pm 0.3	0.48 \pm 0.19	-	70.29 \pm 12.97	-		-0.35
kur	3.42 \pm 0.73	0.14 \pm 0.08	-	36.2 \pm 18.2	-		2.67
p95	31.17 \pm 2.11	0.54 \pm 0.2	-	73.9 \pm 12.78	-		31.69
vp30	0.15 \pm 0.05	0.55 \pm 0.2	-	74.95 \pm 11	-		0.09
forest ¹	-	-	-	-	-	149.57 \pm 26.82	-
popdens ²	-	-	-	-	-	0.24 \pm 0.11	-
Post-breeding season							
max	37.89 \pm 2.54	0.48 \pm 0.17	-	72.45 \pm 12.48	-		38.5
avg	18.78 \pm 1.97	0.51 \pm 0.15	-	73.16 \pm 12.25	-		18.8
qav	445.01 \pm 75.36	0.5 \pm 0.15	-	73.14 \pm 12.96	-		418.72
std	7.42 \pm 0.76	0.47 \pm 0.16	-	67.65 \pm 10.64	-		7.36

Table A.1, continued

Variable plot/pixel level	a) mean	b) prop	c) dist	d) ai	e) nest	f) raw	g) threshold
ske	-0.28±0.26	0.43±0.14	-	67.37±21.01	-		-0.28
kur	3.14±0.59	0.15±0.08	-	39.97±24.95	-		2.63
p95	29.89±2.19	0.49±0.16	-	73.84±12.82	-		30.51
vp30	0.13±0.05	0.49±0.16	-	74.54±12.58	-		0.06
forest ¹	-	-	-	-	-	151.73±24.76	-
popdens ²	-	-	-	-	-	0.25±0.1	-

¹ in ha, calculated in 750-m buffers around the home range centroid

² number of territory centers per 100 ha forest, calculated in 2-km buffers around the home range centroid

Table A.2 Results of four principal component analyses (PCA) conducted for habitat variables obtained from data collected in the field within white-backed woodpecker breeding home ranges in Central Europe. Data were collected between 2016 and 2019. Each PCA was done with 10 variables representing one of four types of resource distribution (mean = mean resource abundance, prop = proportion of sampling plots with high resource abundance, dist = mean distance between plots with high resource abundance, nest = sum of resources around nest tree), e.g., pc1.mean and pc2.mean were produced with mean.vlog, mean.vsnag, mean.tree50 et cetera, pc1.prop and pc2.prop with prop.vlog, prop.vsnag, prop.tree50 et cetera. Shown are rotated factor loadings, eigenvalues, and cumulative variances of the first two principal components per PCA. Variables are described in the methods section and Fig. 1.

Variables	pc1.	pc2.	pc1.	pc2.	pc1.	pc2.	pc1.	pc2.
	mean	mean	prop	prop	dist	dist	nest	nest
mean./prop./dist./nest.vlog	-0.37	0.13	-0.29	0.08	-0.4	0.27	-0.36	-0.09
mean./prop./dist./nest.vsnag	-0.34	0.09	-0.41	-0.28	-0.2	-0.52	-0.32	-0.2
mean./prop./dist./nest.tree50	-0.18	-0.6	-0.12	0.45	-0.02	0.35	-0.33	0.41
mean./prop./dist./nest.beech50	-0.11	-0.3	-0.33	-0.02	-0.27	0.03	-0.2	0.44
mean./prop./dist./nest.bsng	-0.44	0.06	-0.43	-0.2	-0.3	-0.47	-0.4	-0.08
mean./prop./dist./nest.blive	-0.24	-0.5	-0.28	0.19	-0.18	-0.1	-0.29	0.45
mean./prop./dist./nest.log30	-0.33	0.12	-0.17	0.46	-0.38	0.34	-0.31	-0.36
mean./prop./dist./nest.snag30	-0.38	0.16	-0.36	-0.1	-0.41	-0.12	-0.29	-0.25
mean./prop./dist./nest.deadbr	-0.04	-0.46	-0.14	0.64	-0.29	0.39	-0.07	0.4
mean./prop./dist./nest.vdw	-0.44	0.15	-0.42	-0.1	-0.46	-0.12	-0.44	-0.17
eigenvalue	4.68	2.09	4.04	1.8	3.99	2.36	3.87	2.37
% cumulative variance	46.83	67.7	40.44	58.4	39.91	63.48	38.69	62.43

Table A.3 Results of six principal component analyses (PCA) conducted for habitat variables obtained from light detection and ranging (LiDAR) data within white-backed woodpecker breeding and post-breeding home ranges in Central Europe. Home range data were collected between 2016 and 2019. Each PCA was done with eight variables representing one of three types of resource distribution (mean = mean resource abundance, prop = proportion of pixels with high resource abundance, ai = aggregation index of pixels with high resource abundance), e.g., pc1.l.mean and pc2.l.mean were produced with mean.max, mean.avg, mean.qav et cetera, pc1.l.prop and pc2.l.prop with prop.max, prop.avg, prop.qav et cetera. Shown are rotated factor loadings, eigenvalues, and cumulative variances of the first two principal components per PCA. Variables are described in the methods section and Fig. 1.

Variable	breeding season home ranges						post-breeding season home ranges					
	pc1.l. mean	pc2.l. mean	pc1.l.p rop	pc2.l. .prop	pc1.l. ai	pc2.l. ai	pc1.l. mean	pc2.l. mean	pc1.l. prop	pc2.l. prop	pc1.l. ai	pc2.l. ai
mean./prop./ai.max	-0.35	0.35	-0.38	0.22	-0.4	0.23	-0.35	0.35	-0.35	0.25	-0.41	0.23
mean./prop./ai.avg	-0.42	-0.24	-0.34	-0.4	-0.36	-0.41	-0.43	-0.2	-0.36	-0.36	-0.4	-0.15
mean./prop./ai.qav	-0.18	0.53	-0.24	0.53	-0.21	0.52	-0.21	0.52	-0.26	0.5	-0.24	0.51
mean./prop./ai.std	0.25	0.5	-0.28	-0.5	-0.31	-0.47	0.26	0.49	-0.27	-0.51	-0.23	-0.48
mean./prop./ai.ske	-0.15	-0.46	-0.29	0.44	-0.12	0.42	-0.15	-0.51	-0.28	0.46	0.04	0.64
mean./prop./ai.kur	-0.45	-0.15	-0.39	-0.27	-0.42	-0.24	-0.45	-0.13	-0.39	-0.29	-0.42	-0.13
mean./prop./ai.p95	-0.43	0.21	-0.42	0.08	-0.43	0.17	-0.44	0.18	-0.43	0.04	-0.44	0.04
mean./prop./ai.vp30	-0.44	0.12	-0.43	0.02	-0.44	0.15	-0.42	0.1	-0.43	0.04	-0.44	0.05
eigenvalue	4.63	2.55	5.29	2.3	4.68	2.12	4.72	2.46	5.26	2.25	5.04	1.46
% cumulative variance	57.91	89.8	66.07	94.8	58.55	84.99	59.06	89.84	65.74	93.91	62.96	81.23

Table A.4 Models used for investigating variation in breeding home range size of the white-backed woodpecker in Central Europe based on data collected between 2016 and 2019 (n = 27 home ranges). Model selection was performed based on the leave-one-out-cross-validation information criterion LOOIC. Δ LOOIC = difference between a model's LOOIC and the top-ranked model's LOOIC. All models also include the number of tracking days as fixed effect and year as random effect. Explanations of variables are given in the methods section and Fig. 1.

Model	LOOIC	Δ LOOIC
pc1.prop + pc2.prop + forest + popdens + forest:pc1.prop + forest:pc2.prop + popdens:pc1.prop + popdens:pc2.prop	34.3	0.0
pc1.nest + pc2.nest + forest + forest:pc1.nest + forest:pc2.nest	39.6	5.4
pc1.mean + pc2.mean + forest + forest:pc1.mean + forest:pc2.mean	39.7	5.4
pc1.mean + pc2.mean + forest + popdens + forest:pc1.mean + forest:pc2.mean + popdens:pc1.mean + popdens:pc2.mean	41.5	7.2
forest	41.7	7.4
pc1.l.prop + pc2.l.prop + forest	43.2	8.9
pc1.l.prop + pc2.l.prop + forest + popdens	43.4	9.1
pc1.mean + pc2.mean + forest + popdens	44.0	9.7
pc1.l.ai + pc2.l.ai + forest + forest:pc1.l.ai + forest:pc2.l.ai	44.0	9.8
popdens + forest	44.0	9.8

Table A.4, continued.

Model	LOOIC	Δ LOOIC
pc1.mean + pc2.mean + forest	44.6	10.3
pc1.l.mean + pc2.l.mean + forest	44.6	10.3
null model	44.6	10.3
pc1.l.ai + pc2.l.ai + forest	44.8	10.6
pc1.prop + pc2.prop + forest + popdens	44.9	10.7
pc1.l.prop + pc2.l.prop + forest + forest:pc1.l.prop + forest:pc2.l.prop	45.1	10.9
pc1.l.mean + pc2.l.mean + forest + popdens	45.2	11.0
pc1.nest + pc2.nest + forest	45.9	11.6
pc1.prop + pc2.prop + forest + forest:pc1.prop + forest:pc2.prop	45.9	11.7
pc1.prop + pc2.prop + forest	46.3	12.0
pc1.l.prop + pc2.l.prop + popdens	46.3	12.1
pc1.l.ai + pc2.l.ai + forest + popdens	46.5	12.3
pc1.mean + pc2.mean + popdens	46.6	12.3
pc1.l.ai + pc2.l.ai + popdens	47.3	13.0
pc1.nest + pc2.nest + forest + popdens	47.5	13.2
popdens	47.5	13.2
popdens + pc1.prop + pc2.prop + popdens:pc1.prop + popdens:pc2.prop	47.6	13.4
pc1.nest + pc2.nest + forest + popdens + forest:pc1.nest + forest:pc2.nest + popdens:pc1.nest + popdens:pc2.nest	47.8	13.5
pc1.l.mean + pc2.l.mean + popdens	48.7	14.5
pc1.l.mean + pc2.l.mean + forest + forest:pc1.l.mean + forest:pc2.l.mean	49.1	14.8
popdens + pc1.mean + pc2.mean + popdens:pc1.mean + popdens:pc2.mean	49.2	15.0
pc1.dist + pc2.dist + forest	49.5	15.2
pc1.dist + pc2.dist + forest + popdens	50.1	15.9
pc1.nest + pc2.nest + popdens	51.2	16.9
pc1.prop + pc2.prop + popdens	52.7	18.4
popdens + pc1.l.prop + pc2.l.prop + popdens:pc1.l.prop + popdens:pc2.l.prop	52.9	18.6
pc1.dist + pc2.dist + popdens	53.2	19.0
pc1.dist + pc2.dist + forest + forest:pc1.dist + forest:pc2.dist	53.3	19.1
popdens + pc1.l.ai + pc2.l.ai + popdens:pc1.l.ai + popdens:pc2.l.ai	53.5	19.2
pc1.l.prop + pc2.l.prop + forest + popdens + forest:pc1.l.prop + forest:pc2.l.prop + popdens:pc1.l.prop + popdens:pc2.l.prop	54.4	20.1
pc1.dist + pc2.dist + forest + popdens + forest:pc1.dist + forest:pc2.dist + popdens:pc1.dist + popdens:pc2.dist	54.9	20.6
pc1.l.ai + pc2.l.ai + forest + popdens + forest:pc1.l.ai + forest:pc2.l.ai + popdens:pc1.l.ai + popdens:pc2.l.ai	55.4	21.2
popdens + pc1.l.mean + pc2.l.mean + popdens:pc1.l.mean + popdens:pc2.l.mean	56.0	21.8
popdens + pc1.dist + pc2.dist + popdens:pc1.dist + popdens:pc2.dist	56.6	22.4
popdens + pc1.nest + pc2.nest + popdens:pc1.nest + popdens:pc2.nest	57.9	23.6
pc1.l.mean + pc2.l.mean + forest + popdens + forest:pc1.l.mean + forest:pc2.l.mean + popdens:pc1.l.mean + popdens:pc2.l.mean	60.2	25.9

Table A.5 Models used for investigating variation in post-breeding home range size of the white-backed woodpecker in Central Europe based on data collected between 2016 and 2019 (n = 28 home ranges). Model selection was performed based on the leave-one-out-cross-validation information criterion LOOIC. Δ LOOIC = difference between a model's LOOIC and the top-ranked model's LOOIC. All models also include the number of tracking days as fixed effect and year as random effect. Explanations of variables are given in the methods section and Fig. 1.

Model	LOOIC	Δ LOOIC
null model	48.2	0
pc1.l.prop + pc2.l.prop + popdens	49.7	1.5
popdens	49.8	1.6
forest	49.8	1.6
pc1.l.prop + pc2.l.prop + forest	50.2	2
pc1.l.mean + pc2.l.mean + popdens	50.3	2.1
pc1.l.prop + pc2.l.prop + forest + popdens	51.4	3.2
pc1.l.ai + pc2.l.ai + popdens	51.5	3.3
popdens + forest	51.6	3.4
pc1.l.mean + pc2.l.mean + forest	51.8	3.6
pc1.l.ai + pc2.l.ai + forest	52.4	4.2
pc1.l.mean + pc2.l.mean + forest + popdens	52.5	4.3
pc1.l.mean + pc2.l.mean + forest + forest:pc1.l.mean + forest:pc2.l.mean	52.7	4.5
popdens + pc1.l.prop + pc2.l.prop + popdens:pc1.l.prop + popdens:pc2.l.prop	53.7	5.5
pc1.l.ai + pc2.l.ai + forest + popdens	53.7	5.5
pc1.l.prop + pc2.l.prop + forest + forest:pc1.l.prop + forest:pc2.l.prop	54.3	6.1
pc1.l.ai + pc2.l.ai + forest + forest:pc1.l.ai + forest:pc2.l.ai	57.9	9.7
popdens + pc1.l.mean + pc2.l.mean + popdens:pc1.l.mean + popdens:pc2.l.mean	58.3	10.1
popdens + pc1.l.ai + pc2.l.ai + popdens:pc1.l.ai + popdens:pc2.l.ai	59.1	10.9
pc1.l.prop + pc2.l.prop + forest + popdens + forest:pc1.l.prop + forest:pc2.l.prop + popdens:pc1.l.prop + popdens:pc2.l.prop	61.2	13
pc1.l.mean + pc2.l.mean + forest + popdens + forest:pc1.l.mean + forest:pc2.l.mean + popdens:pc1.l.mean + popdens:pc2.l.mean	63.9	15.7
pc1.l.ai + pc2.l.ai + forest + popdens + forest:pc1.l.ai + forest:pc2.l.ai + popdens:pc1.l.ai + popdens:pc2.l.ai	66.7	18.5

Table A.6 Variants of the top-ranked model (Table 1, Table 2) explaining white-backed woodpecker home range size during the breeding season with the principal components replaced by original variables. Home range sizes were calculated using 95% kernel density estimation based on radio-tracking data collected in Central Europe between 2016 and 2019 (n = 27 home ranges). All models also include then number of tracking days as fixed effect and a random intercept for year. Model selection was performed based on the leave-one-out-cross-validation information criterion LOOIC. Δ LOOIC = difference between a model's LOOIC and the top-ranked model's LOOIC. Explanations for variables are given in the methods section/Fig. 1.

Model	LOOIC	Δ LOOIC
popdens + prop.vsnag + popdens:prop.vsnag + prop.deadbr + popdens:prop.deadbr + forest + forest:prop.vsnag + forest:prop.deadbr	26.2	0
popdens + prop.vlog + popdens:prop.vlog + prop.log30 + popdens:prop.log30 + forest + forest:prop.vlog + forest:prop.log30	28.1	1.8
popdens + prop.blive + popdens:prop.blive + prop.deadbr + popdens:prop.deadbr + forest + forest:prop.blive + forest:prop.deadbr	36.4	10.2
popdens + prop.vsnag + popdens:prop.vsnag + prop.log30 + popdens:prop.log30 + forest + forest:prop.vsnag + forest:prop.log30	36.6	10.4
popdens + prop.bsnag + popdens:prop.bsnag + prop.deadbr + popdens:prop.deadbr + forest + forest:prop.bsnag + forest:prop.deadbr	37.3	11
popdens + prop.blive + popdens:prop.blive + prop.log30 + popdens:prop.log30 + forest + forest:prop.blive + forest:prop.log30	38.5	12.3
popdens + prop.vdw + popdens:prop.vdw + prop.log30 + popdens:prop.log30 + forest + forest:prop.vdw + forest:prop.log30	40.7	14.4
popdens + prop.vsnag + popdens:prop.vsnag + prop.tree50 + popdens:prop.tree50 + forest + forest:prop.vsnag + forest:prop.tree50	41.3	15.0
popdens + prop.beech50 + popdens:prop.beech50 + prop.log30 + popdens:prop.log30 + forest + forest:prop.beech50 + forest:prop.log30	42.2	16
popdens + prop.vdw + popdens:prop.vdw + prop.deadbr + popdens:prop.deadbr + forest + forest:prop.vdw + forest:prop.deadbr	42.7	16.5
popdens + prop.snag30 + popdens:prop.snag30 + prop.deadbr + popdens:prop.deadbr + forest + forest:prop.snag30 + forest:prop.deadbr	43.8	17.6
popdens + prop.blive + popdens:prop.blive + prop.tree50 + popdens:prop.tree50 + forest + forest:prop.blive + forest:prop.tree50	44	17.7
popdens + prop.beech50 + popdens:prop.beech50 + prop.deadbr + popdens:prop.deadbr + forest + forest:prop.beech50 + forest:prop.deadbr	45.4	19.1
popdens + prop.vlog + popdens:prop.vlog + prop.tree50 + popdens:prop.tree50 + forest + forest:prop.vlog + forest:prop.tree50	46.0	19.8
popdens + prop.snag30 + popdens:prop.snag30 + prop.tree50 + popdens:prop.tree50 + forest + forest:prop.snag30 + forest:prop.tree50	46.0	19.8
popdens + prop.beech50 + popdens:prop.beech50 + prop.tree50 + popdens:prop.tree50 + forest + forest:prop.beech50 + forest:prop.tree50	46.1	19.8
popdens + prop.snag30 + popdens:prop.snag30 + prop.log30 + popdens:prop.log30 + forest + forest:prop.snag30 + forest:prop.log30	47.2	21
popdens + prop.bsnag + popdens:prop.bsnag + prop.log30 + popdens:prop.log30 + forest + forest:prop.bsnag + forest:prop.log30	47.7	21.4

Table A.6, continued.

Model	LOOIC	Δ LOOIC
popdens + prop.bsna + popdens:prop.bsna + prop.tree50 + popdens:prop.tree50 + forest + forest:prop.bsna + forest:prop.tree50	48.9	22.6
popdens + prop.vdw + popdens:prop.vdw + prop.tree50 + popdens:prop.tree50 + forest + forest:prop.vdw + forest:prop.tree50	49.8	23.6
popdens + prop.vlog + popdens:prop.vlog + prop.deadbr + popdens:prop.deadbr + forest + forest:prop.vlog + forest:prop.deadbr	50.3	24.1

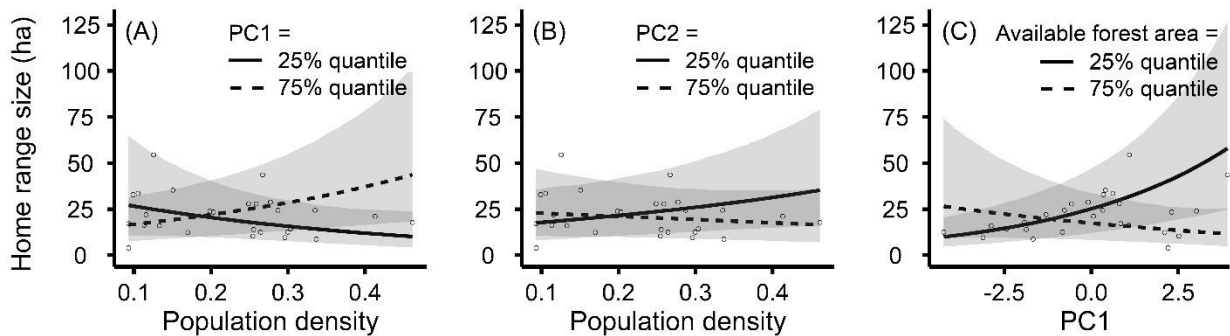


Figure A.1 Relationships between white-backed woodpecker breeding home range size and the interactions between (A) population density and PC1, (B) population density and PC2, and (C) PC1 and available forest area. PC1 and PC2 are the first and second principal components from a principal component analysis summarizing habitat variables on the proportion of habitat with high resource abundance. PC1 was negatively associated with the proportion of plots with high amounts of deadwood (highest loadings for total amount of deadwood and basal area of snags). That is, home range size increased with increasing population density when the proportion of plots with high amounts of deadwood was low but decreased when the proportion of plots with high amounts of deadwood was high (A). Furthermore, home range size decreased with decreasing proportion of plots with high amounts of deadwood when forest cover was high but increased with decreasing proportion of plots with high amounts of deadwood when forest cover was low (C). The second principal component was positively associated with the proportion of habitat with a high number of large-diameter trees and trees with dead branches. That is, home range size tended to increase with increasing population density when the proportion of habitat with high abundance of large-diameter trees and trees with dead branches was high (B). Lines and gray areas are means and 95% credible intervals and were calculated with the 25% and 75% quantiles for PC1 for (A), with the 25% and 75% quantiles for PC2 for (B), and with the 25% and 75% quantiles for available forest area for (C). Circles = raw data, $n = 27$. Data for the analyses were collected in Central Europe between 2016 and 2019.

Chapter 3

Multi-level habitat selection of a forest specialist in a spatially heterogeneous landscape

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Abstract

The habitat of forest species that depend on old-growth structures has become rare due to commercial forestry. Whether integrative conservation measures, e.g., retaining deadwood in managed forests, are sufficient for the conservation of such species is unclear. In heterogeneous forest landscapes, habitat specialists with large area requirements may use a variety of forest stands to meet different biological requirements or to compensate for the lack of habitat of optimal quality. To provide insight into the potential of managed forests as habitat for old-growth forest species, we investigated seasonal habitat selection by the white-backed woodpecker *Dendrocopos leucotos*, a species with large area requirements and highly dependent on deadwood. We radio-tracked 50 individuals in forest habitat types differing in age and vertical structure and analyzed seasonal habitat selection at three levels: a) selection of habitat types for establishing seasonal home ranges within the annual home range; b) selection of habitat types within the seasonal home range; c) selection of foraging trees. Habitat selection occurred at the level of seasonal home range establishment in the pre-breeding and breeding seasons and at the level of foraging trees in all seasons. White-backed woodpeckers selected areas with a high proportion of old deciduous stands for establishing pre-breeding and breeding home ranges, whereas the proportions of all measured habitat types within post-breeding, summer/fall and winter home ranges corresponded to their availability in an area representing the annual home range. Within the seasonal home range, the habitat types were used according to their availability during all seasons. Modeling foraging tree selection revealed that the relative probability of selection increased with the diameter of the tree and was highest for snags; these relationships were similar across habitat types, seasons and sexes. Our findings suggest that managed forest can be used by white-backed woodpeckers as long as suitable foraging trees and close-by (largely) unmanaged old deciduous or mixed stands as breeding habitat are available. Thus, for the conservation of white-backed woodpeckers, integrative measures such as the retention of deadwood and large-diameter trees can be a useful approach in managed stands near old unmanaged stands.

Introduction

Forest management substantially changes the structure and distribution of forest stands, typically decreasing stand age, structural diversity and amount of deadwood (Gibb et al., 2005; Schall et al., 2018) and reducing the proportion of old forest in the landscape. In Europe, the impact of forest management has been particularly strong, and today, only 2.2% of the forested area can be considered as natural (Forest Europe, 2020). While the results of studies comparing the biodiversity of managed and unmanaged forests generally suggest that managed forests can serve as habitat for many forest species (see meta-analysis by Paillet et al., 2010), some species, typically habitat specialists that depend on old-growth forests and their attributes, appear to be sensitive to the changes in forest structure caused by forest management (Moning et al., 2009; Müller et al., 2007). Whether and under which conditions such habitat specialists can persist in managed forests is unclear. On the one hand, integrative conservation approaches, i.e., retaining and creating key habitat elements of old-growth and primary forests (Bauhus et al., 2009; Lindenmayer et al., 2006) or old-growth patches (Bollmann and Braunisch, 2013) in managed forests, have been shown to benefit many species, including habitat specialists, across various taxa. For instance, artificially created deadwood can be a valuable habitat for saproxylic beetles (Jonsell et al., 2004) and fungi (Lindhe et al., 2004) and can significantly increase the diversity and abundance of these taxa in stands managed for timber production (Doerfler et al., 2018; Dufour-Pelletier et al., 2020). According to a meta-analysis of Müller and Bütler (2010), most of the autochthonous species, including red-listed saproxylic beetle species and woodpeckers, appear to be present in deciduous forests with 30 – 50 m³ha⁻¹ of deadwood. Such amounts of deadwood can be found in managed forests with conservation oriented logging (Müller et al., 2007). On the other hand, some specialized species require habitat characteristics that cannot be achieved with integrative measures in managed forests, such as very high amounts of deadwood (Bässler and Müller, 2010; Brunet and Isacson, 2009; Sillett et al., 2000) or stand ages that are incompatible with timber production (Moning and Müller, 2009). The protection of such species requires segregative approaches, i.e., protected areas with no or minimal human intervention, which enable biodiversity conservation by natural dynamics (Bollmann and Braunisch, 2013). Lastly, the value of integrative measures may depend on the quality of the whole landscape. For example, species with low dispersal capacities may benefit from an increase in deadwood in managed forests only when old-growth patches are available nearby (Brunet and Isacson, 2009).

In spatially heterogeneous landscapes such as forest-dominated regions with varying management intensity, habitat specialists with large area requirements may use a variety of forest stands. Firstly, different habitat types might be necessary to meet different biological requirements such as foraging,

breeding, or shelter (Orians and Wittenberger, 1991). Secondly, the lack of one patch with optimal habitat quality might be compensated by increasing the home range and using multiple patches of lower quality (McLoughlin and Ferguson, 2000). Investigating the space use of such species in heterogeneous forest landscapes may help to provide further insight into the potential of managed forests as habitat for old-growth species.

Woodpeckers are well-suited model species for such studies: they are highly susceptible to habitat changes due to their specialization on specific forest habitats (Virkkala, 2006) and have been shown to be good indicators for biodiversity (Martikainen et al., 1998; Mikusiński et al., 2001; Mikusiński and Angelstam, 1998; Roberge and Angelstam, 2006); they have relatively large area requirements, which is one of the reasons why some species have also been proposed as umbrella species (Roberge et al., 2008); and they are charismatic species valuable for the communication and implementation of conservation measures (Virkkala, 2006). One species that represents these general characteristics of woodpeckers particularly well is the white-backed woodpecker *Dendrocopos leucotos*. It is a habitat specialist with large area requirements (with mean yearly home range sizes of 116 - 350 ha, Chapter 1) and is strongly affected by commercial forest management (Virkkala et al., 1993). The species feeds mainly on the larvae of saproxylic beetles (Aulén, 1988) and is associated with old deciduous or mixed forest stands with abundant deadwood (Aulén, 1988; Hogstad and Stenberg, 1994). Due to its habitat requirements, its occurrence in Europe is limited to relicts of primeval forest or regions with low forest management intensity. While previous studies on habitat use and selection during the mating and breeding seasons have consistently concluded that old unmanaged stands are the optimal habitat for white-backed woodpeckers (Czeszczewik and Walankiewicz, 2006; Hogstad and Stenberg, 1994; Kajtoch et al., 2013), the extent to which managed stands can serve as habitat is unclear. Anecdotal observations suggest that the species also uses intensively managed stands at least occasionally (Bühler, 2009; Scherzinger, 1982, personal observations). However, systematically collected data are missing as the species behaves inconspicuously and is thus difficult to observe, particularly in the non-breeding season.

In this study, we radio-tracked white-backed woodpeckers in forest stands differing in age and vertical structure and investigated seasonal habitat selection at three hierarchical levels (corresponding to Johnson's (1980) second-, third-, and fourth-order habitat selection with modifications to account for seasonal differences): a) selection of habitat types for establishing seasonal home ranges within an area representing the annual home range (hereafter second level); b) selection of habitat types within the seasonal home range (third level); c) selection of foraging trees in different habitat types and seasons (fourth level).

Table 1 Expected seasonal differences in habitat selection by the white-backed woodpecker at three levels (level 2: selection of habitat types for establishing seasonal home ranges within an area representing the annual home range; 3: selection of habitat types within seasonal home ranges; 4: selection of foraging trees). DOhet = old deciduous/mixed heterogeneous forest, Dohom = old deciduous/mixed homogeneous forest, Dyhet = young deciduous/mixed heterogeneous forest, Dyhom = young deciduous/mixed homogeneous forest, Con = coniferous forest. Heterogeneous/homogeneous refers to the vertical structure of the stand. Heterogeneous forests are assumed to be managed less intensively and thus to contain more deadwood than homogeneous forests. > preferred over; + more important than in other season; +/- more important than in other season but generally avoided, [...] more important than in other seasons but used according to availability. Tree characteristics not mentioned at level 4 are expected to be used according to their availability without seasonal differences.

Level	Season*	Expected preferences	Explanation for expected habitat preferences
2	Pre-breeding	Dohet > all other habitat types	Movements are restricted to a small area around the nest tree and the home ranges thus have to contain a high proportion of high-quality habitat to provide sufficient food for raising the offspring.
	Breeding	Dohet > all other habitat types	
3	Post-breeding	Dohet > Con > Dyhet/Dohom > Dyhom	Home ranges are larger post-breeding as the individuals do not have to stay close to a central place and also dispersed patches within unsuitable areas can be used. Individuals are less restricted to habitat types with very high amounts of deadwood but still avoid DYhom, which is unlikely to provide food resources. Con is important in the post-breeding season, when the woodpeckers stay close to their unexperienced chicks (which cannot climb well on the smooth bark of beech trees, pers. observation, and need shelter from predators) and in winter, when shelter from weather is needed.
	Summer	DOhet > DYhet/DOhom/Con > DYhom	
	Fall	DOhet > DYhet/DOhom/Con > DYhom	
	Winter	DOhet > Con > DYhet/DOhom > DYhom	
4	Pre-breeding	+snags, +deadbr	Large-diameter trees are important in the breeding season as they contain large larvae used to feed the nestlings. Deadwood is vital throughout the year. In the pre-breeding season and in winter, snags and live trees with dead branches (deadbr) are more important than in the other seasons because logs/stumps are often covered with snow. In the breeding and post-breeding seasons and in summer/fall, snags and logs are equally important, while stumps and live trees with dead branches play a smaller role due to their lower volume of deadwood. Live trees without dead branches (live) are only used from the breeding season to summer/fall when surface-living arthropods are abundant but are generally avoided. Tree species are generally used according to their availability as habitat selection occurs at higher levels.
	Breeding	large diameters; snags, logs, [stumps], +/-live	
	Post-breeding	snags, logs, [stumps], +/-live	
	Summer/fall	snags, logs, [stumps], +/-live	
	Winter	+snags, +deadbr	

*Season in which habitat selection is expected to occur at a given level. In seasons not mentioned at a level, habitats are expected to be used according to their availability.

We expected second-level selection of specific habitat types to occur only in the pre-breeding and breeding seasons, whereas at the third level we expected specific habitat types to be selected during the rest of the year. Moreover, we expected habitat selection at the fourth level to occur throughout

the year but with seasonal differences (see Table 1 for detailed expectations and explanations). As the use of foraging trees has been shown to differ between the sexes (Aulén and Lundberg, 1991; Stenberg and Hogstad, 2004), we also investigated the effect of sex on foraging tree selection. Based on our results, we suggested measures for the conservation of the species and discussed them in the context of integrative and segregative conservation approaches.

Methods

Study area

We conducted the study in western Austria, eastern Switzerland, and the Principality of Liechtenstein (46.8 - 47.5°N, 9.3 - 10°E). About half of the study region is covered with forest; the rest of the area is mainly composed of unforested area in the alpine zone, alpine pastures, and the deforested bottoms of larger valleys. In the study region, white-backed woodpeckers typically occur between 600 and 1300 m a.s.l. in mixed stands dominated by Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) or, less frequently due to their lower availability, in pure deciduous stands dominated by European beech. Forests are mainly managed through single-stem or group selection and irregular shelterwood systems. However, even-aged monocultures are still found in the study area as a result of past forest management, and, depending on the landowner and the accessibility of the stands, forest management intensity can vary considerably at a small scale. As a result, a mosaic of stands differing in age and vertical structure is found in many parts of the study area.

Capturing and tracking

Between 2016 and 2019, we captured 62 adult individuals (40 males, 22 females) using playbacks and mist nets and fitted them with very high frequency (VHF) transmitters (PIP3, Biotrack Ltd., Wareham, UK). Each bird was tracked during a two- and a four-hours session per week until the battery of the transmitter was dead after nine months or until the bird lost the transmitter during the molt in summer. Within a tracking session, the woodpecker's locations and their accuracies (estimated as the radius of the circle in which the woodpecker was assumed to be; mean \pm SD accuracy = 107 \pm 69 m (n = 15047)) were recorded every 15 minutes. For more details regarding capturing and tracking we refer to Chapter 1.

Home range estimation

Seasonal home ranges

First, we divided the year into six seasons: pre-breeding season (February 20 – one day before incubation of the first egg), breeding season (incubation of the first egg – fledging of the last chick);

post-breeding season (for individuals that were observed caring for chicks after fledging: one day after fledging – last observation with a chick; for individuals without chicks: 39 days, as this was the mean time adult birds were observed caring for their fledged chicks); summer (first day without a chick – August 31), fall (September 1 – November 30), and winter (December 1 – February 19). We used the mean dates on which paired individuals started breeding/the last chick fledged as beginning/end dates of the respective seasons for unpaired individuals. We then computed minimum convex polygons (MCPs) for each individual-season combination using all locations with the package *adehabitatHR* (Calenge, 2006) in R 3.6.1 (R Core Team, 2020). We chose MCPs as home range estimator because the habitat types within MCPs are a reasonable measure for availability when assessing habitat selection within home ranges (Aebischer et al., 1993). We excluded all locations with accuracy >200 m (9.5% of the locations) prior to the analyses. Furthermore, we only considered individual-season combinations for which at least 30 locations collected over at least 5 days were available for the home range calculations. When an individual was tracked during the same season in different years (eight woodpeckers were tracked in two years, one in three years), we only used the home range for which the most locations were available. In total, we used 14042 locations and 134 seasonal home ranges (with on average \pm standard deviation 95 ± 50 locations collected over 10 ± 4 days per seasonal home range) of 50 individuals for the analyses.

Annual home ranges

White-backed woodpeckers exhibit high site fidelity, with seasonal home ranges usually overlapping partly (Chapter 1). Thus, to investigate the selection of habitat types for establishing seasonal home ranges within a larger area, we used an approximation of the year-round home ranges as available area. As most individuals were tracked during only one or few seasons, MCPs computed with all locations would underestimate the year-round home range for such individuals. Thus, we used a 1 km buffer (314 ha) around the centroid of each seasonal home range, because this area corresponded to the mean total MCP home range size of six individuals tracked year-round (Chapter 1).

Habitat data

Habitat types

We used two sources of remote sensing data to derive seven habitat types. First, we extracted the land cover types 'Broad-leaved forest', 'Coniferous forest', and 'Mixed forest' from CORINE land cover data (European Environment Agency (EEA), 2019), which were available as vector data with a minimum mapping unit of 25 ha. We defined the area falling into the first or third class as deciduous/mixed forest (*D*), kept the class coniferous forest (*Con*), and defined the rest of the area as unforested (*Unforested*).

In addition, we used two structural parameters derived from airborne light and detection ranging (LiDAR) data (see Chapter 2 for analyses of LiDAR data), maximum vegetation height and standard deviation of the vegetation height, to separate stands by age and vertical structural diversity, respectively. LiDAR variables were computed for 50 x 50 m pixels. We defined each forested pixel with a maximum vegetation height of ≥ 40 m as old forest (*O*) and all other forested pixels as young forest (*Y*). The 40-m threshold was chosen because the dominating tree species found in our study area typically reach this height in mature and old-growth stands (Commarmot et al., 2005). Initially, we had defined a third age class with maximum vegetation height < 20 m; however, most home ranges did not include pixels with such a low maximum vegetation height, and we thus did not distinguish between 20 – 40 m and < 20 m. We are aware that the maximum height varies greatly depending on the growing conditions (Pretzsch et al., 2010) and that our approach probably did not always correctly classify old and young stands. However, positive correlations between tree age and height have been found both for individual trees based on heights measured in the field (Kuuluvainen et al., 2002) and at the stand scale based on parameters obtained from LiDAR data (Maltamo et al., 2020), and we use the terms old and young for convenience here.

Stands with a high variation in vegetation height are likely to contain a high variety of age classes (McElhinny et al., 2005) as found in stands with little human intervention; for instance, the standard deviation of the tree height is usually larger in primeval or unmanaged forests than in managed forests (Commarmot et al., 2005). Hence, we next defined each pixel with a standard deviation larger than the median standard deviation of the respective age class as heterogeneous (*Het*) and with a standard deviation smaller than the median as homogeneous (*Hom*), respectively. Based on the three parameters land cover type, maximum tree height, and standard deviation of the tree height, we created the habitat types 1) *DOHet* (old heterogeneous deciduous/mixed forest), 2) *DOHom* (old homogeneous deciduous/mixed forest), 3) *DYHet* (young heterogeneous deciduous/mixed forest), and 4) *DYHom* (young homogeneous deciduous/mixed forest). We created corresponding habitat types also for coniferous forest; however, as relatively few woodpecker locations were available within each of the four coniferous forest types, we grouped them into one habitat type, 5) *Con* (coniferous forest). We excluded two additional habitat types from further analyses. We did not consider locations in or pixels defined as 6) unforested area (as defined by CORINE land cover data) because we were not interested in habitat selection patterns in unforested areas; it is well-known that the white-backed woodpecker is an obligate forest species (Glutz von Blotzheim and Bauer, 1994), which was also confirmed by our raw data (only 0.8 % of the locations were found in unforested areas). We also did not consider 7) cliffs (=

pixels with a slope > 60° or including vertical cliffs) because in such a terrain the points of the available LiDAR data were partly incorrectly classified and the vegetation height metrics hence unreliable.

Trees used/available for foraging

From 2017 to 2019, we recorded trees used for foraging (as we observed white-backed woodpeckers foraging almost exclusively on live or dead trees in 2016, we only considered trees as foraging sites). Whenever a foraging woodpecker was observed, we recorded the position of the used tree and the following variables (variable names are italicized): tree type (*type*; 5 categories: live = live trees without dead branches > 10 cm diameter, deadbr = live with dead branches > 10 cm, snag = standing deadwood ≥ 1.30 m height, log = lying deadwood, stump = standing deadwood < 1.30 m height), diameter (*diameter*; diameter at breast height for live, deadbr, and snags; diameter in the middle for logs and stumps), and tree species (*species*; 5 categories: beech, spruce, fir, other = other tree species, unknown = not identifiable). To compare used versus available trees, we also recorded tree type, diameter, and species of the closest three trees with a diameter exceeding 10, 5, and 7 cm for live trees, snags, and logs/stumps, respectively. These thresholds were chosen as they were the minimum diameters of trees used during foraging observations made in 2016 (unpublished data). To avoid pseudoreplication in our analyses, we only used observations that were at least one hour apart per individual, resulting in data on 234 used and 702 available trees from 59 individuals for modeling foraging tree selection (mean and standard deviation of characteristics of used and available trees are shown in Table A.1).

Statistical analyses

Selection of habitat types

We investigated habitat selection at the levels of a) habitat types for establishing seasonal home ranges within 1 km buffers and b) habitat types within seasonal home ranges by comparing the proportions of used and available habitat using compositional analysis (Aebischer et al., 1993). For a) we considered the proportions of each habitat type within the seasonal MCPs as used and the proportions within the respective buffers (including the seasonal MCPs) as available habitat. For b) we considered the proportions of locations within each habitat type as used and the proportions of each habitat type within the seasonal MCPs as available habitat. As we excluded unforested area and cliffs, we considered the sum of the five forest habitat types as 100%. We performed compositional analyses for each season at each level (i.e., a total of 12 analyses) in two steps using the package *adehabitatHS* (Calenge, 2006) in R 3.6.1 (R Core Team, 2020). First, we analyzed the mean differences between the used/available log-ratios using MANOVAs to assess whether overall habitat selection differed from random ($p < 0.05$). When habitat selection occurred at a season-level combination, we then performed pairwise

comparisons to determine significant ($p < 0.05$) differences between the habitat types. We applied randomization tests with 1000 iterations and replaced missing proportions of used habitat (i.e., when a habitat type was not used by an individual) by 0.001 for all analyses. To assess the impact of the accuracy of the locations on habitat selection, we performed the analyses once with all locations (accuracy at least 200 m) and once only with locations with an accuracy of at least 100 m. Because both analyses yielded the same results, we kept all locations with an accuracy of at least 200 m for our final analyses.

Selection of foraging trees

We applied logistic regression to examine foraging tree selection. We modeled the binary response variable used/available as a function of the fixed effects diameter (*diameter*), tree type (*type*) and tree species (*species*) and the random effects observation ID (*obs_id*; set of one used and the closest three available trees) nested within individual ID (*ind_id*). Next, we fitted two models additionally including the interactions between *diameter* and *type*, and *diameter* and *species*, respectively, as we expected *diameter* to have a larger effect on the relative probability of selection for live trees than for deadwood and for non-beech trees than for beech trees, respectively. Moreover, we fitted a null model including only the random effects. We compared these four models using the leave-one-out information criterion LOOIC (Vehtari et al., 2019) to find a base model, which turned out to be the model including only the three main effects. To this base model, we added habitat type (*habtype*), season (*season*; summer and fall merged to reduce model size; we did not expect relevant differences between these seasons), or sex (*sex*) as a predictor, always including the interaction with one of the three tree variables from the base model. These nine additional models were also compared using LOOIC. Note that habitat, season, and sex were always the same per observation ID and, hence, the focus was not on their main effects but on the interactions with predictors of the base model (e.g., looking at differences in tree diameter preference between the sexes).

Inspecting the raw data (Table A.1) showed that spruce and fir, the dominating coniferous tree species, made up only 31.5 and 16.9% of the available trees in coniferous forests (coniferous forest is defined as forest with > 75% of coniferous trees). This indicates that white-backed woodpeckers might have selected smaller deciduous patches within coniferous stands, which makes it difficult to detect habitat type-specific selection for a specific tree species based on our used-available trees data. Moreover, seasonal differences in availability (logs and stumps were not available when snow cover was high) complicate comparing habitat selection between seasons. Hence, we additionally explored potential differences in the used tree characteristics (diameter, tree type, tree species) between seasons, habitat types, and sexes by considering only the used trees. We fitted one model per tree characteristic, using

a linear mixed effects model for the log-transformed diameter and multinomial logistic regression models for tree type and tree species. All three models included season, habitat type, and sex as fixed effects and individual ID (as multiple observations per individual were available) as random effect. For the tree species model, we only used data of trees with known tree species, resulting in a slightly smaller sample size than for the diameter and tree type models (239 vs. 277; sample sizes were larger than for the binary logistic regression models as we had additional observations with data on used but not on available trees).

We ran all models in a Bayesian framework in R 3.6.1 (R Core Team, 2020), using Stan through the 'brms' package (v.2.18.0, Bürkner, 2018, 2017). For the binary logistic regression and linear mixed effects models, we used default priors generated by Stan. For the multinomial logistic regression models, we used a normal distribution with mean = 0 and standard deviation = 5 for the fixed effect and intercept priors, and a student-t distribution with $df = 3$, mean = 0 and scale = 2.5 for the variance component priors. We ran four chains with 3000 iterations after 3000 warm-up iterations for each model, which allowed all chains to converge as indicated by rhat values of 1 and effective sample sizes of > 400 for all coefficients (Vehtari et al., 2021). We used the central 95% values of the marginal posterior distributions as 95% credible intervals for parameter estimates.

Results

Selection of habitat types

According to the compositional analyses, habitat selection occurred only at the second level (seasonal home range establishment) and only during the pre-breeding and breeding seasons ($\lambda = 0.39$, $P = 0.002$ and $\lambda = 0.29$, $P = 0.002$, respectively; see Table A.2 and A.3 for results for the other seasons and of the third-level analyses). In both seasons, old deciduous/mixed forests were the most preferred habitat types as shown by the significantly higher mean log-ratio differences than those for the three other habitat types (Table 2; raw data are shown in Fig. 1). The log-ratios of *DOHet* and *DOHom* did not differ significantly, indicating that both habitat types were preferred equally. In the breeding season, *DYHet* had a significantly higher log-ratio difference than *DYHom*, while their log-ratio differences did not differ significantly in the pre-breeding season. *Con* was avoided compared to all other habitat types in both seasons.

Table 2 Results of the compositional analyses addressing selection of habitat types for establishing seasonal home ranges within the annual home range (1 km buffer around centroid of seasonal home range) in the pre-breeding and breeding seasons. Shown are the mean differences \pm standard error between the used/available log-ratios for all pairwise comparisons between the habitat types. Values are positive when the habitat type in the corresponding row was preferred and negative when it was avoided compared to the habitat type in the corresponding column. Significant differences ($p < 0.05$, based on pairwise randomization tests) are printed in bold. Wilk's lambda and p-value from the MANOVAs are given in parentheses.

	DOHet	DOHom	DYHet	DYHom	Con
pre-breeding season ($\lambda = 0.39, p = 0.004$)					
DOHet		0.03 \pm 0.08	0.57 \pm 0.26	0.68 \pm 0.18	2.39 \pm 0.76
DOHom	-0.03 \pm 0.08		0.54 \pm 0.22	0.64 \pm 0.15	2.34 \pm 0.74
DYHet	-0.57 \pm 0.26	-0.54 \pm 0.22		0.10 \pm 0.24	1.72 \pm 0.87
DYHom	-0.68 \pm 0.18	-0.64 \pm 0.15	-0.10 \pm 0.24		1.83 \pm 0.71
Con	-2.39 \pm 0.76	-2.34 \pm 0.74	-1.72 \pm 0.87	-1.83 \pm 0.71	
breeding season ($\lambda = 0.29, p = 0.001$)					
DOHet		-0.10 \pm 0.09	0.35 \pm 0.11	0.66 \pm 0.17	2.45 \pm 0.44
DOHom	0.10 \pm 0.09		0.45 \pm 0.10	0.76 \pm 0.14	2.61 \pm 0.47
DYHet	-0.35 \pm 0.11	-0.45 \pm 0.10		0.31 \pm 0.11	2.09 \pm 0.46
DYHom	-0.66 \pm 0.17	-0.76 \pm 0.14	-0.31 \pm 0.11		1.87 \pm 0.48
Con	-2.45 \pm 0.44	-2.61 \pm 0.47	-2.09 \pm 0.46	-1.87 \pm 0.48	

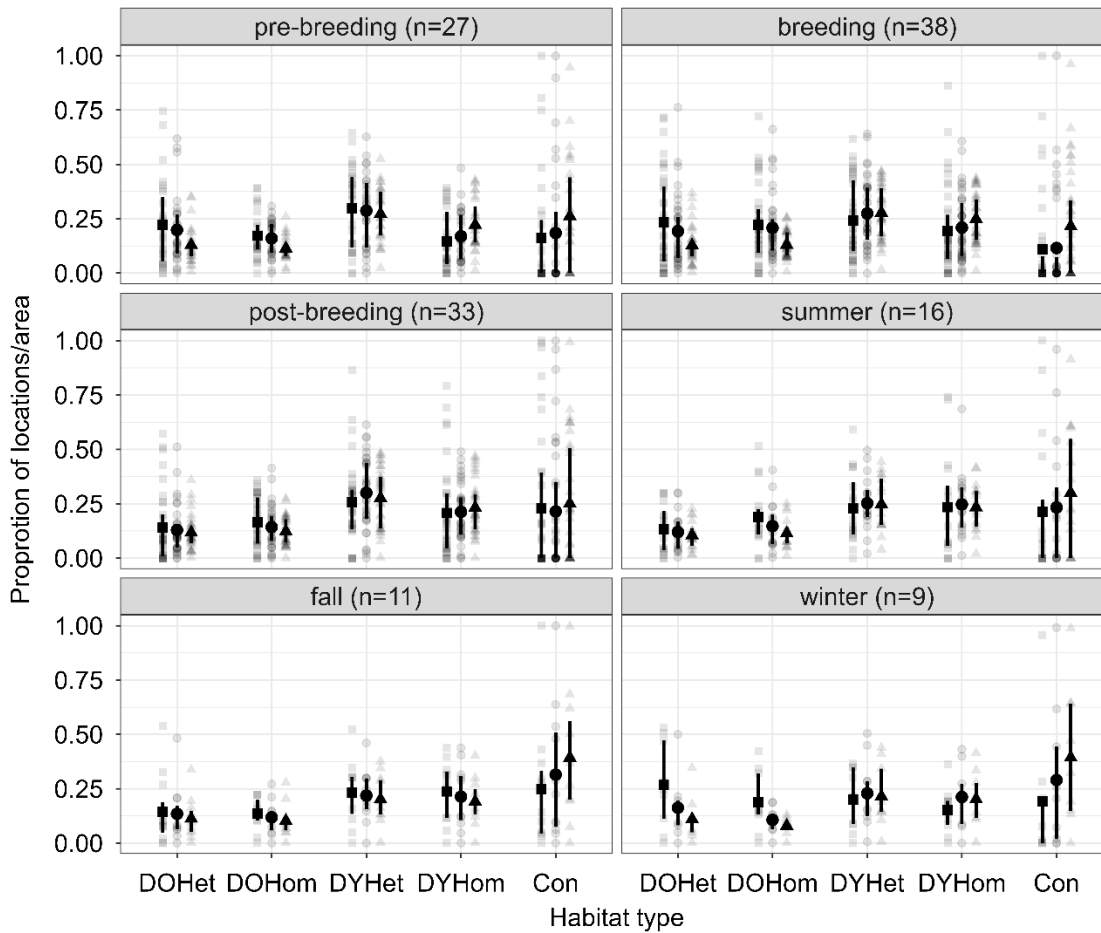


Fig. 1 Mean proportions of white-backed woodpecker telemetry locations within each of five habitat types (black squares, used habitat for investigating 3rd level habitat selection), habitat types within seasonal home ranges (black circles, used habitat for 2nd level selection and available habitat for 3rd level selection), and habitat types within 1 km buffers around home range centroids (black triangles, available habitat for 2nd level selection) per home range in each of six seasons. Sample sizes (number of home ranges) per season are given in parentheses. Vertical lines = interquartile range, gray symbols = raw data at the individual level. DOHet = old and heterogeneous deciduous/mixed forest, DOHom = old and homogeneous deciduous/mixed forest, DYHet = young and heterogeneous deciduous/mixed forest, DYHom = young and homogeneous deciduous/mixed forest, Con = coniferous forest.

Selection of foraging trees

When modeling the selection of foraging trees (fourth-level habitat selection), the model without interactions had the lowest LOOIC (Table 3, Table 4). According to this model, the probability of a tree being selected for foraging (note that selection probabilities in this study refer to the probability that certain tree characteristics will be selected within choice sets of four trees) increased with the diameter of the tree, was highest for snags, followed by logs > stumps > live trees with dead branches > live trees without dead branches, and was similar for all tree species (Table 4, Fig. 2a-c). A model including also the interaction between diameter and tree type ranked similarly high (Δ LOOIC to the top-ranked model

= 0.65) and showed that the effect of diameter on the probability of selection tended to be stronger for logs than for the other tree types (Fig. 2d).

Models additionally including interactions between the tree characteristics and season, habitat type and sex ranked lower than the model including only the tree characteristics (Table 3). Three models that ranked relatively high (ΔLOOIC to the top-ranked model = 3.48 – 5.84) included the interactions between sex and diameter, between sex and tree species, and between diameter and habitat type (Table 3). According to these models, the relation between probability of selection and diameter tended to be slightly stronger for males than for females (Fig. 2e), and males tended to stronger select beech, spruce, and fir than females (Fig. f). Moreover, the probability of selection increased with the tree diameter only in the old forest types and in young heterogeneous forest. However, the sex-specific differences were weak and the credible intervals of the parameter estimates for all interaction terms included zero.

Table 3 Models used for addressing a) the selection of three foraging tree characteristics (diameter, tree type, tree species) by white-backed woodpeckers and b) models for additionally exploring differences in foraging tree selection between seasons, habitat types, and sexes. Each model also included the random effects observation ID (one used and three available trees per observation were recorded) nested within individual ID. Model selection was performed based on the leave-one-out-cross-validation information criterion LOOIC. ΔLOOIC = difference between a model's LOOIC and the top-ranked model's LOOIC.

	Fixed effects	LOOIC	ΔLOOIC
a)	diameter + type + species	912.97	0.00
	diameter + type + diameter*type + species	913.62	0.65
	diameter + type + species + diameter*species	919.85	6.88
	diameter + type + species + diameter*type + diameter*species	920.41	7.44
	null model	1057.64	144.67
b)	sex + diameter + sex*diameter + type + species	916.45	3.48
	sex + species + sex*species + diameter + type	917.92	4.95
	habtype + diameter + habtype*diameter + type + species	918.81	5.84
	sex + type + sex*type + diameter + species	922.02	9.05
	season + diameter + season*diameter + type + species	923.18	10.21
	season + type + season*type + diameter + species	924.46	11.49
	habtype + type + habtype*type + diameter + species	935.40	22.43
	season + species + season*species + diameter + type	944.21	31.24
	habtype + species + habtype*species + diameter + type	944.75	31.78

Table 4 Model coefficients for variables included in the top-ranked model explaining selection of foraging trees by white-backed woodpeckers. Presented are posterior means and 95% credible intervals (CrI). Reference level for type = snag, reference level for species = beech. Variables are explained in the methods section.

Variable	Level	Estimate	Lower CrI	Upper CrI
Fixed effects				
Intercept		-1.87	-2.43	-1.32
diameter		0.30	0.10	0.49
type	log	-0.90	-1.40	-0.41
	stump	-1.51	-2.17	-0.87
	deadbr	-2.15	-2.78	-1.56
	live	-3.34	-4.06	-2.66
species	spruce	-0.30	-0.79	0.20
	fir	-0.40	-1.01	0.20
	other	0.14	-0.47	0.75
	unknown	-0.51	-1.13	0.11
Random effects				
ind_id		0.22	0.01	0.50
ind_id:obs_id		0.09	0.00	0.26

When considering only the used trees, diameter and tree type varied between seasons and habitat types, whereas no differences were found for tree species, and none of the tree characteristics varied between sexes (Fig. 3; see Tables A.4 – A.6 in the appendix for model coefficients). The trees used for foraging tended to be thicker in winter and in the pre-breeding season than during the rest of the year in all habitat types. Moreover, used trees were thicker in old deciduous forests than in young deciduous and coniferous forests in all seasons (Fig. 3). Snags were more likely to be used than the other tree types in the pre-breeding season, summer/fall, and winter in most habitat types, with relative probabilities of use substantially higher than those of the other tree types in summer/fall and winter in all habitat types except DOhet (Fig. 4). In contrast, in the breeding and post-breeding seasons, logs were most likely to be used in all habitat types except DOhet in the post-breeding season; however, in both seasons, the credible intervals included the mean for snags and/or live trees with dead branches in most habitat types. Stumps and live trees without dead branches were seldomly used in all seasons and habitat types except DOhet; in this habitat type, stumps were similarly likely to be used as snags and logs in most seasons (however, the credible intervals were large, Fig. 4).

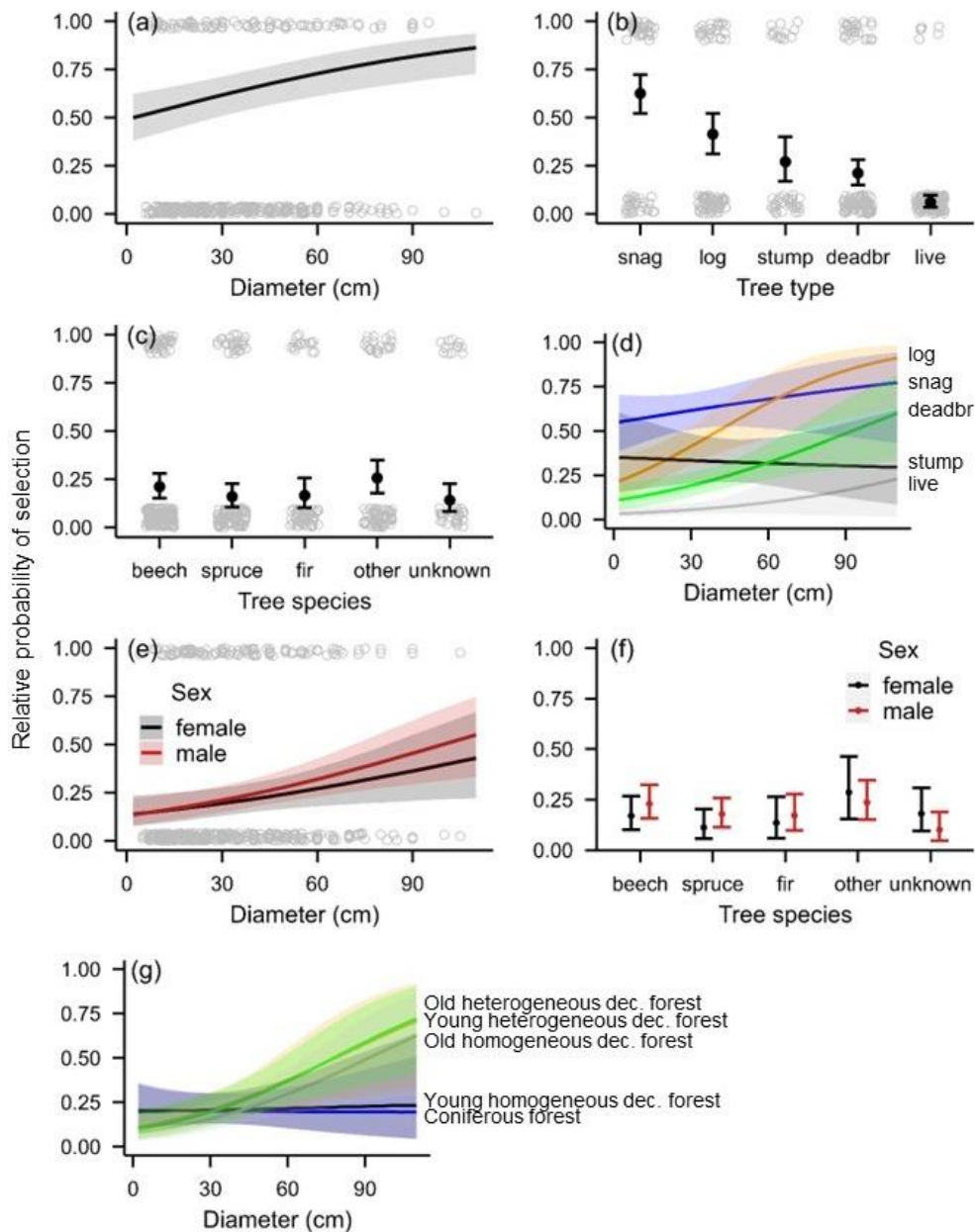


Figure 2 Foraging tree selection of the white-backed woodpecker in relation to various tree characteristics. Shown are relative probabilities of selection in relation to (a) tree diameter, (b) tree type, and (c) tree species based on the top-ranked model, and (d) diameter depending on tree type, (e) diameter and (f) tree species depending on sex, and (g) diameter depending on habitat type based on other high-ranked models. For each tree on which a foraging white-backed woodpecker was observed, the used tree and the closest three unused trees were recorded. Hence, the effect plots show the probability that a tree with certain characteristics will be selected from these sets of four trees. Shown are means of the expected value of the posterior predictive distribution and 95% credible intervals. $N = 936$ (234 used and 702 available trees, based on observations of 59 individuals).

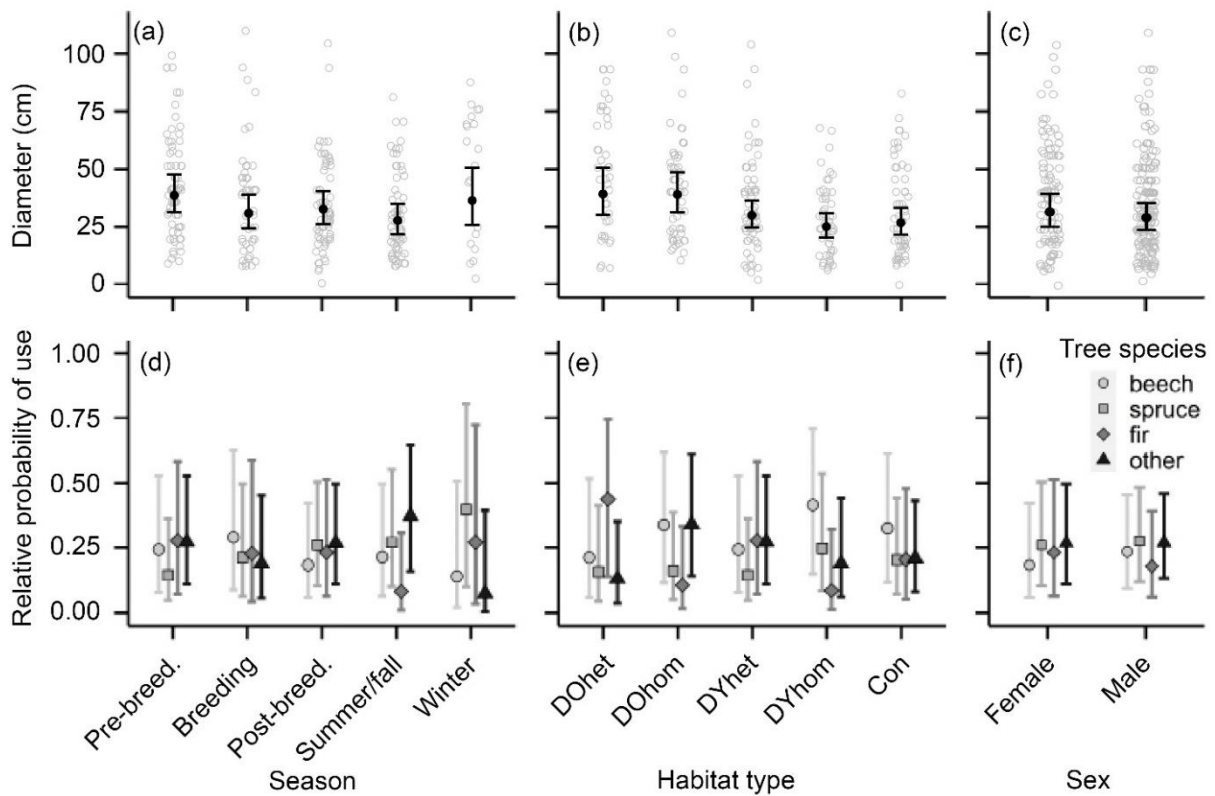


Figure 3 Characteristics of trees used for foraging by white-backed woodpeckers. Mean diameter of trees used for foraging per (a) season, (b) habitat type, and (c) sex (based on a model with diameter as response variable, $n = 277$, observations of 68 individuals) and relative probabilities of a tree used by a foraging white-backed woodpecker being associated with each of four tree species per (d) season, (e) habitat type, and (f) sex (model with tree species as response variable, $n = 239$, observations of 62 individuals). Shown are means and 95% credible intervals (vertical lines). Effect sizes of season were similar in all habitat types and for both sexes and are displayed for habitat type = DYhet and sex = female, estimates of habitat type were similar in all seasons and for both sexes and are displayed for season = post-breeding season and sex = female, estimates of sex were similar in all seasons and habitat types and are displayed for season = post-breeding season and habitat type = DYhet. Circles in (a) - (c) are the raw data. DOhet/DOhom = old deciduous or mixed heterogeneous/homogeneous forest, DYhet/DYhom = young deciduous or mixed heterogeneous/homogeneous forest, Con = coniferous forest.

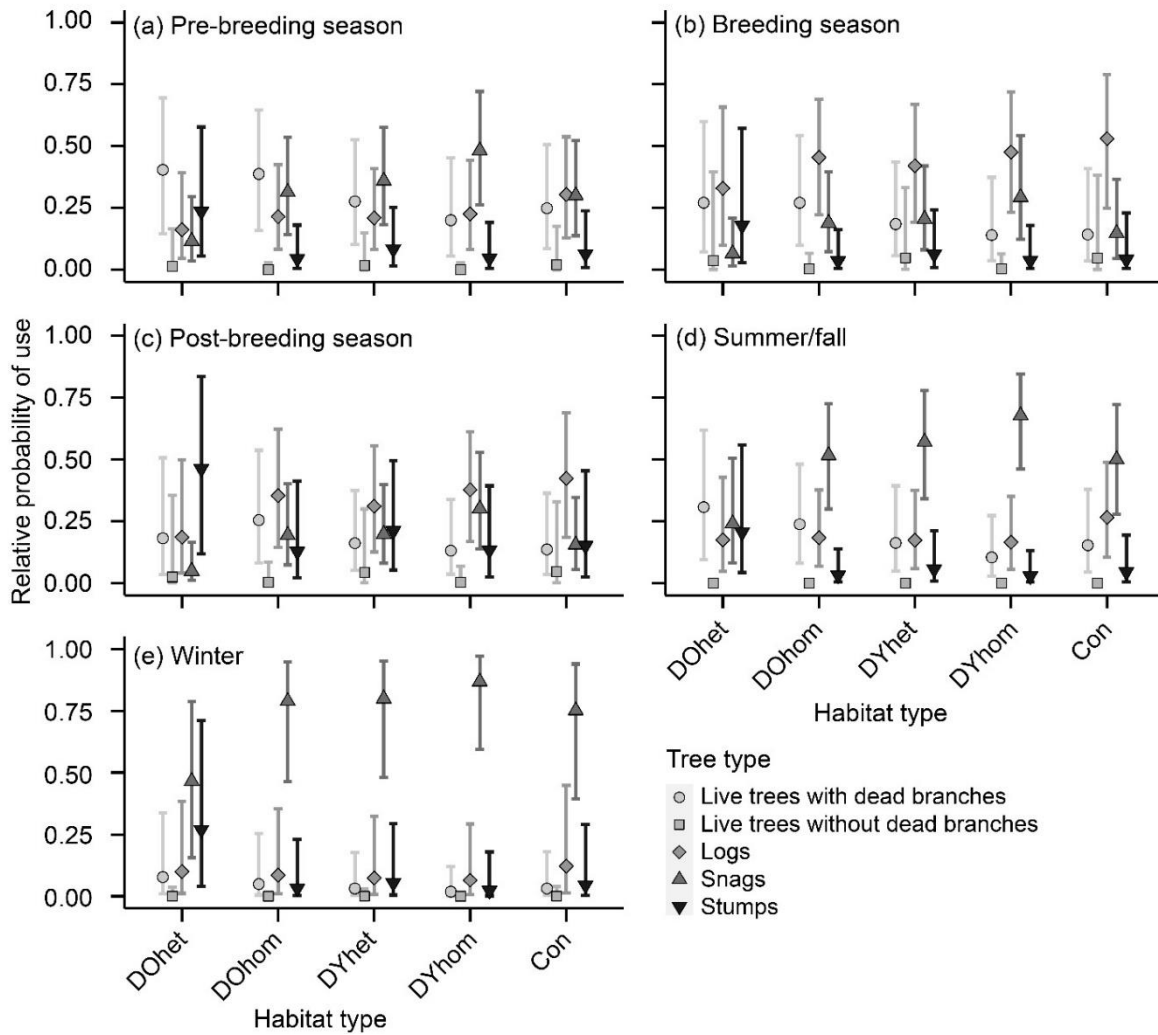


Figure 4 Relative probabilities of a tree used by a foraging white-backed woodpecker being associated with each of five tree types per season and habitat type. Shown are means and 95% credible intervals (vertical lines) of the posterior predictive distribution based on a model explaining variation in the type of used trees in relation to season, habitat type, and sex. Effects are displayed for sex = female. DOhet/DOhom = old deciduous or mixed heterogeneous/homogeneous forest, DYhet/DYhom = young deciduous or mixed heterogeneous/homogeneous forest, Con = coniferous forest. Heterogeneous/homogeneous refer to the vertical structure of the forest stand. N = 277 trees (observations of 68 individuals).

Discussion

In accordance with our expectations, white-backed woodpeckers selected habitats at the second level (selection of habitat types for establishing seasonal home ranges within the annual home range) in the pre-breeding and breeding seasons and at the fourth level (selection of foraging trees) in all seasons. In contrast, we did not find support for the expected third-level habitat selection (selection of habitat types within seasonal home ranges) in the post-breeding season, summer, fall, and winter. Our findings confirm the white-backed woodpecker's preference for old deciduous and mixed forest stands, but only

when considering the selection of the breeding habitat (which is already used in the pre-breeding season) within the annual home range. The woodpeckers showed greater flexibility in the selection of habitat types after fledging of the young but used and selected large-diameter trees and deadwood throughout the year and in all habitat types.

Differences between levels of habitat selection and seasons

White-backed woodpeckers preferred old deciduous or mixed forests for establishing their pre-breeding and breeding home ranges and used the habitat types according to their availability within the home ranges. By contrast, there was no evidence for the selection of specific habitat types during the rest of the year, neither at the second nor at the third level. The lacking evidence for preferences of specific habitat types in the non-breeding season, particularly in summer, fall and winter, might partly be due to the small sample sizes. However, an important factor may also be the high inter-individual variation in the woodpeckers' space use. For example, some individuals shifted their home range almost entirely into coniferous forest in the post-breeding season, while others still mainly used old deciduous forests (Fig. 1). Similarly, some individuals moved over large areas with seasonal minimum convex polygon home ranges up to 300 ha and used only parts of them, whereas others only slightly expanded their breeding home range after fledging of the chicks and used most of the area (unpublished data). Considering that breeding home ranges were relatively small (mean breeding home range size based on 95% Kernel density estimation was 22 ha) compared to post-breeding and annual home ranges (on average 47 and 116 ha, respectively; Chapters 1 and 2), our findings suggest that white-backed woodpeckers select a small area with a relatively high proportion of old forest (compared to what is available within their annual home range) for nesting and use a greater variety of habitat types in the larger non-breeding home ranges. Such a pattern is probably due to the constraint of central place foraging during the breeding season. Increasing traveling distances between the nest and foraging patches are associated with increasing costs, e.g., in terms of time, energy, and mortality risk (Olsson et al., 2008). Therefore, a high density of saproxylic beetle larvae, which are the main prey of the white-backed woodpecker (Aulén, 1988) and typically most abundant in old forests (Grove, 2002; Stenbacka et al., 2010), is particularly important in the breeding season. In contrast, individuals are more flexible in the non-breeding season when they are not constrained by a central place.

This apparent flexibility was limited to second- and third-level habitat selection, whereas fourth-level selection occurred in all seasons. White-backed woodpeckers selected deadwood for foraging year-round and in all habitat types, which shows that the species is a deadwood specialist throughout the year. Hence, the greater flexibility in the use of habitat types in the non-breeding season is unlikely to

be caused by a change in the diet but rather arises from the increased mobility, which enables the birds to use dispersed pieces of deadwood also in habitat types with presumably low deadwood abundance.

Preferred habitat types and foraging trees

Forest height (representing stand age) played a more important role in the selection of forest types than vertical forest structure, with old homogeneous and old heterogeneous deciduous/mixed forests being equally preferred over young deciduous/mixed and coniferous forests for establishing pre-breeding and breeding home ranges. Old deciduous and mixed forests are known to be typical white-backed woodpecker habitats as they can provide a high density of food resources and potential nesting trees (Hogstad and Stenberg, 1994; Scherzinger, 1982). All pre-breeding and breeding home ranges except those of one individual included at least some area of these habitat types (Fig. 5), indicating that old deciduous or mixed forests are essential as part of the breeding territory. However, the old forest types constituted on average only 36 and 40% of the forested area within pre-breeding and breeding home ranges, respectively, indicating a high potential of the other habitat types as breeding habitat as well. Our finding that both old forest types were preferred equally, regardless of their vertical structure and thus presumed management intensity, is contrary to our expectations and might be explained by the high amounts of deadwood in both habitat types. Although the mean deadwood volume was lower in DOhom than in DOhet, both habitat types contained very high amounts of deadwood (on average $80 \text{ m}^3\text{ha}^{-1}$ in DOhom and $90 \text{ m}^3\text{ha}^{-1}$ in DOhet, Table A.7). That the young deciduous/mixed forest types were avoided compared to old forests might also be explained by the available deadwood, particularly by the availability of large-diameter snags and logs (diameter $>30 \text{ cm}$), which were twice as abundant in the old forest types than in the young ones (Table A.7). Young deciduous/mixed forests were still preferred over coniferous forests, confirming the species' specialization on deciduous forests (Glutz von Blotzheim and Bauer, 1994). However, as mentioned above, the variability between individuals was high in all seasons, and some individuals intensively used coniferous forests, with more than half of the telemetry locations found in this habitat type (Fig. 1). This finding shows that white-backed woodpeckers can use coniferous forests when they contain suitable foraging trees.

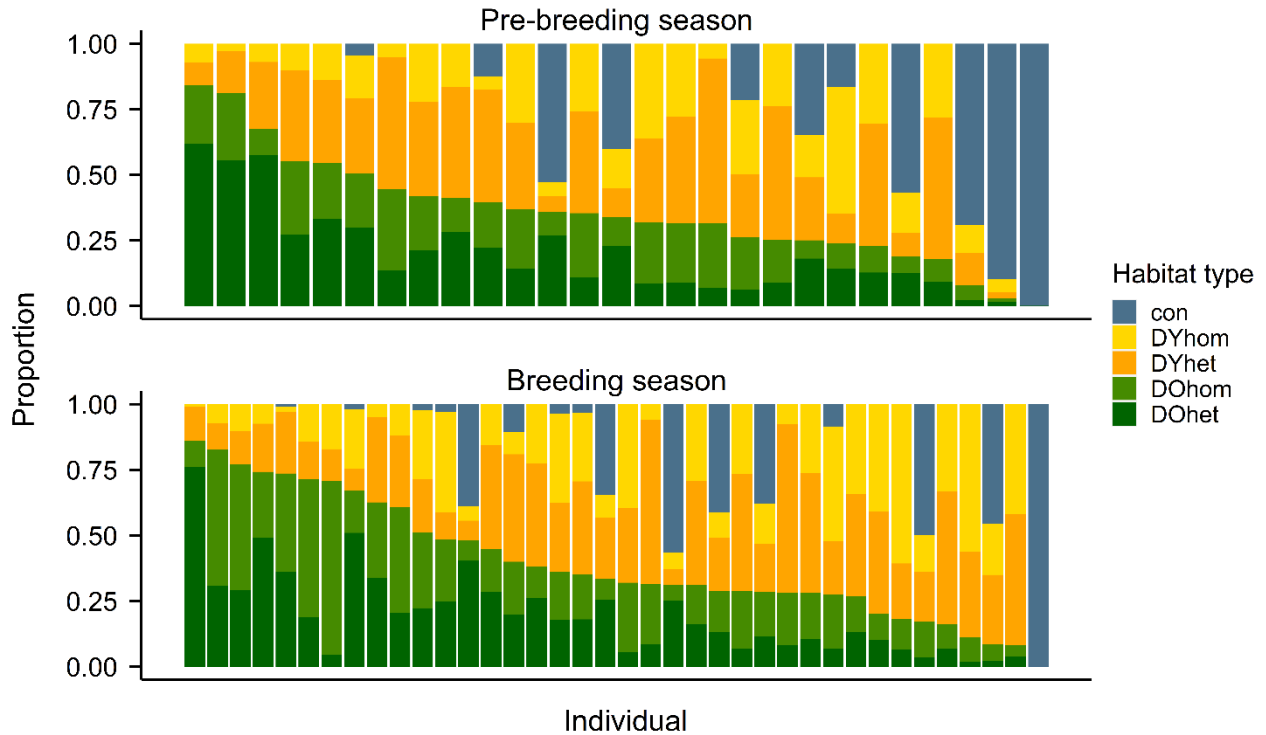


Figure 5 Composition of the forested area within white-backed woodpecker pre-breeding (n=27) and breeding (n=38) home ranges. Each bar represents one individual and the habitat types within its seasonal home range. Con = coniferous forest, DYhom = young homogeneous deciduous or mixed forest, DYhet = young heterogeneous deciduous or mixed forest, DOhom = old homogeneous deciduous or mixed forest, DYhet = old heterogeneous deciduous or mixed forest. Data were sorted by the proportion of old deciduous or mixed forest (DOhet + DOhom), the preferred habitat type in the pre-breeding and breeding seasons.

At the fourth level, deadwood, particularly snags and large-diameter logs, had the highest relative probabilities of being selected for foraging, which confirms the importance of deadwood as foraging substrate (Aulén, 1988; Bühler, 2009; Czeszczewik, 2009; Frank and Hochebner, 2001; Stenberg and Hogstad, 2004) and indirectly the specialization on saproxylic beetle larvae as main prey (Aulén, 1988). Partly in accordance with our expectations, our additional analyses considering only the used trees showed that snags were intensively used throughout the year, whereas the importance of logs varied seasonally. As expected, snags were particularly important in winter, which is probably due to the reduced availability of logs and stumps when the ground is covered with snow and to the reduced availability of surface-living arthropods on live trees. Surprisingly, snags were much more likely to be used than logs and other foraging substrates also in summer and fall. The high importance of snags in summer and fall might be partly explained by the molt, which takes place in summer (Glutz von Blotzheim and Bauer, 1994). Birds often change their behavior during molt to protect the growing feathers from damage, reduce predation risk, or decrease energy expenditure (Jenni and Winkler, 2020), and foraging mainly on snags instead of logs and stumps on the ground could be a strategy to

reduce predation risk. In contrast, in the breeding season, logs had the highest probability of use, which is in accordance with findings of Czeszczewik (2009). It is important to mention that this finding does not necessarily mean that logs are preferred or selected, as we considered only used trees in the respective model and thus did not address habitat selection with this model. A potential explanation for the increased use of logs during the breeding season is that logs contain more beetle larvae. While snags are important for other reasons in the post-breeding season and winter, a high food availability might play the most important role for the selection of foraging trees in the breeding season. However, while studies on saproxylic beetles generally agree that the community composition differs between snags and logs (e.g., Gibb et al., 2006; Hjältén et al., 2010; Jonsell and Weslien, 2003), there is no clear evidence for saproxylic beetles being more abundant in either of them. For instance, Bouget et al. (2012) found that oak snags had a higher abundance of saproxylic beetles than oak logs, whereas Hjältén et al. (2007) found the opposite pattern for spruce. A more likely explanation for the intensive use of logs in the breeding season could be that logs are generally more abundant in our study area (Ettwein et al., 2020) and foraging on all types of deadwood in a small area around the nest is energetically more profitable than moving large areas to forage mainly on the less abundant snags.

Generally, the mentioned seasonal differences in the use of tree types were similar across all habitat types except DOhet, the habitat type that most closely resembled the late successional stages of primeval forests. While in the other habitat types either snags or logs, depending on the season, had markedly higher probabilities of use than the remaining tree types, the differences were less pronounced in DOhet. For instance, stumps and live trees with dead branches were equally likely to be used as snags and logs in most seasons, and stumps had higher probabilities of use in DOhet than in all other habitat types in all seasons. These findings indicate that a wider range of tree types is suitable as foraging substrate in old natural forests than in the presumably managed ones, and that snags and logs are particularly important in managed forests. Moreover, it shows that results of studies conducted in natural forests cannot necessarily be transferred to managed forests. For instance, Czeszczewik (2009) found in a primeval forest that half of the trees used for foraging by white-backed woodpeckers in winter were alive (in our study area 15%). Such differences could be due to habitat differences (e.g., much larger dimensions of and more microhabitats on trees in primeval forests than in managed forests) and concluding that live trees are a suitable winter foraging substrate also in managed forests could be misleading.

Our results show that habitat preferences found in a specific season do not have to be valid in other parts of the year and support Marra's et al. (2015) call for full annual cycle studies. In birds, there is a particularly strong bias towards studies conducted in the breeding season (Marra et al., 2015), although

other parts of the annual cycle might be at least as important for animals. For instance, winter territory quality may affect reproductive success (Rushing et al., 2016) or survival (Duriez et al., 2012) of a species. Thus, if the importance of different resources for birds varies between seasons, focusing on breeding habitat characteristics might be insufficient for the conservation of a species. However, ultimately assessing the critical periods of the year and thus the limiting habitat factors (in our case whether snags or logs or both are limiting individuals and populations) would require also investigating the relationship between habitat and demographic rates (Johnson, 2007) as well as seasonal interactions (Marra et al., 2015).

Lastly, while studies from Scandinavia (Aulén and Lundberg, 1991; Stenberg and Hogstad, 2004) found that foraging tree use differed between males and females, sex was not included in our top-ranked model, and according to lower-ranked models including sex, the sex-specific differences in foraging tree selection and use were small. Additional analyses using similar methods as the mentioned authors revealed significant differences in the trees used by males and females regarding diameter and tree type, indicating that white-backed woodpeckers in our study area also exhibit sexual dimorphism in foraging behavior to some extent. However, while the Scandinavian studies found that males tended to use trees of larger diameters than females (the differences were significant only for some seasons and tree species), in our study area females ($n = 29$ trees) used thicker logs than males ($n = 42$; Mann-Whitney-U-test: $z = 2.67$, $p = 0.008$; data of all tree species and seasons pooled). Moreover, in contrast to findings of Stenberg and Hogstad (2004) but in accordance with those of Aulén and Lundberg (1991), females ($n = 37$ trees) used deadwood in winter and in the pre-breeding season (both seasons combined to enhance comparability with the mentioned studies) more often than males ($n = 57$), which, in turn, used live trees more often ($\chi^2 = 17.5$, $df = 4$, $p = 0.001$; data of all tree species pooled). Investigating further aspects of the white-backed woodpecker's foraging behavior might help to better assess the meaning of the sex-specific differences in foraging and morphology in the context of foraging niche separation.

Integrative or segregative conservation measures?

Our results show that the white-backed woodpecker, previously referred to as “old-growth forest specialist” (Scherzinger, 1982), also uses younger deciduous or mixed and coniferous forests stands, which in our study area are usually managed at least to some extent. Hence, managed forests can serve as habitat for this specialized species. However, there are two constraints. First, the selection of areas with a high proportion of old deciduous and mixed forests during the pre-breeding and breeding season indicates that younger and coniferous forests can serve as habitat when deciduous or mixed forest as breeding habitat are also available, which was also concluded by Scherzinger (1982). Second, our

findings confirm the species' specialization on deadwood, whereas live trees without dead branches (which were significantly thinner than live trees with dead branches; Mann-Whitney-U-test: $z = 8.36$, $p < 0.001$, $n = 522$) do not seem to be suitable as foraging substrate at all. Hence, integrating conservation measures (such as retaining deadwood) into forest management can be a reasonable approach for the protection of a species highly dependent on old-growth forest elements; however, integrative measures are useful only in areas in which old deciduous and mixed forests are also available. In our study area, the old forests within the breeding home ranges were usually protection forests or private forests with very low management intensity and not protected by classical segregative instruments such as the designation as forest reserve. Still, as the old forests contained amounts of deadwood which are not reconcilable with intensive forest management for timber production (see Table A.7), our results support the idea of integrative measures as a supplement to segregative measures as a useful approach for the conservation of the white-backed woodpecker. It is important to note, however, that combining both approaches is only a compromise between ecological and economic interests, at least for the protection of the white-backed woodpecker. In our study area both breeding success (unpublished data) and adult survival (Weber et al., in preparation) of the species are lower than in regions with lower forest management intensity or relicts of primeval forest (e.g., in southwestern Norway (Stenberg, 1997) or Bialowieza Forest (Wesołowski, 1995)). Moreover, adult survival has been shown to decrease with decreasing abundance of deadwood and large-diameter trees within the breeding home range (Weber et al., in preparation), suggesting that the lower survival rate in our study area is related to a higher forest management intensity than in other regions. Negative effects of forest management have been found also for other species preferring unmanaged forests. For instance, the health condition of Siberian tits *Poecile cinctus* was lower (Krams et al., 2010) and physiological stress in Eurasian treecreeper *Certhia familiaris* nestlings (Suorsa et al., 2003) and Northern spotted owls *Strix occidentalis caurina* (Wasser et al., 1997) higher in managed compared to less intensively managed stands. Such differences show that for some species, although occurring and successfully reproducing in managed forests, segregative conservation by providing areas of unmanaged forests large enough to ideally sustain a population would be the optimal solution. However, in the end, the value of a conservation strategy depends on both its feasibility and its impact on other species. At the landscape level, the combination of protected areas and stands with varying silvicultural systems appears to best maintain ecological diversity while fulfilling economic interests (Nolet et al., 2018), and, as indicated by our results, to also provide habitat for deadwood specialists like the white-backed woodpecker.

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References

- Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74, 1313–1325. <https://doi.org/10.2307/1940062>
- Aulén, G., 1988. Ecology and distribution of the white-backed woodpecker *Dendrocopos leucotos* in Sweden (Dissertation). Swedish University of Agricultural Sciences, Uppsala.
- Aulén, G., Lundberg, A., 1991. Sexual dimorphism and patterns of territory use by the white-backed woodpecker *Dendrocopos leucotos*. *Ornis Scand. Scand. J. Ornithol.* 22, 60–64. <https://doi.org/10.2307/3676622>
- Bässler, C., Müller, J., 2010. Importance of natural disturbance for recovery of the rare polypore *Antrodiella citrinella* Niemelä & Ryvarden. *Fungal Biol.* 114, 129–133. <https://doi.org/10.1016/j.funbio.2009.11.001>
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manag.* 258, 525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>
- Bollmann, K., Braunisch, V., 2013. To integrate or to segregate: balancing commodity production and biodiversity conservation in European forests. In *Integrative approaches as an opportunity for the conservation of forest biodiversity*. Kraus D., Krumm F. (eds). European Forest Institute, Freiburg, p. 284.
- Bouget, C., Nusillard, B., Pineau, X., Ricou, C., 2012. Effect of deadwood position on saproxylic beetles in temperate forests and conservation interest of oak snags: Oak snags and saproxylic beetle

- conservation. *Insect Conserv. Divers.* 5, 264–278. <https://doi.org/10.1111/j.1752-4598.2011.00160.x>
- Brunet, J., Isacson, G., 2009. Restoration of beech forest for saproxylic beetles—effects of habitat fragmentation and substrate density on species diversity and distribution. *Biodivers. Conserv.* 18, 2387. <https://doi.org/10.1007/s10531-009-9595-5>
- Bühler, U., 2009. Totholz – existenziell für den Weissrückenspecht in Nordbünden | Dead wood – a vital necessity for the white-backed woodpecker in the Grisons. *Schweiz. Z. Forstwes.* 160, 210–217. <https://doi.org/10.3188/szf.2009.0210>
- Bürkner, P.-C., 2018. Advanced Bayesian multilevel modeling with the R package brms. *R J.* 10, 395–411.
- Bürkner, P.-C., 2017. brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* 80, 1–28. <https://doi.org/10.18637/jss.v080.i01>
- Calenge, C., 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197, 516–519.
- Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Ramp, B., Shparyk, Y., Sukhariuk, D., Viter, R., Zingg, A., 2005. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. *For. Snow Landsc. Res.* 79, 45–56.
- 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 Ornithol.* 44, 109–118. <https://doi.org/10.3161/000164509X482687>
- Czeszczewik, D., Walankiewicz, W., 2006. Logging affects the white-backed woodpecker *Dendrocopos leucotos* distribution in the Białowieża Forest. *Ann. Zool. Fenn.* 43, 221–227.
- Doerfler, I., Gossner, M.M., Müller, J., Seibold, S., Weisser, W.W., 2018. Deadwood enrichment combining integrative and segregative conservation elements enhances biodiversity of multiple taxa in managed forests. *Biol. Conserv.* 228, 70–78. <https://doi.org/10.1016/j.biocon.2018.10.013>
- Dufour-Pelletier, S., A. Tremblay, J., Hébert, C., Lachat, T., Ibarzabal, J., 2020. Testing the effect of snag and cavity supply on deadwood-associated species in a managed boreal forest. *Forests* 11, 424. <https://doi.org/10.3390/f11040424>

- Duriez, O., Ens, B.J., Choquet, R., Pradel, R., Klaassen, M., 2012. Comparing the seasonal survival of resident and migratory oystercatchers: carry-over effects of habitat quality and weather conditions. *Oikos* 121, 862–873. <https://doi.org/10.1111/j.1600-0706.2012.20326.x>
- Ettwein, A., Korner, P., Lanz, M., Lachat, T., Kokko, H., Pasinelli, G., 2020. Habitat selection of an old-growth forest specialist in managed forests. *Anim. Conserv.* 23, 547–560. <https://doi.org/10.1111/acv.12567>
- European Environment Agency (EEA), 2019. Corine Land Cover (CLC) 2018, Version 20. Available at: <https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=download> (accessed 15 July 2019).
- Forest Europe, 2020. State of Europe's forests 2020.
- Frank, G., Hochebner, T., 2001. Erfassung der Spechte - insbesondere des Weißrückenspechtes *Picoides leucotos* - im Rhmen des LIFE-Projektes Wildnisgebiet Dürrenstein. in: LIFE- Projekt Wildnisgebiet Dürrenstein. Amt der Niederösterreichischen Landesregierung (Ed.). Amt der Niederösterreichischen Landesregierung, St. Pölten.
- Gibb, H., Ball, J.P., Johansson, T., Atlegrim, O., Hjältén, J., Danell, K., 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scand. J. For. Res.* 20, 213–222. <https://doi.org/10.1080/02827580510008392>
- Gibb, H., Pettersson, R.B., Hjältén, J., Hilszczański, J., Ball, J.P., Johansson, T., Atlegrim, O., Danell, K., 2006. Conservation-oriented forestry and early successional saproxylic beetles: Responses of functional groups to manipulated dead wood substrates. *Biol. Conserv.* 129, 437–450. <https://doi.org/10.1016/j.biocon.2005.11.010>
- Glutz von Blotzheim, U.N., Bauer, K., 1994. Handbuch der Vögel Mitteleuropas. Band 9: *Columbiformes - Piciformes*, 2nd ed. Aula-Verlag, Wiesbaden.
- Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. *Annu. Rev. Ecol. Syst.* 33, 1–23. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150507>
- Hjältén, J., Johansson, T., Alinvi, O., Danell, K., Ball, J.P., Pettersson, R., Gibb, H., Hilszczański, J., 2007. The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. *Basic Appl. Ecol.* 8, 364–376. <https://doi.org/10.1016/j.baae.2006.08.003>
- Hjältén, J., Stenbacka, F., Andersson, J., 2010. Saproxylic beetle assemblages on low stumps, high stumps and logs: Implications for environmental effects of stump harvesting. *For. Ecol. Manag.* 260, 1149–1155. <https://doi.org/10.1016/j.foreco.2010.07.003>

- Hogstad, O., Stenberg, I., 1997. Breeding success, nestling diet and parental care in the white-backed woodpecker *Dendrocopos leucotos*. J. Für Ornithol. 138, 25–38. <https://doi.org/10.1007/BF01651649>
- Hogstad, O., Stenberg, I., 1994. Habitat selection of a viable population of white-backed woodpeckers *Dendrocopos leucotos*. Fauna Nor. Ser. C Cinclus 17, 75–94.
- Jenni, L., Winkler, R., 2020. The biology of moult in birds. HELM, London.
- Johnson, D., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.
- Johnson, M.D., 2007. Measuring habitat quality: a review. The Condor 109, 489–504. <https://doi.org/10.1650/8347.1>
- Jonsell, M., Nittérus, K., Stighäll, K., 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biol. Conserv. 118, 163–173. <https://doi.org/10.1016/j.biocon.2003.08.017>
- Jonsell, M., Weslien, J., 2003. Felled or standing retained wood—it makes a difference for saproxylic beetles. For. Ecol. Manag. 175, 425–435. [https://doi.org/10.1016/S0378-1127\(02\)00143-3](https://doi.org/10.1016/S0378-1127(02)00143-3)
- Kajtoch, L., Figarski, T., Pelka, J., 2013. The role of forest structural elements in determining the occurrence of two specialist woodpecker species in the Carpathians, Poland. Ornis Fenn. 90, 23–40.
- Krams, I., Cīrule, D., Krama, T., Hukkanen, M., Rytönen, S., Orell, M., Iezhova, T., Rantala, M.J., Tummeleht, L., 2010. Effects of forest management on haematological parameters, blood parasites, and reproductive success of the Siberian tit (*Poecile cinctus*) in Northern Finland. Ann. Zool. Fenn. 47, 335–346. <https://doi.org/10.5735/086.047.0504>
- Kuuluvainen, T., Mäki, J., Karjalainen, L., Lehtonen, H., 2002. Tree age distributions in old-growth forest sites in Vienansalo wilderness, eastern Fennoscandia. Silva Fenn. 36. <https://doi.org/10.14214/sf.556>
- Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433–445. <https://doi.org/10.1016/j.biocon.2006.02.019>

- Lindhe, A., Åsenblad, N., Toresson, H.-G., 2004. Cut logs and high stumps of spruce, birch, aspen and oak – nine years of saproxylic fungi succession. *Biol. Conserv.* 119, 443–454. <https://doi.org/10.1016/j.biocon.2004.01.005>
- Maltamo, M., Kinnunen, H., Kangas, A., Korhonen, L., 2020. Predicting stand age in managed forests using National Forest Inventory field data and airborne laser scanning. *For. Ecosyst.* 7, 44. <https://doi.org/10.1186/s40663-020-00254-z>
- Marra, P.P., Cohen, E.B., Loss, S.R., Rutter, J.E., Tonra, C.M., 2015. A call for full annual cycle research in animal ecology. *Biol. Lett.* 11, 20150552. <https://doi.org/10.1098/rsbl.2015.0552>
- Martikainen, P., Kaila, L., Haila, Y., 1998. Threatened beetles in white-backed woodpecker habitats. *Conserv. Biol.* 12, 293–301.
- McElhinny, C., Gibbons, P., Brack, C., Bauhus, J., 2005. Forest and woodland stand structural complexity: Its definition and measurement. *For. Ecol. Manag.* 218, 1–24. <https://doi.org/10.1016/j.foreco.2005.08.034>
- McLoughlin, P.D., Ferguson, S.H., 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Écoscience* 7, 123–130.
- Mikusiński, G., Angelstam, P., 1998. Economic geography, forest distribution, and woodpecker diversity in Central Europe. *Conserv. Biol.* 12, 200–208. <https://doi.org/10.1111/j.1523-1739.1998.96310.x>
- Mikusiński, G., Gromadzki, M., Chylarecki, P., 2001. Woodpeckers as indicators of forest bird diversity. *Conserv. Biol.* 15, 208–217. <https://doi.org/10.1111/j.1523-1739.2001.99236.x>
- Moning, C., Müller, J., 2009. Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. *Ecol. Indic.* 9, 922–932. <https://doi.org/10.1016/j.ecolind.2008.11.002>
- Moning, C., Werth, S., Dziock, F., Bässler, C., Bradtka, J., Hothorn, T., Müller, J., 2009. Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *For. Ecol. Manag.* 258, 745–751. <https://doi.org/10.1016/j.foreco.2009.05.015>
- Müller, J., Bußler, H., Kneib, T., 2007. Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. *J. Insect Conserv.* 12, 107. <https://doi.org/10.1007/s10841-006-9065-2>

- Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *Eur. J. For. Res.* 129, 981–992. <https://doi.org/10.1007/s10342-010-0400-5>
- Nolet, P., Kneeshaw, D., Messier, C., Béland, M., 2018. Comparing the effects of even- and uneven-aged silviculture on ecological diversity and processes: A review. *Ecol. Evol.* 8, 1217–1226. <https://doi.org/10.1002/ece3.3737>
- Olsson, O., Brown, J.S., Helf, K.L., 2008. A guide to central place effects in foraging. *Theor. Popul. Biol.* 74, 22–33. <https://doi.org/10.1016/j.tpb.2008.04.005>
- Orians, G.H., Wittenberger, J.F., 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* 137, S29–S49. <https://doi.org/10.1086/285138>
- Paillet, Y., Bergès, L., Hjältén, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol. J. Soc. Conserv. Biol.* 24, 101–112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>
- Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., Spellmann, H., Zingg, A., 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Ann. For. Sci.* 67, 712–712. <https://doi.org/10.1051/forest/2010037>
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Roberge, J.-M., Angelstam, P., 2006. Indicator species among resident forest birds – A cross-regional evaluation in northern Europe. *Biol. Conserv.* 130, 134–147. <https://doi.org/10.1016/j.biocon.2005.12.008>
- Roberge, J.-M., Mikusiński, G., Svensson, S., 2008. The white-backed woodpecker: umbrella species for forest conservation planning? *Biodivers. Conserv.* 17, 2479–2494. <https://doi.org/10.1007/s10531-008-9394-4>
- Rushing, C.S., Marra, P.P., Dudash, M.R., 2016. Winter habitat quality but not long-distance dispersal influences apparent reproductive success in a migratory bird. *Ecology* 97, 1218–1227. <https://doi.org/10.1890/15-1259.1>

- Schall, P., Schulze, E.-D., Fischer, M., Ayasse, M., Ammer, C., 2018. Relations between forest management, stand structure and productivity across different types of Central European forests. *Basic Appl. Ecol.* 32, 39–52. <https://doi.org/10.1016/j.baae.2018.02.007>
- Scherzinger, W., 1982. Die Spechte im Nationalpark Bayerischer Wald. Nationalparkverwaltung Bayerischer Wald, Grafenau.
- Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R., Ruchty, A., 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* 10, 789–799. [https://doi.org/10.1890/1051-0761\(2000\)010\[0789:DLOELR\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0789:DLOELR]2.0.CO;2)
- Stenbacka, F., Hjältén, J., Hilszczański, J., Dynesius, M., 2010. Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecol. Appl.* 20, 2310–2321. <https://doi.org/10.1890/09-0815.1>
- Stenberg, I., Hogstad, O., 2004. Sexual dimorphism in relation to winter foraging in the white-backed woodpecker (*Dendrocopos leucotos*). *J. Ornithol.* 145, 321–326. <https://doi.org/10.1007/s10336-004-0045-6>
- Suorsa, P., Huhta, E., Nikula, A., Nikinmaa, M., Jäntti, A., Helle, H., Hakkarainen, H., 2003. Forest management is associated with physiological stress in an old-growth forest passerine. *Proc. R. Soc. Lond. B Biol. Sci.* 270, 963–969. <https://doi.org/10.1098/rspb.2002.2326>
- Vehtari, A., Gabry, J., Yao, Y., Gelman, A., 2019. loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models.” R package version 2.1.0, <https://CRAN.R-project.org/package=loo>.
- Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., Bürkner, P.-C., 2021. Rank-normalization, folding, and localization: An improved $R^{\hat{}}$ for assessing convergence of MCMC. *Bayesian Anal.* 16, 667–718. <https://doi.org/10.1214/20-BA1221>
- Virkkala, R., 2006. Why study woodpeckers? The significance of woodpeckers in forest ecosystems. *Ann. Zool. Fenn.* 43, 82–85.
- Virkkala, R., Alanko, T., Laine, T., Tiainen, J., 1993. Population contraction of the white-backed woodpecker *Dendrocopos leucotos* in Finland as a consequence of habitat alteration. *Biol. Conserv.* 66, 47–53. [https://doi.org/10.1016/0006-3207\(93\)90133-L](https://doi.org/10.1016/0006-3207(93)90133-L)
- Wasser, S.K., Bevis, K., King, G., Hanson, E., 1997. Noninvasive physiological measures of disturbance in the Northern spotted owl. *Conserv. Biol.* 11, 1019–1022.

Weber, P., Korner, P., Ettwein, A., Lanz, M., Pasinelli, G., in preparation. Adult survival of the white-backed woodpecker (*Dendrocopos leucotos*) in relation to sex, topography and habitat.

Wesołowski, T., 1995. Ecology and behaviour of white-backed woodpecker (*Dendrocopos leucotos*) in a primeaval temperate forest (Białowieża National Park, Poland). *Vogelwarte* 38, 61–75.

Appendix

Table A.1 Trees used/available for foraging in different habitat types and seasons and for the two sexes. For diameter mean \pm standard deviation of the used/available trees are presented; numbers for tree type and tree species refer to the percentage of used/available trees in each category. See chapter 2.3 for descriptions of variables and categories. N = sample sizes for used/available trees. Data are from 59 individuals.

	Habitat type					Season					Sex	
	DOHet	DOHom	DYHet	DYHom	Con	pre-br.	breed.	post-br.	sum/fall	winter	f	m
n	40/120	47/141	56/168	49/147	42/126	68/204	39/117	61/183	51/153	22/66	82/ 246	152/ 456
Diameter (cm)	49 \pm 24/ 32 \pm 21	42 \pm 22/ 32 \pm 19	35 \pm 21/ 29 \pm 16	27 \pm 14/ 28 \pm 18	33 \pm 20/ 34 \pm 22	45 \pm 20/ 36 \pm 23	34 \pm 23/ 32 \pm 17	32 \pm 19/ 28 \pm 17	29 \pm 17/ 28 \pm 18	47 \pm 26/ 27 \pm 17	38 \pm 22/ 32 \pm 21	36 \pm 21/ 31 \pm 19
type (% used/available)												
deadbr	35/ 25.8	29.8/ 28.4	21.4/ 22	18.4/ 23.1	19/ 39.5	38.5/ 31.1	23.7/ 23.7	18.3/ 27.2	17.6/ 31.4	15/ 11.7	24.4/ 24	24.3/ 29.1
live	7.5/ 38.3	2.1/ 42.6	10.7/ 38.7	2/ 40.8	9.5/ 22.6	7.7/ 36.8	7.9/ 37.7	11.7/ 32.8	0/ 34.6	0/ 55	3.7/ 35.4	7.9/ 37.9
log	17.5/ 20.8	29.8/ 11.3	25/ 22.6	26.5/ 15.6	31/ 17.7	20/ 18.1	42.1/ 17.5	33.3/ 21.1	19.6/ 13.7	10/ 16.7	29.3/ 20.3	24.3/ 16.3
snag	17.5/ 4.2	36.2/ 14.9	30.4/ 6.5	42.9/ 8.2	31/ 4.8	24.6/ 4.1	18.4/ 7	20/ 7.8	54.9/ 12.4	60/ 10	34.1/ 8.5	30.9/ 7.5
stump	22.5/ 10.8	2.1/ 2.8	12.5/ 10.1	10.2/ 12.2	9.5/ 15.3	9.2/ 9.8	7.9/ 14	16.7/ 11.1	7.8/ 7.8	15/ 6.7	8.5/ 11.8	12.5/ 9.3
species (% used/available)												
beech	20/ 37.5	29.8/ 36.9	25/ 29.8	34.7/ 35.4	45.2/ 33.9	33.8/ 36.3	23.7/ 31.6	31.7/ 33.9	33.3/ 34	25/ 36.7	30.5/ 37.8	30.9/ 32.6
spruce	25/ 19.2	19.1/ 24.1	19.6/ 25	34.7/ 35.4	21.4/ 31.5	12.3/ 16.6	21.1/ 28.9	33.3/ 34.4	25.5/ 29.4	35/ 30	18.3/ 24.4	27/ 28.6
fir	32.5/ 15.8	8.5/ 12.1	17.9/ 16.1	6.1/ 4.8	11.9/ 16.9	23.1/ 21.8	10.5/ 13.2	10/ 10.6	7.8/ 5.9	30/ 10	14.6/ 12.6	15.1/ 13.2
other	7.5/ 10	29.8/ 22.7	19.6/ 15.5	16.3/ 12.2	14.3/ 12.9	16.9/ 15	13.2/ 10.5	20/ 13.3	25.5/ 22.2	5/ 8.3	17.1/ 11.4	18.4/ 16.7
NA	15/ 17.5	12.8/ 4.3	17.9/ 13.7	8.2/ 12.2	7.1/ 4.8	13.8/ 10.4	31.6/ 15.8	5/ 7.8	7.8/ 8.5	5/ 15	19.5/ 13.8	8.6/ 8.8

Table A.2 Results of the compositional analyses addressing selection of habitat types for establishing seasonal home ranges within the annual home range (1 km buffer around centroid of seasonal home range) in the post-breeding season, summer, fall, and winter. Shown are the mean differences \pm standard error between the used/available log-ratios for all pairwise comparisons between the habitat types. Values are positive when the habitat type in the corresponding row was preferred and negative when it was avoided compared to the habitat type in the corresponding column. Significant differences ($p < 0.05$, based on pairwise randomization tests) are printed in bold. Wilk's lambda and p-value from the MANOVAs are given in parentheses.

	decmix_old_div	decmix_old_mon	decmix_middle_div	decmix_middle_mon	con
post-breeding season ($\lambda = 0.67, p = 0.06$)					
decmix_old_div		0.16 \pm 0.10	-0.08 \pm 0.12	0.15 \pm 0.16	0.88 \pm 0.53
decmix_old_mon	0.16 \pm 0.10		0.07 \pm 0.12	0.30 \pm 0.16	1.08 \pm 0.51
decmix_middle_div	0.08 \pm 0.12	-0.07 \pm 0.12		0.23 \pm 0.12	0.87 \pm 0.12
decmix_middle_mon	-0.15 \pm 0.16	-0.30 \pm 0.16	-0.23 \pm 0.12		0.64 \pm 0.56
con	-0.88 \pm 0.53	-1.08 \pm 0.51	-0.87 \pm 0.12	-0.64 \pm 0.56	
summer ($\lambda = 0.80, p = 0.69$)					
decmix_old_div		-0.1 \pm 0.13	-0.02 \pm 0.14	-0.02 \pm 0.20	0.48 \pm 0.42
decmix_old_mon	0.1 \pm 0.13		0.08 \pm 0.12	0.08 \pm 0.17	0.57 \pm 0.50
decmix_middle_div	0.02 \pm 0.14	-0.08 \pm 0.12		0.01 \pm 0.11	0.56 \pm 0.46
decmix_middle_mon	0.02 \pm 0.20	-0.08 \pm 0.17	-0.01 \pm 0.11		0.48 \pm 0.51
con	-0.48 \pm 0.42	-0.57 \pm 0.50	-0.56 \pm 0.46	-0.48 \pm 0.51	
fall ($\lambda = 0.49, p = 0.25$)					
decmix_old_div		-0.11 \pm 0.13	0.15 \pm 0.15	-0.01 \pm 0.25	0.58 \pm 0.23
decmix_old_mon	0.11 \pm 0.13		0.26 \pm 0.21	0.10 \pm 0.15	0.73 \pm 0.26
decmix_middle_div	-0.15 \pm 0.15	-0.26 \pm 0.21		-0.17 \pm 0.29	0.46 \pm 0.26
decmix_middle_mon	0.01 \pm 0.25	-0.10 \pm 0.15	0.17 \pm 0.29		0.71 \pm 0.31
con	-0.58 \pm 0.23	-0.73 \pm 0.26	-0.46 \pm 0.26	-0.71 \pm 0.31	
winter ($\lambda = 0.25, p = 0.10$)					
decmix_old_div		-0.15 \pm 0.32	0.26 \pm 0.17	0.68 \pm 0.32	1.43 \pm 0.67
decmix_old_mon	0.15 \pm 0.32		0.41 \pm 0.20	0.83 \pm 0.59	1.63 \pm 0.59
decmix_middle_div	-0.26 \pm 0.17	-0.41 \pm 0.20		0.42 \pm 0.40	1.21 \pm 0.62
decmix_middle_mon	-0.68 \pm 0.32	-0.83 \pm 0.59	-0.42 \pm 0.40		0.82 \pm 0.85
con	-1.43 \pm 0.67	-1.63 \pm 0.59	-1.21 \pm 0.62	-0.82 \pm 0.85	

Chapter 3

Table A.3 Results of the compositional analyses addressing the selection of habitat types within the seasonal home ranges in six seasons. Shown are the mean differences \pm standard error between the used/available log-ratios for all pairwise comparisons between the habitat types. Values are positive when the habitat type in the corresponding row was preferred and negative when it was avoided compared to the habitat type in the corresponding column. Significant differences ($p < 0.05$, based on pairwise randomization tests) are printed in bold. Wilk's lambda and p-value from the MANOVAs are given in parentheses.

	decmix_old_div	decmix_old_mon	decmix_middle_div	decmix_middle_mon	con
pre-breeding season ($\lambda = 0.57, p = 0.19$)					
decmix_old_div		-0.2 \pm 0.24	-0.18 \pm 0.35	0.6 \pm 0.39	0.2 \pm 0.65
decmix_old_mon	0.2 \pm 0.24		0.2 \pm 0.23	0.8 \pm 0.31	0.37 \pm 0.32
decmix_middle_div	0.18 \pm 0.35	-0.2 \pm 0.23		0.6 \pm 0.34	0.18 \pm 0.57
decmix_middle_mon	-0.6 \pm 0.39	-0.8 \pm 0.31	-0.6 \pm 0.34		-0.45 \pm 0.5
con	-0.2 \pm 0.65	-0.37 \pm 0.32	-0.18 \pm 0.57	0.45 \pm 0.5	
breeding season ($\lambda = 0.87, p = 0.79$)					
decmix_old_div		0.02 \pm 0.34	0.04 \pm 0.29	0.23 \pm 0.41	0.17 \pm 0.44
decmix_old_mon	-0.02 \pm 0.34		0.02 \pm 0.32	0.21 \pm 0.32	-0.27 \pm 0.66
decmix_middle_div	-0.04 \pm 0.29	-0.02 \pm 0.32		0.19 \pm 0.28	-0.34 \pm 0.57
decmix_middle_mon	-0.23 \pm 0.41	-0.21 \pm 0.32	-0.19 \pm 0.28		-0.37 \pm 0.53
con	-0.17 \pm 0.44	0.27 \pm 0.66	0.34 \pm 0.57	0.37 \pm 0.53	
post-breeding season ($\lambda = 0.56, p = 0.06$)					
decmix_old_div		-0.64 \pm 0.37	-0.2 \pm 0.4	-0.28 \pm 0.43	-0.99 \pm 0.51
decmix_old_mon	0.64 \pm 0.37		0.53 \pm 0.3	0.44 \pm 0.26	0.63 \pm 0.4
decmix_middle_div	0.2 \pm 0.4	-0.53 \pm 0.3		-0.09 \pm 0.2	-0.82 \pm 0.62
decmix_middle_mon	0.28 \pm 0.43	-0.44 \pm 0.26	0.09 \pm 0.2		-0.59 \pm 0.5
con	0.99 \pm 0.51	-0.63 \pm 0.4	0.82 \pm 0.62	0.59 \pm 0.5	
summer ($\lambda = 0.58, p = 0.27$)					
decmix_old_div		-0.3 \pm 0.14	0.13 \pm 0.29	0.65 \pm 0.5	0.46 \pm 0.63
decmix_old_mon	0.3 \pm 0.14		0.43 \pm 0.3	0.95 \pm 0.5	0.67 \pm 0.6
decmix_middle_div	-0.13 \pm 0.29	-0.43 \pm 0.3		0.53 \pm 0.39	0.39 \pm 0.63
decmix_middle_mon	-0.65 \pm 0.5	-0.95 \pm 0.5	-0.53 \pm 0.39		-0.5 \pm 0.88
con	-0.46 \pm 0.63	-0.67 \pm 0.6	-0.39 \pm 0.63	0.5 \pm 0.88	
fall ($\lambda = 0.52, p = 0.4$)					
decmix_old_div		-0.56 \pm 0.56	-0.4 \pm 0.54	-0.57 \pm 0.68	-0.14 \pm 0.96
decmix_old_mon	0.56 \pm 0.56		0.17 \pm 0.16	-0.01 \pm 0.34	0.53 \pm 0.44
decmix_middle_div	0.4 \pm 0.54	-0.17 \pm 0.16		-0.17 \pm 0.28	0.32 \pm 0.45
decmix_middle_mon	0.57 \pm 0.68	0.01 \pm 0.34	0.17 \pm 0.28		0.56 \pm 0.48
con	0.14 \pm 0.96	-0.53 \pm 0.44	-0.32 \pm 0.45	-0.56 \pm 0.48	
winter ($\lambda = 0.23, p = 0.08$)					
decmix_old_div		0.13 \pm 0.4	0.81 \pm 0.7	0.49 \pm 0.37	1.57 \pm 0.41
decmix_old_mon	-0.13 \pm 0.4		0.68 \pm 0.7	0.37 \pm 0.52	1.31 \pm 0.67
decmix_middle_div	-0.81 \pm 0.7	-0.68 \pm 0.7		-0.32 \pm 0.51	0.6 \pm 0.94
decmix_middle_mon	-0.49 \pm 0.37	-0.37 \pm 0.52	0.32 \pm 0.51		1.23 \pm 0.46
con	-1.57 \pm 0.41	-1.31 \pm 0.67	-0.6 \pm 0.94	-1.23 \pm 0.46	

Chapter 3

Table A.4 Model coefficients for variables included in a general linear mixed model explaining the diameter of trees used by foraging white-backed woodpeckers. Presented are posterior means and 95% credible intervals (CrI). Variables are explained in the methods section.

Variable	Level	Estimate	Lower CrI	Upper CrI
Fixed effects				
Intercept		3.89	3.64	4.12
Season (reference: pre-breeding)	breeding	-0.21	-0.43	0.01
	post-breeding	-0.16	-0.35	0.03
	summer/fall	-0.32	-0.52	-0.12
	winter	-0.06	-0.35	0.24
Sex (reference: female)	male	-0.07	-0.23	0.09
Habitat type (reference: DOHet)	DOHom	-0.01	-0.26	0.23
	DYHet	-0.26	-0.49	-0.02
	DYHom	-0.43	-0.67	-0.18
	Con	-0.36	-0.6	-0.11
Random effects				
Ind_id		0.09	0	0.22
Residual variance		0.56	0.51	0.61

Table A.5 Model coefficients for variables included in a multinomial logistic regression model explaining the type of trees used by foraging white-backed woodpeckers. Snag was used as reference level of the dependent variable. Presented are posterior means and 95% credible intervals (CrI). Variables are explained in the methods section.

Variable	Level	deadbr vs. snag	live vs. snag	log vs. snag	stump vs. snag
Fixed effects					
Intercept		1.06 [-0.34;2.45]	-2.57 [-6.6;0.27]	0.17 [-1.27;1.55]	0.48 [-1.24;2.12]
Season (reference: pre-breeding)	breeding	0.15 [-1.11;1.43]	1.56 [-0.34;3.55]	1.24 [0.15;2.39]	0.26 [-1.42;1.89]
	post-breeding	0.05 [-1.1;1.18]	1.45 [-0.32;3.22]	0.96 [-0.08;2.03]	1.48 [0.11;2.92]
	summer/fall	-0.98 [-2.07;0.08]	-5.35 [-12.1;-0.86]	-0.65 [-1.7;0.36]	-0.84 [-2.41;0.69]
	winter	-2.86 [-4.88;-1.13]	-4.86 [-11.86;0.02]	-1.76 [-3.82;-0.04]	-1.1 [-3.13;0.79]
Habitat type (reference: DOHet)	DOHom	-0.85 [-2.22;0.45]	-2.89 [-6.23;-0.11]	-0.54 [-1.92;0.81]	-2.42 [-4.31;-0.66]
	DYHet	-1.32 [-2.69;0]	-0.6 [-2.69;1.57]	-0.7 [-2.07;0.64]	-1.95 [-3.61;-0.39]
	DYHom	-1.95 [-3.42;-0.55]	-3.43 [-6.63;-0.69]	-0.92 [-2.32;0.47]	-2.8 [-4.63;-1.1]
	Con	-1.26 [-2.7;0.14]	-0.32 [-2.75;2.23]	-0.16 [-1.58;1.23]	-2.05 [-3.96;-0.33]
Sex (reference: female)	male	0.11 [-0.93;1.14]	0.33 [-2.02;2.85]	-0.16 [-0.96;0.72]	-0.3 [-1.66;1]
Random effect					
ind_id		1.05 [0.28;1.88]	2.42 [0.6;5.12]	0.47 [0.02;1.26]	1.18 [0.16;2.38]

Chapter 3

Table A.6 Model coefficients for variables included in a multinomial logistic regression model explaining the species of trees used by foraging white-backed woodpeckers. Beech was used as reference level of the dependent variable. Presented are posterior means and 95% credible intervals (CrI). Variables are explained in the methods section.

Variable	Level	spruce vs. beech	fir vs. beech	other vs. beech
Fixed effects				
Intercept		-0.5 [-1.99;1.01]	0.55 [-0.75;1.82]	-1.29 [-3.22;0.4]
Season (reference: pre-breeding)	breeding	0.25 [-1.09;1.55]	-0.1 [-1.54;1.29]	-0.25 [-1.73;1.19]
	post-breeding	0.75 [-0.38;1.9]	0.03 [-1.18;1.24]	0.21 [-0.96;1.39]
	summer/fall	0.83 [-0.37;2.09]	-0.92 [-2.44;0.43]	0.71 [-0.55;2.07]
	winter	1.61 [-0.07;3.41]	0.63 [-0.97;2.25]	-0.98 [-4.17;1.61]
Habitat type (reference: DOHet)	DOHom	-0.49 [-1.88;0.9]	-1.87 [-3.47;-0.41]	0.8 [-0.74;2.44]
	DOHet	-0.17 [-1.55;1.24]	-0.52 [-1.82;0.77]	0.81 [-0.75;2.48]
	DYHom	-0.21 [-1.56;1.17]	-2.28 [-4.07;-0.71]	-0.09 [-1.74;1.63]
	DYHet	-0.21 [-1.66;1.29]	-1.24 [-2.63;0.13]	0.26 [-1.38;1.97]
Sex (reference: female)	male	-0.2 [-1.31;0.86]	-0.43 [-1.44;0.64]	-0.12 [-1.37;1.17]
Random effect				
Ind_id		1.11 [0.49;1.88]	0.46 [0.02;1.36]	1.37 [0.51;2.5]

Table A.7 Forest structure characteristics of five habitat types within white-backed woodpecker breeding home ranges (100% minimum convex polygons) based on data from Chapter 1. Data were recorded in the field within 0.05 ha plots (n = 89 plots in DOhet (old heterogeneous deciduous/mixed forest), n = 80 in DOhom (old homogeneous deciduous/mixed forest), n = 132 in DYhet (young heterogeneous deciduous/mixed forest, n = 82 in DYhom (young homogeneous deciduous/mixed forest), n = 58 in Con (coniferous forest)). Presented are means \pm standard deviation per hectare. Dbh = diameter at breast height, d = diameter measured in the middle of the piece.

habitat type	deadwood (m ³)	snags (m ³) ¹	logs (m ³)	stumps (m ³)	snags with dbh>30cm	logs with d>30cm	stumps with d>30cm	trees with dead branches	trees with dbh>50cm
DOhet	93 \pm 90	32 \pm 42	48 \pm 61	13 \pm 15	21 \pm 24	41 \pm 48	67 \pm 75	17 \pm 26	60 \pm 58
DOhom	80 \pm 71	31 \pm 35	40 \pm 48	9 \pm 11	13 \pm 18	30 \pm 56	68 \pm 68	25 \pm 34	79 \pm 61
DYhet	70 \pm 69	26 \pm 42	33 \pm 49	11 \pm 12	12 \pm 18	21 \pm 29	70 \pm 76	24 \pm 37	45 \pm 47
DYhom	55 \pm 60	20 \pm 27	22 \pm 26	13 \pm 47	10 \pm 17	18 \pm 33	52 \pm 70	31 \pm 59	34 \pm 59
Con	102 \pm 131	26 \pm 40	69 \pm 114	7 \pm 10	9 \pm 18	41 \pm 62	56 \pm 71	20 \pm 33	83 \pm 63

Chapter 4

Landscape context plays an important role for the occurrence of the white-backed woodpecker

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Abstract

Habitat models typically relate the occurrence of a species to environmental predictors measured within study sites or home ranges of the studied species (“local habitat”). However, sites with high local habitat quality might be unoccupied when the composition and configuration of the surrounding landscape hamper their colonization. Including landscape context into habitat models may thus be important to correctly identify limiting factors and derive effective conservation measures for endangered species. We examined the occurrence of the white-backed woodpecker *Dendrocopos leucotos*, a species breeding in old forests with abundant deadwood and deciduous trees, in relation to local habitat and landscape context (habitat amount, habitat fragmentation, and matrix quality) in Central Europe. Landscape context explained 2.5 times more of the variance in occurrence probability than local habitat. Occurrence probability increased with the abundance of lying deadwood and trees with dead branches at the local scale. It furthermore increased with the proportion and fragmentation of old deciduous forests (representing habitat amount and habitat fragmentation, respectively) and increasing proportion of coniferous or young deciduous forest (representing matrix quality) at spatial scales ranging from 20 to 64 km² (i.e., 6 to 20 times the annual home range size). Our results show that conservation measures for the white-backed woodpecker might be ineffective in areas with low forest cover at the landscape scale, even if enough high-quality habitat at the local scale is available. Consequently, conservation measures should focus on the conservation of and habitat improvements in areas with enough forest to sustain multiple breeding pairs. These areas should contain a high proportion of old deciduous and of coniferous or young deciduous forest and should ideally be connected via dispersed patches of old deciduous forest. As local habitat quality was generally high and the study population at the species’ range edge, more studies explicitly comparing the relative importance of local habitat and landscape context are needed to assess whether incorporating landscape context into habitat models is generally important for white-backed woodpeckers and other species.

Introduction

Habitat models typically relate the occurrence or abundance of a species to environmental predictors and are an important basis for various conservation applications such as adapting forest management or agricultural practices (Bütler et al., 2004; Franco and Sutherland, 2004) or planning habitat networks (Angelstam et al., 2004). The outcome and quality of the model and therefore the effectiveness of the applied conservation measures may vary depending on the spatial scale, i.e., the extent (area or radius), at which the environmental predictors were measured (de Knecht et al., 2010; Jackson and Fahrig, 2015). Although the importance of scale in species-environment relationships has long been acknowledged (e.g., Wiens, 1989), most habitat selection studies are based on environmental data recorded at rather small spatial scales, e.g., within study sites or home ranges of the studied species (“local habitat”), and scale optimization for environmental predictors is rarely done (McGarigal et al., 2016). Local habitat quality undoubtedly affects the occurrence and abundance of most species. However, a site with high local habitat quality might be unoccupied by a species if habitat amount at the landscape level is too low to sustain a population or if the colonization of the site is impeded by habitat fragmentation or poor quality of the matrix (i.e., the area between patches of the habitat type of interest or relevant to a species). Incorporating landscape context, that is, the composition and configuration of the landscape surrounding a given site, into habitat models may thus be crucial to better understand the processes affecting the occurrence or abundance of a species.

The influences of landscape context, mainly on community-level responses such as species richness, have been intensively studied by landscape ecologists. However, despite decades of research, there is no general consent about the relative importance of landscape composition and landscape configuration (Banks-Leite et al., 2022). This is partly due to the confounded effects of habitat amount and habitat fragmentation; fragmentation does not only change the spatial configuration of a habitat type but simultaneously causes habitat loss, which complicates our ability to disentangle these two processes (Fahrig, 2019). While habitat amount has consistently positive effects on biodiversity (Fahrig, 2003), the role of habitat fragmentation is still heavily debated (Fahrig, 2013, 2017; Fletcher et al., 2018; Hanski, 2015; Saura, 2021). Simulation studies and empirical research suggest that habitat fragmentation may have either negative, positive, or no effects on species’ responses, which has led to a number of competing hypotheses.

According to the *habitat fragmentation hypothesis*, the occurrence of a species is affected by habitat fragmentation, independent of the effect of habitat amount. In the context of the present study, we define fragmentation as spatial pattern rather than as process (Fahrig, 2019) and use the term habitat fragmentation hypothesis for both negative and positive predicted effects of fragmentation. Negative

effects may arise due to reduced dispersal (Schtickzelle and Baguette, 2003) or negative edge effects (Deng and Gao, 2005). Positive fragmentation effects may arise from small inter-patch distances in landscapes with many small instead of few large patches, positive edge effects (e.g., because of higher productivity and structural diversity of edges than of habitat interiors), or reduced competition (Fahrig, 2017). By contrast, the *habitat amount hypothesis* proposed by Fahrig (2013) states that the occurrence of a species in equal-sized sample sites located in habitat patches (and thus containing the same amount of habitat) is unaffected by habitat configuration and driven by one single factor, the amount of habitat within an ecologically meaningful distance to the site. The hypothesis posits that the effects of local patch size and isolation are both contained within the effect of habitat amount and that there is no effect of habitat fragmentation when habitat amount is accounted for. This hypothesis has received support by some empirical studies (see meta-analysis by Watling et al., 2020) but has also been criticized, particularly for its inability to predict effects of habitat fragmentation at scales larger than the study sites (Hanski, 2015; Saura, 2021). While the habitat fragmentation and habitat amount hypotheses state that there either are effects or no effects of habitat fragmentation, the *fragmentation threshold hypothesis* (Andrén, 1994; Fahrig, 1998; Flather and Bevers, 2002) posits that fragmentation effects only occur below a certain threshold of habitat amount. Such thresholds have been found for some species (e.g., Betts et al., 2006; Bosco et al., 2021) but are generally rare (Fahrig, 2017). Lastly, while the three hypotheses presented so far assume a binary landscape consisting of the focal habitat type and the matrix (which comprises all other habitat types), the *matrix quality hypothesis* states that the quality of the intervening landscape influences the occurrence of a species in habitat patches. For instance, high matrix quality may increase survival during dispersal (Schtickzelle and Baguette, 2003) or movement rates (Eycott et al., 2012) and thus facilitate patch colonization.

Here, we examined the occurrence of the white-backed woodpecker *Dendrocopos leucotos* in relation to local habitat and landscape context in Western Austria, Eastern Switzerland and Liechtenstein, where the species reaches its western range edge in Central Europe. The white-backed woodpecker prefers old-growth deciduous or mixed forests with abundant deadwood (Aulén, 1988; Czeszczewik, 2009a; Scherzinger, 1982), mainly because its diet largely consists of wood-boring larvae (Aulén, 1988; Hogstad and Stenberg, 1997). The species is distributed over the entire Palearctic but has a disjunct distribution in Europe as a result of deforestation and intensive forest management (Virkkala et al., 1993). Accordingly, the occurrence of the species in Europe is limited to regions with generally low forest management intensity, and within a population, the presence and abundance of the species is associated with factors typically found in old-growth forests (Ettwein et al., 2020; Kajtoch et al., 2013; Walankiewicz et al., 2011). Today, the white-backed woodpecker is of high conservation concern in

many European countries (e.g., it is listed in Annex 1 of the European Union's Birds Directive). Current conservation recommendations and action plans focus on the maintenance and creation of old forest stands with abundant deadwood and deciduous trees within areas of the size of a home range (Löhmus et al., 2010; Nagel et al., 2017) or without reference to the spatial extent at which the measures should be implemented (Ettwein et al., 2020). While it is known that habitat amount at the landscape level determines population persistence (Angelstam et al., 2004; Carlson, 2000), it is unknown how suitable habitats should be spatially distributed or how the landscape surrounding habitat patches should be composed.

We used similar habitat variables as in previous studies addressing white-backed woodpecker habitat preferences (forest structure characteristics recorded in the field within sites with the size of a breeding home range; e.g., Ettwein et al., 2020; Hogstad and Stenberg, 1994; Kajtoch et al., 2013) to describe local habitat, and variables representing habitat fragmentation, habitat amount and matrix quality (derived from remote sensing data at spatial scales ranging from 1 – 25 times the annual home range size) to describe landscape context. The aims of the study were (1) to evaluate which variables describing local habitat and which hypotheses describing effects of landscape context (habitat fragmentation hypothesis, habitat amount hypothesis, fragmentation threshold hypothesis, matrix quality hypothesis) explain occurrence probability of the white-backed woodpecker; (2) to assess the relative importance of local habitat and landscape context for modeling white-backed woodpecker occurrence probability; and (3) to complement existing conservation recommendations for this species by addressing how suitable habitats should be embedded in the surrounding landscape.

Methods

Study area and study sites

The study area was located in the Eastern Alps in Austria (State of Vorarlberg), Eastern Switzerland (Cantons of Grisons and St Gallen), and the Principality of Liechtenstein (46.8 - 47.5°N, 9.3 - 10°E). Forest cover is naturally limited by the partly high elevations (elevations range from 400 to 3000 m a.s.l., tree line at approximately 1600 – 1800 m) and has been additionally reduced by deforestation, particularly in the bottoms of larger valleys. Today, about 40% of the study area is covered with forest. Deciduous and mixed forests, dominated by European beech *Fagus sylvatica*, Norway spruce *Picea abies*, and silver fir *Abies alba*, comprise about 10 and 43% of the forested area and are found in lower elevations. Coniferous forests naturally occur in higher elevations up to the tree line but are also found as spruce plantations in lower elevations. Forest management intensity in the study area varies with accessibility of the terrain and landownership; it ranges from intensive management for timber

production in easily accessible stands to the occasional logging of single trees or management abandonment in steep protection forests or some privately owned stands.

We selected 30 sites with and 30 sites without known white-backed woodpecker presence. Presence sites corresponded to the breeding home ranges of white-backed woodpeckers radio-tracked between 2016 and 2019 (see Chapter 1 for details regarding capturing and tracking). We used minimum convex polygons based on all locations collected between egg-laying and fledging to compute these breeding home ranges. We selected only home ranges that did not overlap with another breeding home range from the same or another year and used only one breeding home range per individual for the analyses. Absence sites were selected in 2018 using the following procedure. We first created a 550 x 550 m grid to obtain potential absence sites (= 30.25 ha) corresponding in size to a white-backed woodpecker breeding home range (mean breeding home range size of 12 individuals tracked in 2016 and 2017 was 29 ha). Next, we calculated the proportions of deciduous or mixed forest area and of total forest area from CORINE Land Cover data (European Environment Agency 2019, CORINE Land Cover (CLC) 2018, Version 20, Copenhagen, Denmark) for the breeding home ranges of birds tracked in 2016 and 2017 and for all potential absence sites. We then calculated the 25% quantiles of the proportions of deciduous or mixed forest and of total forest area, respectively, in the breeding home ranges. To obtain absence sites that contain at least some potential white-backed woodpecker habitat, we omitted all potential absence sites in which the proportion of deciduous or mixed forest and of total forest was below these 25% quantiles. Moreover, we omitted potential absence sites that were closer than 1000 m to a previous white-backed woodpecker observation. These observations were mainly made while searching individuals for the telemetry study (Chapter 1, Chapter 2) and were complemented by data from ornitho.ch, inatura Dornbirn, and BirdLife Vorarlberg. Finally, we selected all potential absence sites that overlapped with absence sites used by Ettwein et al. (2020; n = 8; only sites in which no white-backed woodpecker was detected in both years of the study were used) and 22 of the remaining potential absence sites that were considered accessible based on the inspection of topographic maps. We checked whether white-backed woodpeckers were present in the 30 absence sites in two surveys between February and April 2018. During each survey, a field worker used playbacks of drumming and calls (1 minute of drumming, 1 minute of calls, and again 1 minute of drumming; 1 minute of waiting for a reaction of a white-backed woodpecker after playing each sound) every 200 m. In two absence sites, white-backed woodpeckers were detected during the first survey. These sites were not used for the analyses and replaced by two new randomly chosen potential absence site, which then were also checked for white-backed woodpeckers in two surveys.

Habitat data

Local habitat

We selected similar variables describing local habitat (habitat within the presence and absence sites) as in previous studies addressing white-backed woodpecker habitat preferences (e.g., Ettwein et al., 2020; Frank and Hochebner, 2001; Hogstad and Stenberg, 1994; Kajtoch et al., 2013). We recorded forest structure characteristics in the field within circular 500 m² sampling plots whose centers were situated at the intersections of a 200 x 200 m grid. We recorded diameter at breast height (DBH) and tree species of all live trees with a DBH \geq 30 cm. We furthermore recorded whether the tree had dead branches with a diameter \geq 10 cm. Moreover, we recorded diameter in the middle and length of all pieces of lying deadwood (= logs) with a diameter \geq 7 cm and DBH and height of all pieces of standing deadwood (= snags) with a DBH \geq 5 cm and height \geq 130 cm. We used the formula of a cylinder to calculate the volume of individual snags and logs. The variables derived from these data and used for the analyses are shown in Table 1. We additionally computed the mean potential annual insolation for each site based on digital elevation models using SAGA 2.1.4 (Conrad et al., 2015) as white-backed woodpeckers have been shown to prefer sun-exposed slopes (Frank, 2002; Hogstad and Stenberg, 1994; Scherzinger, 1982). Lastly, we calculated the proportion of old deciduous or mixed forest, the habitat type preferred by white-backed woodpeckers during the breeding season (Chapter 3; see “Landscape context” for the definition of this habitat type) in 500 m buffers around the site centroids. We did not calculate this variable within the sites because the home ranges varied in size. 500 m buffers resulted in areas of 78 ha, which approximately corresponded to the size of the largest breeding home range.

Landscape context

We used remote sensing data to create variables representing landscape context because mapping forest characteristics in the field was not feasible at the landscape scale. We used Corine Land Cover data and LiDAR-based digital surface models (provided in a 0.5 m resolution by the responsible authorities in Austria and Liechtenstein and by the Federal Institute for Forest, Snow and Landscape Research WLS in Switzerland), to create a 50 x 50 m raster with five habitat types: old deciduous or mixed deciduous/coniferous forest (proportion of deciduous trees $>$ 25%, maximum tree height \geq 40 m), young deciduous or mixed deciduous/coniferous forest (proportion of deciduous trees $>$ 25%, maximum tree height $<$ 40 m), old coniferous forest (proportion of deciduous trees \leq 25%, maximum tree height \geq 40 m), young coniferous forest (proportion of deciduous trees \leq 25%, maximum tree height $<$ 40 m), and unforested (unforested area, cliffs, slopes $>$ 60°; details can be found in Chapter 3).

Table 1 Variables used for modeling white-backed woodpecker occurrence probability based on data recorded for breeding season home ranges and absence sites (550 x 550 m squares without white-backed woodpeckers). Local habitat was recorded within the study sites apart from dec_old_500, which was recorded in a 500 m buffer around the site centroid; landscape context was recorded within circular buffers around the site centroid ranging from 1000 to 5000 m radii in 500 m increments (i.e., 9 variables per landscape metric).

Variable name	Description	Represented aspect of landscape context
Local habitat		
logs	Mean volume of lying deadwood per ha	-
snags	Mean volume of standing deadwood per ha	-
basallive	Mean basal area of live trees with DBH > 30 cm per ha	-
deadbr	Mean number of trees with dead branches per ha	-
beech50 ¹	Mean number of beech trees with DBH > 50 cm per ha	-
sun	Mean potential annual insolation (kWh/m ²)	-
dec_old_500	Proportion of old deciduous/mixed forest	
Landscape context		
dec_old	Proportion of old deciduous/mixed forest (proportion of deciduous trees > 25%, maximum tree height ≥ 40 m)	Habitat amount
clumpy	Clumpiness index for old deciduous/mixed forest (deviation of the proportion of adjacent old deciduous forest cell pairs from that expected under a spatially random distribution)	Habitat fragmentation
con_dec_young	Proportion of young and old coniferous forest and young deciduous/mixed forest (proportion of forest minus dec_old)	Matrix quality
dec_young	Proportion of young deciduous/mixed forest (proportion of deciduous trees > 25%, maximum tree height < 40 m)	Matrix quality
con_old	Proportion of old coniferous forest (proportion of deciduous trees ≤ 25%, maximum tree height ≥ 40 m)	Matrix quality

¹ Used because the white-backed woodpecker prefers old deciduous forests and beech is the dominating deciduous tree species in the study area.

We then calculated five landscape metrics describing habitat amount, habitat fragmentation, and matrix quality (see below) at nine spatial scales ranging from 1000 m to 5000 m radii (in increments of 500 m) around the site centroids. The smallest radius (1000 m) resulted in an area of 314 ha, which approximately corresponded to the annual minimum convex polygon home range size of a white-backed woodpecker (Chapter 1), while the largest radius (5000 m) corresponded to an area 25 times the annual home range size. Based on the well-known preference for old-growth deciduous and mixed forest as breeding habitat (e.g., Scherzinger, 1982; Wesołowski, 1995; Hogstad and Stenberg, 1994; Chapter 3), we considered old deciduous or mixed forests (henceforward referred to as “old deciduous forest”) as focal habitat type to calculate metrics representing habitat amount and habitat fragmentation and considered all other habitat types as matrix. We used the R package *landscapemetrics* v1.5.5 (Hesselbarth et al., 2019) to calculate the five landscape metrics at each spatial

scale. First, we calculated the proportion of old deciduous forest as metric representing habitat amount. Next, we used a clumpiness index for old deciduous forest as metric representing habitat fragmentation. This metric describes the deviation of the proportion of adjacent old deciduous forest cell pairs from that expected under a spatially random distribution and ranges from -1 when the habitat type is maximally disaggregated (i.e., maximally fragmented) to 1 when it is maximally clumped (McGarigal et al., 2012). Lastly, we calculated the proportions of coniferous or young deciduous forest, of young deciduous forest, and of old coniferous forest as metrics representing matrix quality, assuming that forest habitat types are associated with higher matrix quality for a forest specialist than unforested area (Brotons et al., 2003). We considered the proportions of young deciduous forest and of old coniferous forest as separate variables in our analyses to evaluate if a specific forest type is associated with high matrix quality (Table 1).

Statistical analyses

We modeled white-backed woodpecker occurrence probability in three steps to select relevant local habitat variables (step 1), to evaluate the most relevant spatial scale(s) for each landscape metric (step 2), and to evaluate the hypotheses explained in the introduction (step 3). As our response variable (presence/absence) was binary, we used binomial generalized linear mixed models with a log-link function. We fitted the models in a Bayesian framework using *rstanarm* v.2.21.3 (Goodrich et al., 2020) and performed model selection in each step. All variables were centered to mean = 0 and scaled to standard deviation = 1 prior to the analyses. As the sites were partly spatially clustered (e.g., several breeding home ranges close to each other), we created the variable `cluster_id` using the DBSCAN clustering tool in QGIS 3.22.8, which resulted in 17 site clusters being at least 5 km apart from each other. We fitted a random intercept for `cluster_id` in each model of all steps to account for pseudoreplication due to the overlapping buffers of neighboring sites.

In step 1, we first fitted a model including all seven local habitat variables. We then fitted four additional models with different combinations of `dec_old_500` (which was kept in all models to account for varying habitat amount at the local scale) and variables that had coefficient estimates $> |0.5|$ in the first model and compared the five models via the leave-one-out cross-validation information criterion (LOOIC, Vehtari et al., 2019). To select the most relevant spatial scale per landscape metric (step 2), we applied a ridge regression, a form of regularized linear regression that shrinks the regression coefficients towards zero by constraining the sum of the squared values of the coefficients (Hooten and Hobbs, 2015). Ridge regression is particularly useful when multicollinearity among the covariates is present or when fewer observations than variables are available (Brown et al., 2002). This approach allowed us to include all (partly highly correlated) landscape metrics at all spatial scales into one model

Table 2 Models examined for testing predictions of the habitat fragmentation hypothesis, fragmentation threshold hypothesis, habitat amount hypothesis, and matrix quality hypothesis (1: high importance of coniferous or young deciduous forest as matrix habitat; 2: high importance of young deciduous forest as matrix habitat; 3: high importance of old coniferous forest as matrix habitat). Clumpy = clumpiness index (metric representing habitat fragmentation), dec_old = proportion of old deciduous forest (metric representing habitat amount), con_dec_young, dec_young, and con_old = proportions of coniferous or young deciduous forest, of young deciduous forest, and of old coniferous forest, respectively (metrics representing matrix quality).

Hypothesis	Prediction	Models
Habitat fragmentation	Occurrence probability is positively or negatively related to clumpiness index	clumpy dec_old + clumpy
Fragmentation threshold	Occurrence probability is positively related to clumpiness index (i.e., negative effect of habitat fragmentation) when habitat amount is low; model including interaction between dec_old and clumpy performs better than model without interaction	dec_old + clumpy + dec_old:clumpy
Habitat amount	Occurrence probability is positively related to habitat amount at the landscape level (after accounting for habitat amount at the local scale) and not related to clumpiness index; model including only dec_old performs better than model additionally including clumpy	dec_old
Matrix quality 1	Occurrence probability is positively related to proportion of coniferous or young deciduous forest; the effect of matrix quality may be stronger when habitat amount is low	con_dec_young dec_old + con_dec_young dec_old + con_dec_young + dec_old:con_dec_young
Matrix quality 2	Occurrence probability is positively related to proportion of young deciduous forest; the effect of matrix quality may be stronger when habitat amount is low	dec_young dec_old + dec_young dec_old + dec_young + dec_old:dec_young
Matrix quality 3	Occurrence probability is positively related to proportion of old coniferous forest; the effect of matrix quality may be stronger when habitat amount is low	con_old dec_old + con_old dec_old + con_old + dec_old:con_old

and hence to control for effects of other potentially relevant variables while evaluating the most relevant spatial scale for each metric. We constructed a model with the local habitat variables of the top-ranked model from step 1 and the five landscape metrics at all spatial scales (i.e., 45 landscape context variables). We then performed the ridge regression in a Bayesian framework by gradually increasing the width of the priors on the coefficients of the landscape context variables (Hooten and Hobbs, 2015). We used normal priors with mean = 0 and standard deviation (SD) = 0.1 to 2.5 (in increments of 0.05, i.e., 49 different priors and models) for the landscape context variables and with mean = 0 and SD = 2.5 for the local habitat variables (same priors in all models), with wide prior distributions resulting in weak regularization and narrow prior distributions in strong regularization.

We compared the 49 models via the k-fold cross-validation information criterion (KFOLDIC). Using the top-ranked model, we selected each landscape metric the spatial scale at which it had the largest absolute coefficient estimate for step 3. If the absolute coefficient estimates were similar at two spatial scales, we kept both variables. In step 3, we used the landscape context variables at the spatial scales selected in step 2 to build models representing the hypotheses presented in the introduction (see Table 2 for an overview of the predictions of each hypothesis and the corresponding models) and performed model selection via LOOIC. If a landscape metric was equally important at two scales according to the top-ranked model of step 2, we ran two models, using one of the two spatial scales per model. Each model also included the variables selected in step 1 to control for effects of local habitat and a random intercept for *cluster_id*.

To assess the relative importance of local habitat and landscape context for modeling white-backed woodpecker occurrence probability, we used the top-ranked model from step 3 as model representing both local habitat and landscape context (*m.full*). We also fitted one model (*m.local*) including only the local habitat variables from step 1 and *cluster_id* and one model (*m.landscape*) including only the important landscape context variables from step 3 and *cluster_id*. We then calculated 1) the LOOIC for each of the three models, 2) the proportion of sites for which white-backed woodpecker presence/absence was correctly predicted by each of the three models, and 3) the proportion of variance explained a) by local habitat and landscape context while controlling for *cluster_id*, b) by local habitat while controlling for landscape context and *cluster_id*, and c) by landscape context while controlling for local habitat and *cluster_id*. We additionally fitted a model including only *cluster_id* as random effect (*m.ranef*) and calculated the proportion of explained variance following Gelman and Pardoe (2006):

$$R^2(\text{local habitat} + \text{landscape context}) = 1 - \frac{\text{residual variance under } m.\text{full}}{\text{residual variance under } m.\text{ranef}}$$

$$R^2(\text{local habitat}) = 1 - \frac{\text{residual variance under } m.\text{full}}{\text{residual variance under } m.\text{landscape}}$$

$$R^2(\text{landscape context}) = 1 - \frac{\text{residual variance under } m.\text{full}}{\text{residual variance under } m.\text{local}}$$

Results

According to our local habitat models (step 1), white-backed woodpecker occurrence probability was positively associated with the volume of lying deadwood and the number of live trees with dead branches (Table 3, Table 4a, Fig. 1). Occurrence probability was also positively related to the proportion

of old deciduous forest, which was used in all models. None of the credible intervals in this model included zero (Table 4a). The top-ranked model from the Bayesian ridge regression (step 2) showed that habitat amount best explained white-backed woodpecker occurrence at the relatively small spatial scales of 1000 to 2500 m (highest coefficient estimate at the 2500 m scale, Fig. 2a). White-backed woodpecker occurrence probability was negatively related to the clumpiness index (i.e., it was positively related to habitat fragmentation) across all spatial scales (largest coefficient estimates at the 3500 and 4500 m scales) except for the 1000 m radius (Fig. 2b). The coefficient estimates for proportion of coniferous and young deciduous forest were positive at all spatial scales (Fig. 2c), whereas those for the proportion of young deciduous forest and for the proportion of old coniferous forest were close to zero across almost all spatial scales (Fig. 2d - e).

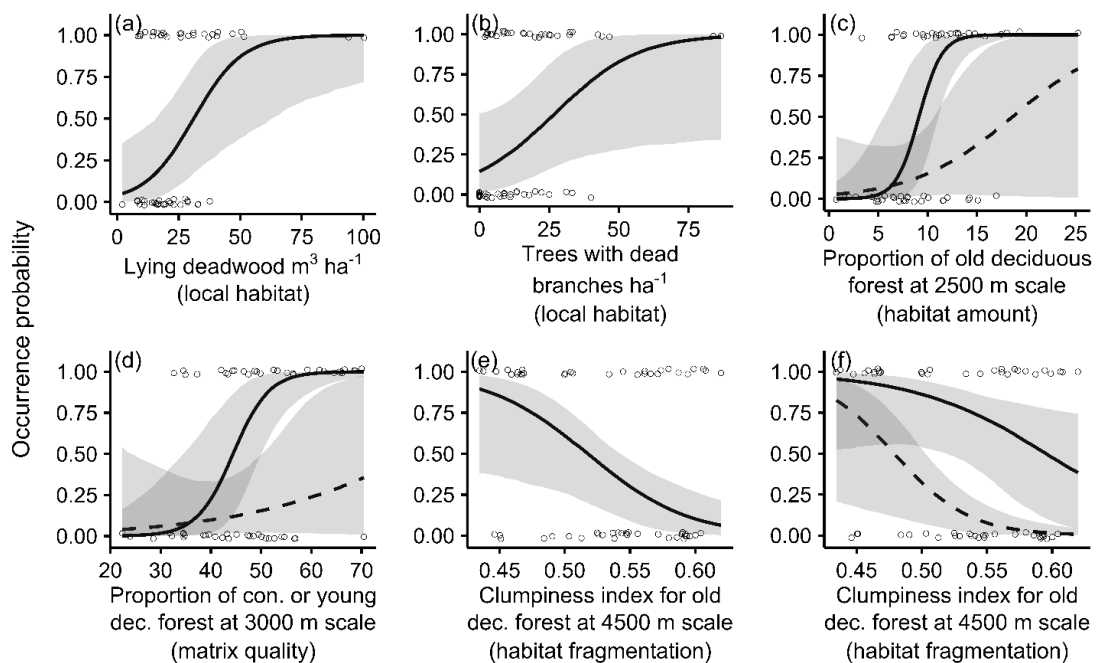


Figure 1 Relationships between white-backed woodpecker occurrence probability and variables representing (a) and (b) local habitat and (c) – (f) landscape context. Shown are medians and 95% credible intervals using the joint posterior distribution of (a) – (d) the top-ranked model, (e) a high-ranked model representing the habitat fragmentation hypothesis, and (f) a model representing the fragmentation threshold hypothesis. Estimates were calculated with other variables set to their means, except when the variable on the x-axis was in interaction with another predictor (proportion of coniferous and young deciduous forest in (c) and proportion of old deciduous forest in (d) and (f)), where the 25% (dashed line) and 75% quantiles (solid line) of the interacting predictor were used. $N = 60$.

Comparing the models representing the landscape context hypotheses (step 3) showed that white-backed woodpecker occurrence was best explained by a model including habitat amount and matrix quality variables and their interaction (Table 3), with none of the credible intervals including zero (Table 4b). Occurrence probability increased with increasing proportion of old deciduous forest at the 1000

m scale and increasing proportion of coniferous and young deciduous forest at the 3000 m scale. The interaction between the two variables showed that occurrence probability was only high when both habitat amount and the proportion of coniferous and young deciduous forest (referring to matrix quality) were high (Fig. 1c, d). A model including habitat amount and old coniferous forest as matrix habitat also ranked relatively high (ΔLOOIC to the top-ranked model = 6.63) but the credible interval for the proportion of old coniferous forest included zero (Table 4c). A similarly ranked model (ΔLOOIC to the top-ranked model = 7.13) included habitat amount and habitat fragmentation variables and none of the credible intervals included zero (Table 4d). According to this model, occurrence probability increased with increasing proportion of old deciduous forest at the 2500 m scale and decreased with increasing clumpiness index at the 4500 m scale (Fig. 1e). There was no evidence for a threshold in habitat amount below which occurrence probability was negatively related to habitat fragmentation; the model including the interaction between habitat amount and habitat fragmentation ranked lower than the model without the interaction (Table 3), and occurrence probability decreased with increasing clumpiness index (i.e., decreasing fragmentation) regardless of habitat amount (Fig. 1f). Lastly, comparing the models including both local habitat and landscape context (*m.full*), only local habitat (*m.local*), and only landscape context (*m.landscape*) showed that *m.landscape* explained white-backed woodpecker occurrence substantially better than *m.local* and almost as well as *m.full* (Table 5).

Table 3 Models used to relate white-backed woodpecker occurrence to local habitat and to landscape context (represented by four hypotheses: HA = Habitat amount hypothesis; HF = Habitat fragmentation hypothesis; FT = Fragmentation threshold hypothesis; MQ = Matrix quality hypothesis: 1: high importance of all non-old deciduous forest types, 2: high importance of young deciduous forest, 3: high importance of old coniferous forest as matrix habitat). Model selection was performed based on the leave-one-out cross-validation information criterion (LOOIC). Δ LOOIC: Difference between the model's and the top-ranked model's LOOIC. Dec_old = proportion of old deciduous forest, con_dec_young = proportion of coniferous and young deciduous forest, clumpy = clumpiness index for dec_old, con_old = proportion of old coniferous forest, dec_young = proportion of young deciduous forest. The numbers at the end of a variable name refer to the spatial scale at which it was measured. If a landscape metric was used at two spatial scales, only the higher ranked model is presented (see Table A.1 in the Appendix for full list of models and Table A.2 for correlations between the variables). N = 60.

Hypothesis	Model	LOOIC	Δ LOOIC
Local habitat			
-	dec_old_500 + vollog + deadbr	73.05	0
-	dec_old_500 + vollog + deadbr + insolation	74.42	1.37
-	dec_old_500 + deadbr + insolation	75.19	2.14
-	dec_old_500 + vollog + insolation	78.57	5.52
-	dec_old_500 + beech50 + basallive + vollog + volsnag + deadbr + insolation	83.98	10.93
Local habitat + landscape context (all models also include dec_old_500 + vollog + deadbr)			
MQ1	dec_old_2500 + con_dec_young_3000 + dec_old_2500:con_dec_young_3000	50.18	0
MQ1	dec_old_2500 + con_dec_young_3000	54.24	4.05
MQ3	dec_old_2500 + con_old_1500	56.81	6.63
HF	dec_old_2500 + clumpy_4500	57.31	7.13
FT	dec_old_2500 + clumpy_4500 + dec_old_2500:clumpy_4500	58.38	8.19
HA	dec_old_2500	58.82	8.63
MQ1	con_dec_young_3000	59.72	9.54
MQ2	dec_old_2500 + dec_young_3000	60.81	10.62
MQ2	dec_old_2500 + dec_young_3000 + dec_old_2500:dec_young_3000	61.39	11.2
MQ3	dec_old_2500 + con_old_1500 + dec_old_2500:con_old_1500	61.48	11.3
HF	clumpy_4500	69.09	18.9
MQ2	dec_young_3000	71.17	20.98
-	Only local habitat	73.05	22.87
MQ3	con_old_1500	74.94	24.75

Figure 2 Results of the top-ranked model of a Bayesian ridge regression relating white-backed woodpecker occurrence probability to landscape metrics at spatial scales ranging from 1000 to 5000 m. Each dot is the coefficient estimate (median of the marginal posterior distribution) of one landscape metric at a given spatial scale. The ridge regression was used to evaluate the most relevant spatial scale per landscape metric, with the largest absolute coefficient estimate indicating the most relevant scale per metric.

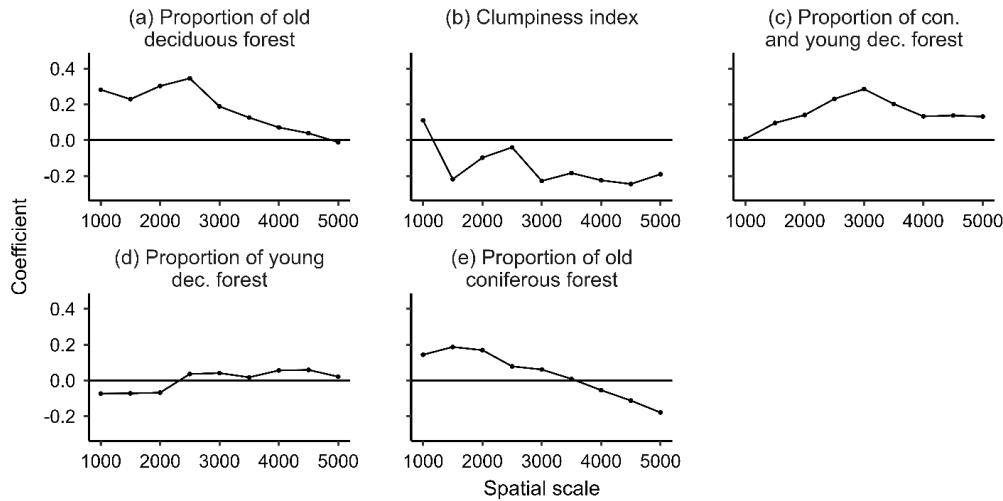


Table 4 Occurrence of the white-backed woodpecker in relation local habitat and landscape context. Shown are coefficient estimates and credible intervals (medians and 2.5 and 97.5% quantiles of the joint posterior distribution) of variables included in a) the top-ranked local habitat-only model, b) the top-ranked model including local habitat and landscape context variables, c) and d) two other high-ranked models. Variable names are given in Table 1.

Variable	a)	b)	c)	d)
Intercept	-0.19 [-1.3; 0.65]	-0.67 [-2.29; 0.71]	-0.37 [-1.81; 0.93]	-0.44 [-1.84; 0.7]
vollog	0.8 [0.05; 1.72]	1.79 [0.39; 3.64]	1.2 [0.09; 2.49]	1.68 [0.48; 3.14]
deadbr	1.06 [0.3; 1.99]	1.21 [0.04; 2.84]	1.8 [0.61; 3.53]	0.9 [-0.22; 2.41]
dec_old_500	0.84 [0.03; 1.88]	0.54 [-0.83; 2]	-0.06 [-1.34; 1.18]	0.41 [-0.9; 1.76]
dec_old_2500	-	2.40 [0.83; 4.84]	2.71 [1.27; 4.65]	2.42 [1.06; 4.07]
con_dec_young_3000	-	1.7 [0.38; 3.68]	-	-
dec_old_2500:con_dec_young_3000	-	2.35 [0.53; 4.66]	-	-
con_old_1500	-	-	1 [-0.01; 2.39]	-
clumpy_4500	-	-	-	-1.39 [-2.96; -0.13]
Variance cluster_id	0.68 [0; 7.54]	1.72 [0.01; 13.79]	2.25 [0.01; 16.08]	1.18 [0; 9.2]

Table 5 Performance of three models relating white-backed woodpecker occurrence to variables describing both local habitat and landscape context, only local habitat, or only landscape context. LOOIC = leave one out cross-validation information criterion. All models also include a random intercept for cluster_id.

Model	LOOIC	% of sites for which presence/absence was correctly predicted	Explained variance
Local habitat + landscape context	50.2	90%	66%
Landscape context	58	87%	50%
Local habitat	73.1	78%	20%

Discussion

In the present study, we examined white-backed woodpecker occurrence probability in relation to local habitat and to four hypotheses describing potential effects of landscape context: the habitat fragmentation hypothesis, the fragmentation threshold hypothesis, the habitat amount hypothesis, and the matrix quality hypothesis. Landscape context explained 2.5 times more of the variance in occurrence probability than local habitat. The relation between occurrence probability and landscape context was explained by the matrix hypothesis and, albeit with weaker support, the habitat fragmentation hypothesis. Although occurrence probability was strongly related to habitat amount, the habitat amount hypothesis was not supported as this hypothesis predicts no relation with habitat fragmentation (i.e., with the clumpiness index; Table 2).

White-backed woodpecker occurrence is related to local forest characteristics and to landscape composition and configuration

In accordance with previous studies addressing the white-backed woodpecker's habitat preferences (e.g., Czeszczewik et al., 2013; Ettwein et al., 2020; Hogstad and Stenberg, 1994; Kajtoch et al., 2013), occurrence probability increased with the abundance of structural elements found in old-growth forests (lying deadwood and trees with dead branches) at the local scale. However, it is important to note that data on the abundance and spatial distribution of these structural elements at the landscape scale were not available and we thus do not know whether deadwood and trees with dead branches are important at larger spatial scales as well.

Complementing the existing knowledge about the white-backed woodpecker's breeding habitat preferences, we found that occurrence probability was also related to the landscape composition and configuration at spatial scales beyond the home range scale. According to our top-ranked model, white-backed woodpecker occurrence probability increased with the proportion of old deciduous forest (representing habitat amount) at the 2500 m (= 20 km²) scale and, in line with the matrix quality hypothesis, with the proportion of coniferous or young deciduous forest at the 3000 m (= 28 km²) scale.

The interaction between matrix quality and habitat amount showed that for high occurrence probabilities both habitat amount and matrix quality needed to be high, with both variables exhibiting thresholds above which occurrence probability strongly increased (Fig. 1). For instance, at average local habitat quality and high matrix quality, occurrence probability increased from 10 to 90% when the proportion of old deciduous forest in the landscape increased from 6.5 to 11.7% (Fig. 1c). Moreover, at average local habitat quality and high habitat amount at the landscape scale, occurrence probability increased from 10 to 90% when the proportion of coniferous or young deciduous forest increased from 37 to 52% (Fig. 1d). The proportion of old deciduous forest at the 500 m (= 0.8 km²) scale, which we used in all models to account for varying habitat amount at the local scale and which was an important variable in the local habitat-only model, became unimportant once habitat amount at larger scales was also included (Table 4). That habitat amount is important at spatial scales beyond the home range scale is consistent with studies on the occurrence of many other species including forest birds (e.g., Betts et al., 2007, 2010; Smith et al., 2011), some of which also found thresholds for habitat amount (Betts et al., 2007, 2010). Considering that the annual home range size of the white-backed woodpecker is approximately 100 - 350 ha (Chapter 1), the importance of habitat amount at a large spatial scale suggests that the individuals establish their home ranges in areas with enough habitat to sustain multiple breeding pairs. Indeed, in our study area usually at least three to five breeding territories were found next to each other.

Matrix quality was important at a similar spatial scale as habitat amount. This might either be because white-backed woodpeckers supplement their resource intake by foraging also in the matrix (“landscape supplementation hypothesis”, Dunning et al., 1992) or because forest as matrix habitat facilitates movement between habitat patches. It likely is a combination of both: On the one hand, white-backed woodpeckers are known to forage also in coniferous and young deciduous forests, particularly in the non-breeding season (Chapter 3), and high forest cover at large spatial scales thus provides additional habitat for multiple breeding pairs. On the other hand, the species strongly avoids unforested area (Chapter 3), and old deciduous stands within larger forested areas are thus more likely to be reached than stands surrounded by unforested area. The latter aspect may be particularly important for dispersal. Translocation experiments (Aben et al., 2012; Bélisle et al., 2001), tracking of dispersing juveniles (Cox and Kesler, 2012), and studies addressing occupancy and abundance (Watling et al., 2011) have consistently concluded that matrix composition strongly influences movements and ultimately connectivity in many species. The importance of matrix composition for movement and connectivity tends to be stronger when the contrast between matrix types is high (Eycott et al., 2012).

In our study area, where forest cover is relatively low (approximately 40%), matrix quality may thus be particularly important.

Lastly, in line with the habitat fragmentation hypothesis, white-backed woodpecker occurrence probability decreased with increasing clumpiness (i.e., decreasing fragmentation) of old deciduous forest at the 4500 m (= 64 km²) scale. Contrary to the fragmentation threshold hypothesis, there was no evidence for a threshold in habitat amount below which fragmentation effects were negative, and occurrence probability increased with increasing habitat fragmentation also when habitat amount was low (Fig. 1f). Similar to the positive effects of matrix quality, positive effects of habitat fragmentation may be related to enhanced connectivity (Fahrig, 2017). Distances between habitat patches tend to be smaller in landscapes with many small instead of few large patches, and dispersed patches of old deciduous forest in a matrix of other forest types may serve as stepping stones between occupied sites. However, considering that the coefficient estimates of the clumpiness index were smaller than those of the proportions of old deciduous forest and of coniferous and young deciduous forest, and that the difference between the LOOIC values of the habitat fragmentation model and the matrix quality model was relatively large, habitat fragmentation appeared to be less important than habitat amount and matrix quality.

Altogether, the relationships between white-backed woodpecker occurrence and landscape context suggest that occurrence probability within a study site is affected by the likelihood that the site is colonized by a dispersing bird. Dispersal of juvenile white-backed woodpeckers has not been studied yet, but studies on other woodpecker species avoiding unforested area also suggest that landscape context strongly affects site colonization through modifying dispersal. For instance, prospecting juvenile red-bellied woodpeckers (*Melanerpes carolinus*) chose foray paths and dispersal directions with high forest cover (Cox and Kesler, 2012), suggesting a high importance of matrix composition for dispersal. Moreover, juvenile red-cockaded woodpeckers (*Picoides borealis*) and middle spotted woodpeckers (*Dendrocoptes medius*) dispersed across forests resembling the species' breeding habitat (Ciudad et al., 2009; Kesler and Walters, 2012), supporting the idea that habitat patches in the matrix may serve as stepping stones for dispersing birds.

Landscape context is more important than local habitat

According to our models including both local habitat and landscape context, landscape context explained about 2.5 times more of the variance in occurrence probability than local habitat. Moreover, the models including only landscape context variables performed substantially better than the local habitat-only model and almost as well as the model including both local habitat and landscape context

variables. The high importance of landscape context in our models does not only show that the occurrence of the white-backed woodpecker in a given site may strongly depend on its surrounding landscape as discussed above but also illustrates that identifying important habitat factors requires consideration of variables at various spatial scales. Considering only local habitat may lead to the overemphasis of local habitat characteristics and ineffective conservation guidelines. For instance, our study confirmed that old-growth structures (logs and trees with dead branches) are important elements of the white-backed woodpecker's breeding habitat. According to our top-ranked model, at intermediate habitat amount and matrix quality at the landscape scale, white-backed woodpecker occurrence probability exceeded 50% when 31 m³ of logs and 27 trees with dead branches per hectare were available. However, if a site with 31 m³ of logs and 27 trees with dead branches per hectare was in a landscape with intermediate habitat amount at the local scale but low habitat amount and matrix quality at the landscape scale (25% quantiles), our model predicted an occurrence probability of only 30%. By contrast, when we set the proportions of old deciduous forest and of coniferous and young deciduous forest to the respective 75% quantiles, occurrence probability exceeded 50% at minimum local habitat quality (in our dataset 2 m³ of logs and no trees with dead branches; however, note that predicted values are associated with some uncertainty and none of the occupied sites in our study contained neither logs nor trees with dead branches). Although thresholds are helpful tools for conservation planning, thresholds based on univariate models (e.g., Büttler et al., 2004; Kajtoch et al., 2013) may thus be misleading. We do not conclude that local habitat quality is generally unimportant for white-backed woodpeckers. Deadwood is used for foraging throughout the year (Czeszczewik, 2009, Chapter 3) and thus crucial for this species. The low importance of local habitat in our models was rather a result of the generally high habitat quality in most absence sites, which also contained deciduous or mixed mountain forest with relatively high amounts of deadwood. Moreover, the effect of the landscape context may differ between regions. For instance, Orme et al. (2019) showed that the negative effect of deforestation on the occurrence of forest birds was stronger near the range edge than in the range core, and the high importance of landscape context found in our study might be due to the study population being at the range edge. Similarly, our results may not be transferable to other species. In a similar study system as ours (spatially structured woodpecker population at the range edge), Robles and Ciudad (2012) found that local habitat was more important than landscape context for occupancy dynamics of the middle spotted woodpecker. More studies explicitly comparing the relative importance of local habitat and landscape context are needed to assess whether incorporating landscape context into habitat models is generally important for white-backed woodpeckers and other species.

Conservation implications

The high importance of the landscape context for the occurrence of the white-backed woodpecker shows that conservation measures for this species might be ineffective in areas with low forest cover, even when enough habitat for a breeding pair is available. As afforesting currently unforested areas over large extents is not feasible in most of Europe, management measures for the white-backed woodpecker should focus on the conservation of and habitat improvements in large forested areas with known occurrence of the species or on unoccupied areas that contain enough forest to potentially sustain multiple breeding pairs. In our study region, a high proportion of old deciduous or mixed forest as well as of other forest types was important in areas of 20 to 28 km² surrounding a given occupied site. For example, occurrence probability exceeded 90% when 230 ha of old deciduous forest and 16 km² of other forest types were available within areas of 20 and 28 km², respectively. Therefore, conservation measures at the landscape level should focus on the protection or creation of old deciduous or mixed stands (e.g., by establishing forest reserves) embedded in large forested areas. The positive relationship between white-backed woodpecker occurrence probability and habitat fragmentation within 64 km² areas suggests that these forests large enough to sustain multiple breeding pairs should ideally be connected by dispersed patches of old deciduous or mixed forest. At the scale of the breeding home range (approximately 30 ha), logs and trees with dead branches appeared to be important and should thus be retained. However, as the yearly home ranges are larger and deadwood is the main foraging substrate not only within the home ranges but probably also during dispersal, white-backed woodpeckers will benefit from the availability of deadwood and old trees in much larger areas and in all forest types.

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References

Aben, J., Adriaensen, F., Thijs, K.W., Pellikka, P., Siljander, M., Lens, L., Matthysen, E., 2012. Effects of matrix composition and configuration on forest bird movements in a fragmented Afromontane biodiversity hot spot. *Anim. Conserv.* 15, 658–668. <https://doi.org/10.1111/j.1469-1795.2012.00562.x>

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–366. <https://doi.org/10.2307/3545823>
- Angelstam, P., Roberge, J.-M., Löhmus, A., Bergmanis, M., Brazaitis, G., Dönn-Breuss, M., Edenius, L., Kosinski, Z., Kurlavicius, P., Lārmanis, V., Lūkins, M., Mikusiński, G., Račinskis, E., Strazds, M., Tryjanowski, P., 2004. Habitat modelling as a tool for landscape-scale conservation: a review of parameters for focal forest birds. *Ecol. Bull.* 51, 427–453.
- Aulén, G., 1988. Ecology and distribution of the white-backed woodpecker *Dendrocopos leucotos* in Sweden (Dissertation). Swedish University of Agricultural Sciences, Uppsala.
- Banks-Leite, C., Betts, M.G., Ewers, R.M., Orme, C.D.L., Pigot, A.L., 2022. The macroecology of landscape ecology. *Trends Ecol. Evol.* 37, 480–487. <https://doi.org/10.1016/j.tree.2022.01.005>
- Bélisle, M., Desrochers, A., Fortin, M.-J., 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82, 1893–1904. [https://doi.org/10.1890/0012-9658\(2001\)082\[1893:IOFCOT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1893:IOFCOT]2.0.CO;2)
- Betts, M.G., Forbes, G.J., Diamond, A.W., 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conserv. Biol.* 21, 1046–1058. <https://doi.org/10.1111/j.1523-1739.2007.00723.x>
- Betts, M.G., Forbes, G.J., Diamond, A.W., Taylor, P.D., 2006. Independent effects of fragmentation on forest songbirds: an organism-based approach. *Ecol. Appl.* 16, 1076–1089. [https://doi.org/10.1890/1051-0761\(2006\)016\[1076:IEFOF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1076:IEFOF]2.0.CO;2)
- Betts, M.G., Hagar, J.C., Rivers, J.W., Alexander, J.D., McGarigal, K., McComb, B.C., 2010. Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecol. Appl.* 20, 2116–2130. <https://doi.org/10.1890/09-1305.1>
- Bosco, L., Cushman, S.A., Wan, H.Y., Zeller, K.A., Arlettaz, R., Jacot, A., 2021. Fragmentation effects on woodlark habitat selection depend on habitat amount and spatial scale. *Anim. Conserv.* 24, 84–94. <https://doi.org/10.1111/acv.12604>
- Brotans, L., Mönkkönen, M., Martin, J.L., 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *Am. Nat.* 162, 343–357. <https://doi.org/10.1086/376887>
- Brown, P.J., Vannucci, M., Fearn, T., 2002. Bayes model averaging with selection of regressors. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 64, 519–536. <https://doi.org/10.1111/1467-9868.00348>

- Bütler, R., Angelstam, P., Ekelund, P., Schlaepfer, R., 2004. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. *Biol. Conserv.* 119, 305–318. <https://doi.org/10.1016/j.biocon.2003.11.014>
- Carlson, A., 2000. The effect of habitat loss on a deciduous forest specialist species: the white-backed woodpecker (*Dendrocopos leucotos*). *For. Ecol. Manag.* 131, 215–221. [https://doi.org/10.1016/S0378-1127\(99\)00215-7](https://doi.org/10.1016/S0378-1127(99)00215-7)
- Ciudad, C., Robles, H., Matthysen, E., 2009. Postfledging habitat selection of juvenile middle spotted woodpeckers: a multi-scale approach. *Ecography* 32, 676–682. <https://doi.org/10.1111/j.1600-0587.2009.05806.x>
- Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., Böhner, J., 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. *Geosci. Model Dev.* 8, 1991–2007. <https://doi.org/10.5194/gmd-8-1991-2015>
- Cox, A.S., Kesler, D.C., 2012. Prospecting behavior and the influence of forest cover on natal dispersal in a resident bird. *Behav. Ecol.* 23, 1068–1077. <https://doi.org/10.1093/beheco/ars076>
- Czeszczewik, D., 2009a. Marginal differences between random plots and plots used by foraging white-backed woodpeckers demonstrates supreme primeval quality of the Białowieża National Park, Poland. *Ornis Fenn.* 86, 30–37.
- Czeszczewik, D., 2009b. Foraging behaviour of white-backed woodpeckers *Dendrocopos leucotos* in a primeval forest (Białowieża National Park, NE Poland): dependence on habitat resources and season. *Acta Ornithol.* 44, 109–118. <https://doi.org/10.3161/000164509X482687>
- Czeszczewik, D., Walankiewicz, W., Mitrus, C., Tumiel, T., Stański, T., Sahel, M., Bednarczyk, G., 2013. Importance of dead wood resources for woodpeckers in coniferous stands of the Białowieża Forest. *Bird Conserv. Int.* 23, 414–425. <https://doi.org/10.1017/S0959270912000354>
- de Knegt, H.J., van Langevelde, F., Coughenour, M.B., Skidmore, A.K., de Boer, W.F., Heitkönig, I.M.A., Knox, N.M., Slotow, R., van der Waal, C., Prins, H.H.T., 2010. Spatial autocorrelation and the scaling of species–environment relationships. *Ecology* 91, 2455–2465. <https://doi.org/10.1890/09-1359.1>
- Deng, W.-H., Gao, W., 2005. Edge effects on nesting success of cavity-nesting birds in fragmented forests. *Biol. Conserv.* 126, 363–370. <https://doi.org/10.1016/j.biocon.2005.06.013>
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169–175. <https://doi.org/10.2307/3544901>

- Ettwein, A., Korner, P., Lanz, M., Lachat, T., Kokko, H., Pasinelli, G., 2020. Habitat selection of an old-growth forest specialist in managed forests. *Anim. Conserv.* 23, 547–560. <https://doi.org/10.1111/acv.12567>
- Eycott, A.E., Stewart, G.B., Buyung-Ali, L.M., Bowler, D.E., Watts, K., Pullin, A.S., 2012. A meta-analysis on the impact of different matrix structures on species movement rates. *Landsc. Ecol.* 27, 1263–1278. <https://doi.org/10.1007/s10980-012-9781-9>
- Fahrig, L., 2019. Habitat fragmentation: a long and tangled tale. *Glob. Ecol. Biogeogr.* 28, 33–41. <https://doi.org/10.1111/geb.12839>
- Fahrig, L., 2017. Ecological responses to habitat fragmentation per se. *Annu. Rev. Ecol. Evol. Syst.* 48, 1–23. <https://doi.org/10.1146/annurev-ecolsys-110316-022612>
- Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* 40, 1649–1663. <https://doi.org/10.1111/jbi.12130>
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>
- Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? *Ecol. Model.* 105, 273–292. [https://doi.org/10.1016/S0304-3800\(97\)00163-4](https://doi.org/10.1016/S0304-3800(97)00163-4)
- Flather, C.H., Bevers, M., 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *Am. Nat.* 159, 40–56. <https://doi.org/10.1086/324120>
- Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., Holt, R.D., Gonzalez, A., Pardini, R., Damschen, E.I., Melo, F.P.L., Ries, L., Prevedello, J.A., Tschardtke, T., Laurance, W.F., Lovejoy, T., Haddad, N.M., 2018. Is habitat fragmentation good for biodiversity? *Biol. Conserv.* 226, 9–15. <https://doi.org/10.1016/j.biocon.2018.07.022>
- Franco, A.M.A., Sutherland, W.J., 2004. Modelling the foraging habitat selection of lesser kestrels: conservation implications of European Agricultural Policies. *Biol. Conserv.* 120, 63–74. <https://doi.org/10.1016/j.biocon.2004.01.026>
- Frank, G., 2002. Brutzeitliche Einnischung des Weissrückenspechtes *Dendrocopos leucotos* im Vergleich zum Buntspecht *Dendrocopos major* in montanen Mischwäldern der nördlichen Kalkalpen. *Vogelwelt* 123, 225–239.

Frank, G., Hochebner, T., 2001. Erfassung der Spechte - insbesondere des Weißrückenspechtes *Picoides leucotos* - im Rhmen des LIFE-Projektes Wildnisgebiet Dürrenstein. in: LIFE- Projekt Wildnisgebiet Dürrenstein. Amt der Niederösterreichischen Landesregierung (Ed.). Amt der Niederösterreichischen Landesregierung, St. Pölten.

Gelman, A., Pardoe, I., 2006. Bayesian measures of explained variance and pooling in multilevel (hierarchical) models. *Technometrics* 48, 241–251. <https://doi.org/10.1198/004017005000000517>

Goodrich, B., Gabry, J., Ali, I., Brilleman, S., 2020. “rstanarm: Bayesian applied regression modeling via Stan.” R package version 2.19.3, <https://mc-stan.org/rstanarm>.

Hanski, I., 2015. Habitat fragmentation and species richness. *J. Biogeogr.* 42, 989–993. <https://doi.org/10.1111/jbi.12478>

Hesselbarth, M.H., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J., 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* 42, 1648–1657.

Hogstad, O., Stenberg, I., 1997. Breeding success, nestling diet and parental care in the white-backed woodpecker *Dendrocopos leucotos*. *J. Für Ornithol.* 138, 25–38. <https://doi.org/10.1007/BF01651649>

Hogstad, O., Stenberg, I., 1994. Habitat selection of a viable population of white-backed woodpeckers *Dendrocopos leucotos*. *Fauna Nor. Ser. C Cinclus* 17, 75–94.

Hooten, M.B., Hobbs, N.T., 2015. A guide to Bayesian model selection for ecologists. *Ecol. Monogr.* 85, 3–28. <https://doi.org/10.1890/14-0661.1>

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? *Glob. Ecol. Biogeogr.* 24, 52–63. <https://doi.org/10.1111/geb.12233>

Kajtoch, L., Figarski, T., Pelka, J., 2013. The role of forest structural elements in determining the occurrence of two specialist woodpecker species in the Carpathians, Poland. *Ornis Fenn.* 90, 23–40.

Kesler, D.C., Walters, J.R., 2012. Social composition of destination territories and matrix habitat affect red-cockaded woodpecker dispersal. *J. Wildl. Manag.* 76, 1028–1035. <https://doi.org/10.1002/jwmg.330>

Lõhmus, A., Kinks, R., Soon, M., 2010. The importance of dead-wood supply for woodpeckers in Estonia. *Balt. For.* 16, 76–86.

McGarigal, K., Cushman, S., Ene, E., 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the

University of Massachusetts, Amherst. Available at the following web site:
<http://www.umass.edu/landeco/research/fragstats/fragstats.html>.

McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. *Landsc. Ecol.* 31, 1161–1175. <https://doi.org/10.1007/s10980-016-0374-x>

Nagel, T.A., Firm, D., Pisek, R., Mihelic, T., Hladnik, D., de Groot, M., Rozenbergar, D., 2017. Evaluating the influence of integrative forest management on old-growth habitat structures in a temperate forest region. *Biol. Conserv.* 216, 101–107. <https://doi.org/10.1016/j.biocon.2017.10.008>

Orme, C.D.L., Mayor, S., dos Anjos, L., Develey, P.F., Hatfield, J.H., Morante-Filho, J.C., Tylianakis, J.M., Uezu, A., Banks-Leite, C., 2019. Distance to range edge determines sensitivity to deforestation. *Nat. Ecol. Evol.* 3, 886–891. <https://doi.org/10.1038/s41559-019-0889-z>

Robles, H., Ciudad, C., 2012. Influence of habitat quality, population size, patch size, and connectivity on patch-occupancy dynamics of the middle spotted woodpecker. *Conserv. Biol.* 26, 284–293.

Saura, S., 2021. The Habitat Amount Hypothesis implies negative effects of habitat fragmentation on species richness. *J. Biogeogr.* 48, 11–22. <https://doi.org/10.1111/jbi.13958>

Scherzinger, W., 1982. Die Spechte im Nationalpark Bayerischer Wald. Nationalparkverwaltung Bayerischer Wald, Grafenau.

Schtickzelle, N., Baguette, M., 2003. Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration–patch area relationships in fragmented landscapes. *J. Anim. Ecol.* 72, 533–545. <https://doi.org/10.1046/j.1365-2656.2003.00723.x>

Smith, A.C., Fahrig, L., Francis, C.M., 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography* 34, 103–113. <https://doi.org/10.1111/j.1600-0587.2010.06201.x>

Vehtari, A., Gabry, J., Yao, Y., Gelman, A., 2019. loo: efficient leave-one-out cross-validation and WAIC for Bayesian models." R package version 2.1.0, <https://CRAN.R-project.org/package=loo>.

Virkkala, R., Alanko, T., Laine, T., Tiainen, J., 1993. Population contraction of the white-backed woodpecker *Dendrocopos leucotos* in Finland as a consequence of habitat alteration. *Biol. Conserv.* 66, 47–53. [https://doi.org/10.1016/0006-3207\(93\)90133-L](https://doi.org/10.1016/0006-3207(93)90133-L)

Walankiewicz, W., Czeszczewik, D., Tumiel, T., Stański, T., 2011. Woodpeckers abundance in the Białowieża Forest – a comparison between deciduous, strictly protected and managed stands. *Ornis Pol.* 52, 161–168.

Watling, J.I., Arroyo-Rodríguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L.M., Fang, R., Hamel-Leigue, A.C., Lachat, T., Leal, I.R., Lens, L., Possingham, H.P., Raheem, D.C., Ribeiro, D.B., Slade, E.M., Urbina-Cardona, J.N., Wood, E.M., Fahrig, L., 2020. Support for the habitat amount hypothesis from a global synthesis of species density studies. *Ecol. Lett.* 23, 674–681. <https://doi.org/10.1111/ele.13471>

Watling, J.I., Nowakowski, A.J., Donnelly, M.A., Orrock, J.L., 2011. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Glob. Ecol. Biogeogr.* 20, 209–217. <https://doi.org/10.1111/j.1466-8238.2010.00586.x>

Wesołowski, T., 1995. Ecology and behaviour of white-backed woodpecker (*Dendrocopos leucotos*) in a primeval temperate forest (Białowieża National Park, Poland). *Vogelwarte* 38, 61–75.

Wiens, J.A., 1989. Spatial scaling in ecology. *Funct. Ecol.* 3, 385–397. <https://doi.org/10.2307/2389612>

APPENDIX

Table A.1 Full list of models used to relate white-backed woodpecker occurrence to local habitat and to landscape context. All models also include the proportion of old deciduous forest at the 500 m scale, volume of lying deadwood and number of trees with dead branches as variables representing local habitat. Model selection was performed based on the leave-one-out cross-validation information criterion (LOOIC). Δ LOOIC: Difference between the model's and the top-ranked model's LOOIC. Dec_old = proportion of old deciduous forest, con_dec_young = proportion of coniferous and young deciduous forest, clumpy = clumpiness index for dec_old, con_old = proportion of old coniferous forest, dec_young = proportion of young deciduous forest. The numbers at the end of a variable name refer to the spatial scale at which it was measured.

Model	LOOIC	Δ LOOIC
dec_old_2500 + con_dec_young_3000 + dec_old_2500:con_dec_young_3000	50.18	0
dec_old_1000 + con_dec_young_3000 + dec_old_1000:con_dec_young_3000	53.43	3.24
dec_old_2500 + con_dec_young_3000	54.24	4.05
dec_old_1000 + con_dec_young_3000	54.83	4.64
dec_old_2500 + con_old_1500	56.81	6.63
dec_old_2500 + clumpy_4500	57.31	7.13
clumpy_4500 + dec_old_2500 + clumpy_4500:dec_old_2500	58.38	8.19
dec_old_2500	58.82	8.63
dec_old_2500 + clumpy_1500	59.38	9.19
con_dec_young_3000	59.72	9.54
dec_old_2500 + con_old_5000	60.47	10.29
clumpy_1500 + dec_old_2500 + clumpy_1500:dec_old_2500	60.69	10.5
dec_old_2500 + dec_young_3000	60.81	10.62
dec_old_2500 + dec_young_3000 + dec_old_2500:dec_young_3000	61.39	11.2
dec_old_2500 + con_old_1500 + dec_old_2500:con_old_1500	61.48	11.3
dec_old_1000 + clumpy_4500	62.89	12.71
dec_old_2500 + con_old_5000 + dec_old_2500:con_old_5000	65.07	14.88
clumpy_4500 + dec_old_1000 + clumpy_4500:dec_old_1000	65.44	15.26
dec_old_1000 + dec_young_3000	65.76	15.57
dec_old_1000 + clumpy_1500	65.99	15.81
dec_old_1000 + con_old_1500	68.33	18.15
dec_old_1000 + dec_young_3000 + dec_old_1000:dec_young_3000	69.05	18.86
clumpy_4500	69.09	18.9
clumpy_1500 + dec_old_1000 + clumpy_1500:dec_old_1000	69.2	19.02
dec_old_1000 + con_old_5000	69.89	19.7
clumpy_1500	71.11	20.93
dec_young_3000	71.17	20.98
dec_old_1000 + con_old_1500 + dec_old_1000:con_old_1500	71.41	21.22
dec_old_1000 + con_old_5000 + dec_old_1000:con_old_5000	73.22	23.04
LH	73.48	23.3
con_old_1500	74.94	24.75
con_old_5000	75.21	25.03

Table A.2 Correlations between variables used for modeling white-backed woodpecker occurrence probability (Pearson correlation coefficient). Variable names are given in Table 1.

	logs	snags	basallive	deadbr	beech50	sun	dec_old_500	dec_old_1000	dec_old_2500	clumpy_1500	clumpy_4500	con_dec_young_3000	dec_young_3000	con_old_1500
logs	1	0.5	0.19	0.32	0.43	-0.08	0.03	0.02	-0.15	0.07	0.12	-0.19	-0.12	-0.1
snags	0.5	1	0.29	0.39	0.28	0.1	0.25	0.34	0.18	0.04	0.15	-0.02	-0.02	-0.28
basallive	0.19	0.29	1	0.41	0.19	0.06	-0.12	-0.03	0	-0.06	-0.14	0.23	0.11	-0.02
deadbr	0.32	0.39	0.41	1	0.22	0.24	-0.05	0	0.04	-0.17	-0.27	0.05	0.09	-0.1
beech50	0.43	0.28	0.19	0.22	1	-0.13	0.27	0.19	-0.08	0.1	0.02	-0.27	0.12	-0.29
sun	-0.08	0.1	0.06	0.24	-0.13	1	-0.35	-0.3	-0.19	-0.37	-0.32	-0.09	0.17	-0.25
dec_old_500	0.03	0.25	-0.12	-0.05	0.27	-0.35	1	0.85	0.51	0.43	0.43	-0.13	-0.21	-0.06
dec_old_1000	0.02	0.34	-0.03	0	0.19	-0.3	0.85	1	0.67	0.34	0.36	-0.04	-0.07	-0.11
dec_old_2500	-0.15	0.18	0	0.04	-0.08	-0.19	0.51	0.67	1	0.07	0.12	0.24	0.26	-0.06
clumpy_1500	0.07	0.04	-0.06	-0.17	0.1	-0.37	0.43	0.34	0.07	1	0.59	-0.26	-0.51	0.18
clumpy_4500	0.12	0.15	-0.14	-0.27	0.02	-0.32	0.43	0.36	0.12	0.59	1	-0.14	-0.5	0.21
con_dec_young_3000	-0.19	-0.02	0.23	0.05	-0.27	-0.09	-0.13	-0.04	0.24	-0.26	-0.14	1	0.37	0.34
dec_young_3000	-0.12	-0.02	0.11	0.09	0.12	0.17	-0.21	-0.07	0.26	-0.51	-0.5	0.37	1	-0.55
con_old_1500	-0.1	-0.28	-0.02	-0.1	-0.29	-0.25	-0.06	-0.11	-0.06	0.18	0.21	0.34	-0.55	1

General discussion

The range expansion of the white-backed woodpecker into my study area in Western Austria, Liechtenstein and Eastern Switzerland shows that this old-growth forest specialist may also colonize regions with predominately managed forests. By studying home range size and habitat selection of adult white-backed woodpeckers in forest stands differing in management intensity and forest structure, I aimed to close knowledge gaps in this species' spatial ecology and to assess how the occurrence of the white-backed woodpecker and forest management can be reconciled.

Given the white-backed woodpecker's conservation relevance in Europe and its role as umbrella species, I use this last section of the thesis to synthesize and discuss the key results of the four chapters in a conservation context (in the order in which planning a conservation strategy for the white-backed woodpecker seems most reasonable to me). I present numbers regarding the white-backed woodpecker's habitat requirements whenever I feel they could be helpful for conservation and forestry practitioners. These numbers should not be interpreted as exact thresholds but should rather serve as rough guidelines. Moreover, it is important to note that the presented conservation suggestions do not refer to ideal conditions for the white-backed woodpecker, but rather to a compromise between ecological and economic interests. In my study area, white-backed woodpeckers appeared to maintain a stable population at least during the study period (between 2015 and 2021, the majority of the known territories was occupied each year, apart from areas close to the range edge; Chapter 2), but population density, reproductive success (unpublished data), and adult survival (Weber et al., in preparation) were lower than in other studied populations (e.g., in Finland (Virkkala et al., 1993), southwestern Norway (Stenberg, 1990), Białowieża Forest in Poland (Wesołowski, 1995), and Wildnisgebiet Dürrenstein wilderness area in Austria (Frank and Hochebner, 2001)). This suggests that the habitat in our study area is not optimal, both in terms of its amount at the landscape scale and its quality at the home range scale.

Key results of the thesis and their implications for conservation and forest management

- 1. Landscape context played an important role for the occurrence of the white-backed woodpecker in sites with the size of a breeding home range → large spatial scales need to be considered for planning and implementing conservation measures.*

In Chapter 4, we found that the occurrence of the white-backed woodpecker within study sites corresponding in size to a breeding home range was partly explained by environmental predictors recorded at large spatial scales compared with the home range size of the species. In addition to local

forest structure characteristics, occurrence probability was positively related to the proportion of old deciduous or mixed forest (representing habitat amount), the proportion of non-old deciduous/mixed forest (representing matrix quality), and to the fragmentation of old deciduous/mixed forest at spatial scales ranging from 20 to 64 km², i.e., 6 to 20 times the annual home range size. The sites had only high probabilities of being occupied by a white-backed woodpecker when both habitat amount and matrix quality were high; at least 11% of 20 km² and 50% of 28 km² needed to be covered by old deciduous or mixed forest and by other forest types, respectively. We concluded that white-backed woodpeckers preferably colonize sites in areas with enough breeding and non-breeding habitat for multiple breeding pairs, and that such areas should ideally be connected through dispersed patches of old deciduous or mixed forest. Furthermore, these results showed that conservation actions in areas with low forest cover might be ineffective, even if enough habitat for a breeding pair is available. Consequently, large areas with high forest cover (>60% forest cover within 20-28 km²) should be selected for the implementation of conservation measures. Within this area, enough old deciduous or mixed forest to sustain multiple breeding pairs should be available or created. The positive relation between white-backed woodpecker occurrence and habitat fragmentation indicates that old deciduous or mixed forests should ideally be dispersed at large spatial scales (64 km²) to enhance connectivity; therefore, the creation or protection of many small rather than few large old-growth patches within the managed-forest matrix may be a useful measure at such large scales. This conclusion supports findings from other studies on effects of habitat fragmentation (when considered independent of habitat amount), which show that ecological responses to habitat fragmentation are generally positive (reviewed by Fahrig, 2017) and suggest high conservation value of small protected areas (Fahrig, 2020). However, as Hanski (2015) and Saura (2021) stressed, the direction of the effect of habitat fragmentation may be scale-dependent; at larger spatial scales than those addressed in this thesis, habitat fragmentation might negatively affect white-backed woodpeckers, and my results indicate that that old deciduous forests should rather be clumped at the small scale of the breeding home range as discussed further below.

Whether our results on the importance of landscape context are transferable to other populations still needs to be examined. Habitat selection may differ between populations at the range edge and in the range core (Fuller, 2012) and depend on population density (Elkin and Reid, 2010; Mobæk et al., 2009). Since my study population is at the range edge and population density is low, the results might not be transferable to high-density populations in the range core. However, at least for low-density populations, our findings might be an important conservation-relevant complement to the existing knowledge about the importance of habitat availability in areas large enough to sustain a population

(Angelstam et al., 2004; Carlson, 2000) and of local breeding habitat quality (e.g., Czeszczewik et al., 2013; Hogstad and Stenberg, 1994; Kajtoch et al., 2013; Nagel et al., 2017, Chapters 2-4 of this thesis).

I deliberately present our results on the importance of the landscape context first because I believe that considering large spatial scales is not only one of the most important but also the most difficult step when planning and implementing conservation measures. While it may be relatively easy to set aside single forest stands or to motivate a number of forest managers to reduce forest management intensity, it gets more complicated when a high proportion of the forest within a larger area needs to be of high habitat quality and when the spatial distribution of these high-quality stands needs to be considered. Such large-scale planning is challenging since it requires involving many landowners, forest managers, and authorities. In fact, these challenges may be one of the reasons why the largest white-backed woodpecker conservation project, which aims to recover the Swedish white-backed woodpecker population by restoring forests and releasing captive-bred individual, has not been successful to date. For instance, Hof and Hjältén (2018) found that the current (high) conservation effort is not sufficient to create enough habitat for a viable population. Furthermore, the selection and distribution of the restoration sites partly did not meet ecological criteria due to the organizational, economic and logistical constraints such large-scale projects are faced with (Hof et al., 2021).

2. *Breeding home ranges were small and the habitat composition within the breeding home range was important → a high proportion of a relatively small area should be managed at low intensity or not at all (segregative/land sparing approaches useful for providing breeding habitat).*

During the breeding season in April and May, white-backed woodpeckers used only a small area within their annual home range (depending on the home range estimator, about 30 – 55 ha within an area of 116 to 350 ha, Chapter 1). Furthermore, the results of Chapters 2-4 suggest that the habitat composition within the home ranges is important particularly in the breeding season. In Chapter 2, we showed that in areas with low forest cover, breeding home range size decreased with increasing proportion of habitat with high resource abundance (standing deadwood and trees with dead branches). Mean resource abundance within the home range was less important than the proportion of resource-rich habitat, indicating that resources should ideally be clumped. In Chapter 3, we found that old deciduous and mixed forests were preferred for establishing the pre-breeding and breeding home ranges within the annual home range. Lastly, analyses from Chapter 4 revealed that white-backed woodpecker occurrence probability within breeding home range-sized sites increased with the amount of lying deadwood and trees with dead branches within the site (however, note that we considered

these variables only at the breeding home range scale and that they might be important at larger scales as well).

These results of the four chapters suggest that white-backed woodpeckers select a small area with high habitat quality as breeding territory, while they appear to be somewhat more flexible in their space use in the non-breeding season (see key result 3 below). This conclusion is plausible considering that white-backed woodpeckers are bound to a central place (the nest tree) only during the breeding season. Foraging costs increase with the distance to the central place; for breeding birds, such costs may not only include increased energy expenditure or predation risk (Olsson et al., 2008) but also decreased provisioning rates of the nestlings (Séchaud et al., 2022; Staggenborg et al., 2017) or fledging success (Pfeiffer and Meyburg, 2015; Séchaud et al., 2022). Thus, selecting small breeding home ranges with high resource abundance may increase individual fitness.

The following numbers may provide some guidance what “high resource abundance” means in our study population. In Chapter 2, we found that about half of the breeding home ranges (mean home range size from egg laying until fledging was 22 ha) comprised forest with high resource abundance, i.e., $> 51 \text{ m}^3 \text{ ha}^{-1}$ of total deadwood, $>15 \text{ m}^3 \text{ ha}^{-1}$ of snags, $>20 \text{ m}^3 \text{ ha}^{-1}$ of logs, and at least 1 tree with thick dead branches ha^{-1} . The mean deadwood volume within the breeding home ranges was $73 \text{ m}^3 \text{ ha}^{-1}$ (Chapter 2). The habitat types old deciduous/mixed forest with a heterogeneous vertical structure and with a homogeneous vertical structure, which were preferred for establishing pre-breeding and breeding home ranges, comprised on average 40% of the breeding home range and had a mean deadwood volume of 90 and $80 \text{ m}^3 \text{ ha}^{-1}$, respectively (Chapter 3). Lastly, occurrence probability within breeding home range-sized sites exceeded 50% when 31 m^3 of logs and 27 trees with dead branches per hectare were available (Chapter 4).

Such amounts of deadwood are much higher than those found in commercial forests and are typically found in stands with low management intensity or in forest reserves (Bouget et al., 2014; Christensen et al., 2005). This indicates that part of the forest should be managed at low intensity or not at all. In our study area, the forests used as breeding habitat were often protection forests or private forests managed through single-tree or group selection. However, that reproductive success in our study area was lower than in other regions indicates that even low management intensity might not be ideal for the white-backed woodpecker. Hence, segregative or land sparing approaches (e.g., via forest reserves) would probably be most beneficial to this species, at least for providing suitable breeding habitat.

3. *White-backed woodpeckers appeared to be more flexible in their space use in the non-breeding season but selected deadwood for foraging in all forest types and throughout the year → integrative/land sharing approach useful for providing non-breeding habitat.*

While breeding home ranges were small and the habitat composition within these home ranges important, the radio-tracked white-backed woodpeckers appeared to be somewhat more flexible in their space use in the non-breeding season (Chapters 2 and 3). First, seasonal home ranges in the non-breeding season were much larger than in the pre-breeding and breeding seasons. Predicted median seasonal home range sizes from June to January ranged from 48 to 67 ha and from 136 to 184 ha when estimated with kernel density estimation and autocorrelated kernel density estimation, respectively, and were 1.6 to 3.3 times larger than during the breeding season in April and May. Moreover, the variability in home range size between the individuals was high. Second, while variation in breeding home range size was explained by resource distribution and intraspecific competition, post-breeding home range size was related to neither factor. Lastly, while old deciduous or mixed forests were preferred during the breeding season, no forest type was significantly preferred over another one in the post-breeding season, summer, fall, and winter.

While the conclusions on the importance of old deciduous or mixed forests with abundant deadwood as breeding habitat are well-supported by our data, the apparently higher flexibility in the white-backed woodpecker's space use in the non-breeding season should be considered with some caution. Sample sizes were low in late summer, fall, and winter, and data on deadwood not available for the large non-breeding home ranges. Still, the high variability in space use between the individuals, particularly regarding the use of the different forest types (for example, some individuals used almost exclusively coniferous forest in the post-breeding season, whereas others did not use coniferous forest at all) suggests that white-backed woodpeckers are not as strictly bound to old deciduous or mixed forest in the non-breeding season as in the breeding season.

Such seasonal shifts in habitat specialization, resulting in seasonal differences in space use, appear to be common among animals; only few studies addressing seasonal variation in habitat selection found that habitat specialization is relatively constant throughout the year across levels of habitat selection (e.g., in the crested tit *Lophophanes cristatus*; Berlusconi et al., 2022). On the one hand, seasonal shifts in habitat specialization have been frequently explained by seasonal differences in the species' dietary preferences or by varying environmental conditions. For instance, some species target high-energy food resources in the breeding season to meet the increased nutritional demands during this period but use a wider food spectrum in the non-breeding season (Bettega et al., 2020; Booth et al., 2018). This may result in greater flexibility in the use of different habitat types in the non-breeding season

than in the breeding season (Bettega et al., 2020; however, note that the opposite pattern can also be found when winter is the more limiting season, e.g., Squires et al., 2010). Moreover, habitat specialists may use alternative food resources in the non-breeding season when the availability of the preferred food type is low, which can result in seasonal differences in habitat selection (Rolstad and Rolstad, 1995). On the other hand, some food specialists have been shown to feed on the same food type throughout the year but to shift their movement strategy or foraging behavior seasonally (e.g., from central place foraging in the breeding season to nomadism in the non-breeding season; Lenz et al., 2015). In Chapter 3, we showed that white-backed woodpeckers strongly selected deadwood for foraging throughout the year and in all habitat types; living trees were only used when they had dead branches. This indicates that the lower specialization on old deciduous and mixed forest in the non-breeding season is not related to a major shift in its diet but to its movement behavior. Almost all tracked white-backed woodpeckers showed home range behavior also in the non-breeding season; however, the higher mobility after fledging of the chicks appeared to enable white-backed woodpeckers to increase their home range and forage also on dispersed pieces of deadwood in habitat types with presumably low deadwood availability.

These findings suggest that integrative measures in stands managed for wood production (including young deciduous or mixed stands and coniferous forest) may be suitable for providing non-breeding habitat and a useful complement to the presence of (almost) unmanaged stands as breeding habitat. Standing deadwood was clearly preferred over lying deadwood and stumps (i.e., standing deadwood lower than 1.30 m). Furthermore, the probability of selection increased with the diameter of the tree; this effect was particularly pronounced for lying deadwood, while standing deadwood was likely to be used regardless of its diameter. Therefore, integrative measures should focus on the creation or retention of standing deadwood, large-diameter lying deadwood, and old trees.

In summary, these three key results show that addressing multiple seasons, spatial scales, and levels of habitat selection might be necessary to gain a comprehensive understanding of a species' space use. Reviews by Marra et al. (2015) and McGarigal et al. (2016) demonstrated that the majority of the reviewed ecological studies focused on the breeding season and addressed only one spatial scale and/or level of habitat selection, respectively. However, the resulting incomplete knowledge about a species' requirements might lead to ineffective conservation measures. The present thesis provides an example how knowledge gained from assessing the space use of an old-growth forest specialist across multiple seasons, scales, and levels of habitat selection could be used to make better informed conservation and forest management decisions.

Conclusion

By analyzing the space use of radio-tracked white-backed woodpeckers in a heterogeneous landscape I showed that (1) the occurrence of the white-backed woodpecker in the study area is related to landscape composition and configuration at large spatial scales, (2) old deciduous or mixed forests with abundant deadwood are important as breeding habitat, and (3) white-backed woodpeckers appeared to be less bound to old deciduous or mixed forest in the non-breeding season but selected deadwood for foraging in all forest types and seasons. For the conservation of the white-backed woodpecker in landscapes with relatively high human impact (compared to large primeval forests), I suggest the following procedure as compromise between ecological and economic interests. First, large areas with high forest cover (in our study area > 60% forest cover within an 20-28 km²) should be selected; within this area, enough old deciduous or mixed forest to sustain multiple breeding pairs (> 11% within 20 km²) should be available or created. These old deciduous or mixed forests should ideally be dispersed at large spatial scales (64 km²) to enhance connectivity. By contrast, a high proportion of old deciduous or mixed forest within a small area is required at the relatively small spatial scale of the breeding home range (0.3 – 0.5 km²), and within the breeding home range, high amounts of standing deadwood, lying deadwood, and trees with dead branches should be available. Therefore, part of the forest at the breeding home range scale should be managed at very low intensity (e.g., through single-tree selection) or not at all to provide sufficient breeding habitat, supporting the idea of segregative measures as useful approach. Lastly, when the amount of old (almost) unmanaged deciduous or mixed forest is sufficiently high both at the landscape and the breeding home range scales, integrative measures such as the retention of deadwood and habitat trees in more intensively managed stands (including coniferous and young deciduous or mixed stands) may be a useful supplement.

References

- Angelstam, P., Roberge, J.-M., Löhmus, A., Bergmanis, M., Brazaitis, G., Dönn-Breuss, M., Edenius, L., Kosinski, Z., Kurlavicius, P., Lärmanis, V., Lūkins, M., Mikusiński, G., Račinskis, E., Strazds, M., Tryjanowski, P., 2004. Habitat modelling as a tool for landscape-scale conservation: a review of parameters for focal forest birds. *Ecol. Bull.* 51, 427–453.
- Berlusconi, A., Martinoli, Alessio, Wauters, L.A., Tesoro, G., Martini, S., Clerici, E., Guenzani, G., Pozzi, G., Rubolini, D., Morganti, M., Martinoli, Adriano, 2022. Year-round multi-scale habitat selection by crested tit (*Lophophanes cristatus*) in lowland mixed forests (northern Italy). *Avian Res.* 13, 100058. <https://doi.org/10.1016/j.avrs.2022.100058>

- Bettega, C., Fernández-González, Á., Ramón Obeso, J., Delgado, M.D.M., 2020. Circannual variation in habitat use of the white-winged snowfinch *Montifringilla nivalis nivalis*. *Ibis* 162, 1251–1261. <https://doi.org/10.1111/ibi.12829>
- Booth, J.M., Steinfurth, A., Fusi, M., Cuthbert, R.J., McQuaid, C.D., 2018. Foraging plasticity of breeding Northern rockhopper penguins, *Eudyptes moseleyi*, in response to changing energy requirements. *Polar Biol.* 41, 1815–1826. <https://doi.org/10.1007/s00300-018-2321-6>
- Bouget, C., Parmain, G., Gilg, O., Noblecourt, T., Nusillard, B., Paillet, Y., Pernot, C., Larrieu, L., Gosselin, F., 2014. Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? *Anim. Conserv.* 17, 342–353. <https://doi.org/10.1111/acv.12101>
- Carlson, A., 2000. The effect of habitat loss on a deciduous forest specialist species: the white-backed woodpecker (*Dendrocopos leucotos*). *For. Ecol. Manag.* 131, 215–221. [https://doi.org/10.1016/S0378-1127\(99\)00215-7](https://doi.org/10.1016/S0378-1127(99)00215-7)
- Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenberger, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., 2005. Dead wood in European beech (*Fagus sylvatica*) forest reserves. *For. Ecol. Manag.* 210, 267–282. <https://doi.org/10.1016/j.foreco.2005.02.032>
- Czeszczewik, D., Walankiewicz, W., Mitrus, C., Tumiel, T., Stański, T., Sahel, M., Bednarczyk, G., 2013. Importance of dead wood resources for woodpeckers in coniferous stands of the Białowieża Forest. *Bird Conserv. Int.* 23, 414–425. <https://doi.org/10.1017/S0959270912000354>
- Domínguez, J., Carbonell, R., Ramírez, A., 2017. Seasonal changes in habitat selection by a strict forest specialist, the Middle Spotted Woodpecker (*Leiopicus medius*), at its southwestern boundary: implications for conservation. *J. Ornithol.* 158, 459–467. <https://doi.org/10.1007/s10336-016-1415-6>
- Elkin, C.M., Reid, M.L., 2010. Shifts in breeding habitat selection behaviour in response to population density. *Oikos* 119, 1070–1080. <https://doi.org/10.1111/j.1600-0706.2009.18010.x>
- Fahrig, L., 2020. Why do several small patches hold more species than few large patches? *Glob. Ecol. Biogeogr.* 29, 615–628. <https://doi.org/10.1111/geb.13059>
- Fahrig, L., 2017. Ecological responses to habitat fragmentation per se. *Annu. Rev. Ecol. Evol. Syst.* 48, 1–23. <https://doi.org/10.1146/annurev-ecolsys-110316-022612>
- Frank, G., Hochebner, T., 2001. Erfassung der Spechte - insbesondere des Weißrückenspechtes *Picoides leucotos* - im Rhmen des LIFE-Projektes Wildnisgebiet Dürrenstein. in: LIFE- Projekt

- Wildnisgebiet Dürrenstein. Amt der Niederösterreichischen Landesregierung (Ed.). Amt der Niederösterreichischen Landesregierung, St. Pölten.
- Fuller, R.J., 2012. Birds and habitat: relationships in changing landscapes. Cambridge University Press, New York.
- Galende, G.I., Raffaele, E., 2012. Diet selection of the southern vizcacha (*Lagidium viscacia*): a rock specialist in north western Patagonian steppe, Argentina. *Acta Theriol. (Warsz.)* 57, 333–341. <https://doi.org/10.1007/s13364-012-0078-9>
- Hanski, I., 2015. Habitat fragmentation and species richness. *J. Biogeogr.* 42, 989–993. <https://doi.org/10.1111/jbi.12478>
- Hof, A.R., Hjältén, J., 2018. Are we restoring enough? Simulating impacts of restoration efforts on the suitability of forest landscapes for a locally critically endangered umbrella species. *Restor. Ecol.* 26, 740–750. <https://doi.org/10.1111/rec.12628>
- Hof, A.R., Zachrisson, A., Polvi, L.E., 2021. Forest restoration: do site selection and restoration practices follow ecological criteria? A case study in Sweden. *Forests* 12, 988. <https://doi.org/10.3390/f12080988>
- Hogstad, O., Stenberg, I., 1994. Habitat selection of a viable population of white-backed woodpeckers *Dendrocopos leucotos*. *Fauna Nor. Ser. C Cinclus* 17, 75–94.
- Kajtoch, L., Figarski, T., Pelka, J., 2013. The role of forest structural elements in determining the occurrence of two specialist woodpecker species in the Carpathians, Poland. *Ornis Fenn.* 90, 23–40.
- Lenz, J., Böhning-Gaese, K., Fiedler, W., Mueller, T., 2015. Nomadism and seasonal range expansion in a large frugivorous bird. *Ecography* 38, 54–62. <https://doi.org/10.1111/ecog.00522>
- Marra, P.P., Cohen, E.B., Loss, S.R., Rutter, J.E., Tonra, C.M., 2015. A call for full annual cycle research in animal ecology. *Biol. Lett.* 11, 20150552. <https://doi.org/10.1098/rsbl.2015.0552>
- McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. *Landsc. Ecol.* 31, 1161–1175. <https://doi.org/10.1007/s10980-016-0374-x>
- Mobæk, R., Myrnerud, A., Egil Loe, L., Holand, Ø., Austrheim, G., 2009. Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. *Oikos* 118, 209–218. <https://doi.org/10.1111/j.1600-0706.2008.16935.x>

- Nagel, T.A., Firm, D., Pisek, R., Mihelic, T., Hladnik, D., de Groot, M., Rozenbergar, D., 2017. Evaluating the influence of integrative forest management on old-growth habitat structures in a temperate forest region. *Biol. Conserv.* 216, 101–107. <https://doi.org/10.1016/j.biocon.2017.10.008>
- Olsson, O., Brown, J.S., Helf, K.L., 2008. A guide to central place effects in foraging. *Theor. Popul. Biol.* 74, 22–33. <https://doi.org/10.1016/j.tpb.2008.04.005>
- Pfeiffer, T., Meyburg, B.-U., 2015. GPS tracking of Red Kites (*Milvus milvus*) reveals fledgling number is negatively correlated with home range size. *J. Ornithol.* 156, 963–975. <https://doi.org/10.1007/s10336-015-1230-5>
- Rolstad, J., Rolstad, E., 1995. Seasonal patterns in home range and habitat use of the greyheaded woodpecker *Picus canus* as influenced by the availability of food. *Ornis Fenn.* 72, 1–13.
- Saura, S., 2021. The Habitat Amount Hypothesis implies negative effects of habitat fragmentation on species richness. *J. Biogeogr.* 48, 11–22. <https://doi.org/10.1111/jbi.13958>
- Séchaud, R., Schalcher, K., Almasi, B., Bühler, R., Safi, K., Romano, A., Roulin, A., 2022. Home range size and habitat quality affect breeding success but not parental investment in barn owl males. *Sci. Rep.* 12, 6516. <https://doi.org/10.1038/s41598-022-10324-7>
- Squires, J.R., Decesare, N.J., Kolbe, J.A., Ruggiero, L.F., 2010. Seasonal resource selection of Canada lynx in managed forests of the Northern Rocky Mountains. *J. Wildl. Manag.* 74, 1648–1660.
- Staggenborg, J., Schaefer, H.M., Stange, C., Naef-Daenzer, B., Gruebler, M.U., 2017. Time and travelling costs during chick-rearing in relation to habitat quality in Little Owls *Athene noctua*. *Ibis* 159, 519–531. <https://doi.org/10.1111/ibi.12465>
- Stenberg, I., 1990. Preliminary results of a study on woodpeckers in More and Romsdal Country, western Norway, in: Carlson, A, Aulén, G. (Eds): Conservation and Management of Woodpecker Populations. Report 17, Uppsala. Departement of Wildlife Ecology, Swedish University of Agricultural Sciences, Uppsala, pp. 67–79.
- Virkkala, R., Alanko, T., Laine, T., Tiainen, J., 1993. Population contraction of the white-backed woodpecker *Dendrocopos leucotos* in Finland as a consequence of habitat alteration. *Biol. Conserv.* 66, 47–53. [https://doi.org/10.1016/0006-3207\(93\)90133-L](https://doi.org/10.1016/0006-3207(93)90133-L)
- Weber, P., Korner, P., Ettwein, A., Lanz, M., Pasinelli, G., in preparation. Adult survival of the white-backed woodpecker (*Dendrocopos leucotos*) in relation to sex, topography and habitat.

Wesołowski, T., 1995. Value of Białowieża Forest for the conservation of white-backed woodpecker *Dendrocopos leucotosi* in Poland. Biol. Conserv. 71, 69–75. [https://doi.org/10.1016/0006-3207\(94\)00022-1](https://doi.org/10.1016/0006-3207(94)00022-1)

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