



Seasonal variation in home-range size of the White-backed Woodpecker

Antonia Ettwein^{1,2} · Michael Lanz¹ · Gilberto Pasinelli^{1,2}

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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 Central Europe 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 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). Moreover, home-range sizes varied between seasons. 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 ha, AKDE: 136–184 ha). The mean home-range size of six individuals tracked in all seasons (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 also of other species. 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 116–350 ha of forest should be present for a pair.

Keywords Autocorrelated kernel density estimation · *Dendrocopos leucotos* · Radio-tracking · VHF telemetry · Territory size · Piciformes

Zusammenfassung

Saisonale Veränderungen in der Aktionsraumgrösse des Weissrückenspechts

Die Raumansprüche einer Art zu kennen, ist für den Artenschutz wichtig. Für die Nominatform des Weissrückenspechts *Dendrocopos leucotos*, eine Art von hoher Naturschutzrelevanz in Europa, gibt es bisher keine Schätzungen der saisonalen und ganzjährigen Aktionsraumgrößen basierend auf Telemetriedaten. In der vorliegenden Studie haben wir adulte Weissrückenspechte in Mitteleuropa mittels Radiotelemetrie lokalisiert und die zweimonatlichen Aktionsraumgrößen anhand von drei Aktionsraum-Schätzmethoden in Abhängigkeit von Saison, Geschlecht, Körpergewicht und Jahr untersucht. Die Aktionsraumgrösse von 49 besenderten Individuen variierte je nach verwendeter Methode, wobei die

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✉ Gilberto Pasinelli
gilberto.pasinelli@vogelwarte.ch

¹ Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

² Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

Minimum-Convex-Polygon-Methode (MCP) und die Autocorrelated-Kernel-Density-Estimation-Methode (AKDE) saisonale Aktionsräume erzeugten, die 1,6 bis 1,8 bzw. 2 bis 3,3 Mal grösser waren als bei der traditionellen Kernel-Density-Estimation-Methode (KDE). Zudem variierten die Aktionsraumgrößen zwischen den Saisons. Die kleinsten Aktionsräume wurden im Februar/März (die Medianwerte der vorhergesagten Aktionsraumgrößen reichten von 35 ha mit KDE bis 88 ha mit AKDE) und April/Mai (KDE: 30 ha, AKDE: 55 ha) festgestellt, während sie den Rest des Jahres über grösser waren (KDE: 48–67 ha, AKDE: 136–184 ha). Die mittlere Aktionsraumgrösse von sechs Individuen, die über alle Saisons hinweg verfolgt wurden (berechnet mit allen Lokalisationen pro Individuum), betrug 116 ha mit KDE, 304 ha mit MCP und 350 ha mit AKDE. Unsere Ergebnisse zeigen, dass es bei der Ermittlung der Raumansprüche des Weissrückenspechts und wahrscheinlich auch anderer Arten wichtig ist, den gesamten Jahreszyklus zu berücksichtigen. Darüber hinaus zeigt unsere Studie, dass die Verwendung mehrerer Methoden zur Schätzung der Aktionsräume nützlich sein kann, um Ergebnisse zu erhalten, die sowohl mit denen anderer Studien vergleichbar sind als auch den Bereich abdecken, in dem die tatsächliche Aktionsraumgrösse wahrscheinlich liegt. Für den Schutz des Weissrückenspechts schlussfolgern wir, dass mindestens 116 bis 350 ha Wald für ein Brutpaar vorhanden sein sollten.

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 size or density (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 commercial forest management 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; Wesołowski 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 larger home ranges in males than in females (Campion et al. 2020). Home-range sizes in fall and winter are completely unknown.

The aim of the present study was to estimate seasonal home-range sizes and, for individuals that were tracked in all seasons, total (annual) home-range sizes. We expected the home ranges to be 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. We furthermore explored differences in home-range size between the sexes, expecting that males have larger home ranges than females. As home-range size might be related to body weight [either negatively (Focardi et al. 2006), positively (Relyea et al. 2000), or with the direction of the effect differing between the sexes (Palomares 1994)] and might differ between years, we also investigated relationships between home-range size and these two 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 spatial 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 2 years, one individual in 3 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. 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-hour 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 were recorded every 15 min. Due to the often difficult and inaccessible terrain, the birds were mostly located by triangulation (by one person from different positions). As the exact position of the bird was mostly not known, the center of the circular area in

which the woodpecker was assumed to be was considered as location. To describe the accuracy of each location, the field worker estimated the radius of this area on a digital map (with a 100 × 100-m grid as guideline) using the categories 10 m, 25 m, 50 m, 100 m, 200 m, and > 200 m. The average estimated accuracy of the remaining locations ($\pm$ standard deviation SD) was 107 ± 69 m ($n = 15,047$; excluding locations with accuracy > 200 m). It was also noted when a woodpecker could not be located after 15 min. 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. S1, Online Resource 1).

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 computed home ranges for individual-season combinations with at least 30 locations ($n = 144$). We then tested the sensitivity of home-range size to the number of locations using area-location plots (based on the KDE home ranges). We visually assessed whether an asymptote was reached (Kenward 2001) and 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 in all seasons 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). When a woodpecker was captured in 2 or 3 different years, we related the seasonal home ranges with the body weight of the respective year. Four woodpeckers were captured and weighed twice in the same year. In these cases, we used the first measurement. 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 restrictions that we included the interaction between *season* and *sex* only in models with the respective main effects and that we used *weight* only in combination with *sex* (to account for differences in body weight between the sexes [males: 104.0 ± 5.1 g, females: 99.2 ± 5.7 g; t test: $t(37.1) = -3.04$, $p = 0.004$, $n = 61$]). As the body weight of males increased in the course of spring (Pearson's correlation coefficient = 0.44, $p = 0.006$, $n = 38$, two individuals captured in fall excluded), all

Table 1 Fixed and random effects used for modeling bi-monthly White-backed Woodpecker home-range sizes

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

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 and trackdays² = number of days an individual was tracked as linear and quadratic terms, signal = proportion of unsuccessful location attempts, weight = body weight, day_captured = day of the year on which the individual was captured and weighed, ind_id = individual id of each woodpecker

models including *weight* additionally included the variable *day_captured*, (with 1 January being day 1 of the year). 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_id*) 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 affected 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 48 individuals with enough locations to reliably represent home-range size (120 ± 44 locations recorded during 22 ± 17 weeks per individual; depending on the season, up to 70–100 locations were necessary until bi-monthly home-range size stabilized). Six individuals were tracked in all seasons, which resulted in 836 ± 193 locations recorded during 50–78 weeks per individual.

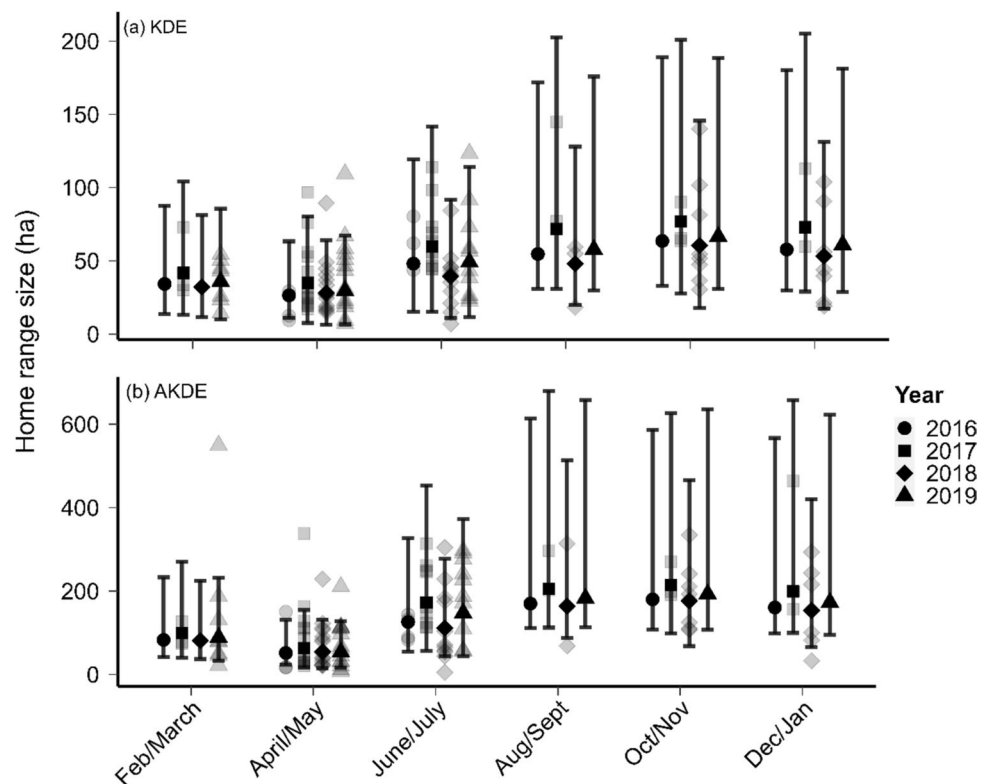
The home-range estimator had little effect on the model ranking, with Δ LOOIC values comparing models using AKDE home-range size differing only marginally from those with KDE home-range sizes (Table 1). After controlling for year, individual ID, and number of tracking

Table 2 Results of four models explaining variation in the logarithm of bi-monthly White-backed Woodpecker home-range size

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_id	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]

Shown are estimates and credible intervals [CrI] of all fixed and random effects included in each model. 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. $n = 115$

Fig. 1 Bi-monthly home-range sizes of radio-tracked White-backed Woodpeckers per year. Shown are predicted median home-range sizes (with 95% credible intervals) 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



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 over 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. This trend was consistent across seasons (Fig. 1), as shown by a model with a random slope for season per year ranking similarly high as the top-ranked one ($\Delta\text{LOOIC} = 0.32$ and 0.18 for KDE and AKDE home ranges, respectively; Table 1). 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 large (Fig. 1).

According to the highest-ranked model including body weight and sex (ΔLOOIC 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 3 for predicted bi-monthly home-range sizes of males and females). All trends were similar for both home-range estimators (Table 4, Fig. 1). 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

Table 3 Bi-monthly home-range sizes (ha) of male and female White-backed Woodpeckers radio-tracked in Central Europe

Season	m (KDE)	f (KDE)	m (AKDE)	f (AKDE)	m (MCP)	f (MCP)	<i>n</i> (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 ± 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 ± 41.5	57 ± 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 ± 52.5	103.3 ± 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 ± 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 ± 38.9	156.4 ± 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 ± 41.8	55.9 ± 38.9	7/2

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, 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)

Table 4 Bi-monthly home-range sizes (ha) of radio-tracked White-backed Woodpeckers

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

Shown are predicted median home-range sizes (with 95% credible intervals) after accounting for individual ID, number of tracking days, 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)

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 period (Table 4). 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 4).

Lastly, the mean home-range size of six individuals tracked in all seasons (see Fig. S1 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 six individuals showed marked site fidelity, with large overlaps between the bi-monthly home ranges (Fig. S2).

Discussion

Using 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 based on telemetry. 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, Fig. S3 in Online Resource 1), which suggests territoriality throughout the year.

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. The ratios for seasonal differences in pre-breeding, breeding, and post-breeding home-range size of the Three-toed Woodpecker (*Picoides tridactylus*; Pechacek 2004) and in winter, pre-breeding, and breeding home-range size of the Middle Spotted Woodpecker (*Dendrocoptes medius*; Pasinelli et al. 2001) were similar as in our study. In addition, similar increases in home-range size after nesting as in our study have been reported for the Helmeted Woodpecker (*Celeus galeatus*; Lammertink and Fernández 2022), the Robust Woodpecker (*Campephilus robustus*; Lammertink and Fernández 2022), and the White-headed Woodpecker (*Leuconotopicus albolarvatus*; only in females, while males had slightly smaller home ranges post-breeding, Lorenz et al. 2015). As opposed to our studied White-backed Woodpeckers, Lesser Spotted Woodpeckers (*Dryobates minor*; Höntsch 2004; Wiktander et al. 2001) and Grey-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; Wiktander et al. 2001). Hence, the hypothesis that territorial behavior restricts winter home-range size does 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' diets and foraging behaviors. However, all 3 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 foraging on deadwood

throughout the year (Ettwein 2024). 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-range 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 2 different years ($n=8$ seasonal home ranges of 6 individuals) are in accordance with this trend: Individuals 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 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 2 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 only partly overlapped (see Fig. S2 in Online Resource 1 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; Wesolowski 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 in Spain, where breeding and post-breeding KDE home ranges of the subspecies *lilfordi* were 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, using cross validation Noonan et al. (2019) demonstrated 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 of 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 of values (30–55 ha to 67–184 ha for bi-monthly and 116–350 ha for annual home-range sizes) instead of single values should be considered as the mean area requirements of the White-backed Woodpecker in our study area. The annual home-range estimates refer to the home-range sizes of a single individual, but they may also correspond to the area requirements of a breeding pair. For 4 breeding pairs, radio-tracking data for both partners were available. In all 4 pairs, the home ranges of the male and female strongly overlapped, even when the individuals were tracked in different years (Fig. S4). Moreover, the annual home ranges of individuals that were tracked in 2 or 3 years strongly overlapped ($n=8$, Fig. S5). Therefore, in our study population, the mean area requirements for a breeding pair over multiple years are likely to be within the range of 116–350 ha.

Lastly, 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 3). 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 (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; Wiktander 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 other species as well. Importantly, the calculated home-range sizes also greatly depended on the used home-range estimator, suggesting 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 116–350 ha of forest should be present for one breeding pair.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-024-02240-6>.

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Data availability Analyses reported in this article can be reproduced using the datasets and R codes provided in the [vogelwarte.ch Open Repository and Archive](https://doi.org/10.5281/zenodo.13860448) at <https://doi.org/10.5281/zenodo.13860448>.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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