WILDLIFE BIOLOGY

Research article

Home range and habitat selection of wolves recolonising central European human-dominated landscapes

Aleš Vorel[1], Ivo Kadlec[1], Tadeáš Toulec[1], Aldin Selimovic[2], Jan Horníček[1], Oldřich Vojtěch[3], Jan Mokrý[3], Lukáš Pavlačík[4], Walter Arnold[2], Jessica Cornils[2], Miroslav Kutal[5,6], Martin Duľa[6], Lukáš Žák[1,7] and Vojtěch Barták[1]

[1]Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic
[2]Department of Interdisciplinary Life Sciences, Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, Vienna, Austria
[3]Department of Zoology, Šumava National Park Administration, Vimperk, Czech Republic
[4]Wildlife Photo, Dvůr Králové, Czech Republic
[5]Friends od the Earth Czech Republic, Carnivore Conservation Programme, Olomouc, Czech Republic
[6]Department of Forest Ecology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic
[7]Senckenberg Museum of Natural History, Görlitz, Germany

Correspondence: Aleš Vorel (vorel@fzp.czu.cz)

Wildlife Biology
2024: e01245
doi: 10.1002/wlb3.01245
Subject Editor: Aimee Tallian
Editor-in-Chief: Ilse Storch
Accepted 02 May 2024

Decades of persecution has resulted in the long-term absence of grey wolves *Canis lupus* from most European countries. However, recent changes in both legislation and public attitudes toward wolves has eased the pressure, allowing wolves to rapidly re-establish territories in their previous central European habitats over the last 20 years. Unfortunately, these habitats are now heavily altered by humans. Understanding the spatial ecology of wolves in such highly modified environments is crucial, given the high potential for conflict and the need to reconcile their return with multiple human concerns. We equipped 20 wolves, originating from seven packs in six central European regions, with GPS collars, allowing us to calculate monthly average home range sizes for 14 of the animals of 213.3 km^2 using autocorrelated kernel density estimation. We then used ESA WorldCover data to assess the mosaic of available habitats used within each home range. Our data confirmed a general seasonal pattern for breeding individuals, with smaller apparent home ranges during the reproduction phase, and no specific pattern for non-breeders. Predictably, our wolves showed a general preference for remote areas, and especially forests, though some wolves within military training areas also showed a broader preference for grassland, possibly influenced by local land use and high availability of prey. Our results provide a comprehensive insight into the ecology of wolves during their re-colonisation of central Europe. Though wolves are spreading relatively quickly across central European landscapes, their permanent reoccupation remains uncertain due to conflicts with the human population. To secure the restoration of European wolf populations, further robust biological data, including data on spatial ecology, will be needed to clearly identify any management implications.

Keywords: Autocorrelated kernel density estimation, canis lupus, habitat preference, seasonal dynamics, territoriality

NORDIC SOCIETY OIKOS

www.wildlifebiology.org

© 2024 The Authors. Wildlife Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

Centuries of persecution against European large carnivores has resulted in the virtual extirpation of the grey wolf *Canis lupus* from large parts of its original distribution (Boitani 2000, Ripple et al. 2014), with the remaining intact populations limited to the remotest and least accessible forested and mountainous areas (Breitenmoser 1998). However, in recent decades, changes in legislation (Linnell et al. 2001, Mech 2017), socioeconomic development detaching people from rural areas (thus improving habitat and prey abundance; Breitenmoser 1998) and a general improvement in the perception of large carnivores (Glikman et al. 2012, Dressel et al. 2015), together with evolutionary high adaptability of the wolf itself, has enabled the wolf to return to many parts of its historical range (Wabakken et al. 2001, Kojola et al. 2006, Chapron et al. 2014, Fabbri et al. 2014, Hulva et al. 2018, Reinhardt et al. 2019, Kaczensky et al. 2021).

The central European region is bordered by three major wolf populations, the 'Central European' (Nowak and Mysłajek 2016), the 'Carpathian' (Hulva et al. 2018) and the 'Italian-Alpine' (Fabbri et al. 2007); nevertheless, the region has been one of the last to be recolonised, with wolves only reaching the heavily human-altered landscapes of western Poland (Mysłajek et al. 2018), Germany (Reinhardt et al. 2019), Austria (Rauer and Blaschka 2021) and Czechia (Czech Republic; Kutal et al. 2017) between 2015 and 2020. At the same time, game management and agricultural intensification, along with several decades with no large predators, has resulted in an increase in wild ungulate density in many European ecosystems (Borkowski et al. 2019, Carpio et al. 2021). Though this has created favourable conditions for rapid recolonisation by wolves, they are returning to a heavily altered environment. Though wolves generally tend to avoid people, the current profile of the human-dominated landscapes makes conflicts almost inevitable (Ronnenberg et al. 2017, Khorozyan and Heurich 2022). On the other hand, changes in legislation and a greater tendency to tolerate wildlife also offer opportunities to find the means to coexist sustainably with such large carnivores (Fritts et al. 2003, Kuijper et al. 2019).

Wolves are territorial, apex predators that live in packs, usually centred on a mated pair (Mech and Boitani 2003). Males and females can disperse at any age, though most commonly as yearlings or subadults (Gese and Mech 1991, Kojola et al. 2006, Morales-González et al. 2022), after which they may disperse over vast distances to acquire suitable territory (Wabakken et al. 2001, Mech and Boitani 2003, Ražen et al. 2016). Once suitable territory is found, colonisation success is increased by their highly flexible diet (Newsome et al. 2016) and rapid reproduction (Packard 2003). In the Northern Hemisphere, wolves have historically occurred in almost all habitats with sufficient food resources, though they generally display a preference for two complementary features, presence of forests and an absence of human settlements and roads (Kaartinen et al. 2005, Jedrzejewski et al. 2008, Ronnenberg et al. 2017). In more recent years, however, as wolves have returned to areas with a high human population density, they have also been recorded in predominantly treeless agricultural land (Blanco and Cortés 2007, Eggermann et al. 2011) and meadows and pastures (Jedrzejewski et al. 2008), with their territories often incorporating small and large human settlements (Zanni et al. 2023).

Gaining a detailed knowledge of wolf territorial systems not only offers a comprehensive insight into their population structure, spatial distribution and dynamics (Ciucci et al. 1997, Okarma et al. 1998), it also represents an important element in the process of understanding wolf population ecology within human-dominated landscapes (Dickie et al. 2022). In a broader context, a territory can be understood as that part of an individual's home range (HR) that it defends (Powell 2000); however, in the case of wolves, both terms carry almost the same amount of information (Mech 1994, Mech and Boitani 2003). Owing to the species' strong territoriality, the level of overlap between individual HRs and pack territory is usually high (Benson and Patterson 2015). A wolf's HR can vary in size across populations, with larger HRs commonly seen with increasing latitude, human density and pack size, and smaller HRs observed with increasing prey abundance (Fuller et al. 2003, Jedrzejewski et al. 2007, Mattisson et al. 2013, Mysłajek et al. 2018). Features such as choice of prey (Fuller et al. 2003), landscape topography (Kauffman et al. 2007, Kittle et al. 2015) and phase of colonisation (Mech and Boitani 2003) can also act as important determinants. Finally, the HR of each individual in the pack may show substantial variation throughout the year, with reproduction status, which generally peaks in late spring (Packard 2003), being the main factor influencing such variation, with HRs reducing in size as individuals stay closer to the den (Kusak et al. 2005, Jedrzejewski et al. 2007, Roffler and Gregovich 2018). Once the pups gain mobility in late summer, HRs usually increase once again, reaching their maximum size in winter (Ciucci et al. 1997). Note that individuals following prey over large distances (Walton et al. 2001), or dispersal away from the pack, could also adversely affect 'perceived HR size' during the study period (Reinhardt and Kluth 2016).

Though wolf biology has been relatively well studied, there is a general lack of robust studies documenting spatial patterns in the human-dominated landscapes of central Europe (mainly due to low sample sizes), despite numerous ongoing telemetry projects in Germany, Austria, Poland, Slovakia and Switzerland over the last decade using precise GPS collars (Reinhardt and Kluth 2016, Mysłajek et al. 2018). Gaining a better understanding of wolf spatial ecology in these highly modified environments, therefore, will be crucial for better informing national or European level management decisions regarding protection of this large conflict species.

This study aims to provide a comprehensive description of the spatial ecology of returning central European wolves establishing new populations in human-dominated landscapes. Using GPS telemetry-collared animals, we aim to 1)

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

describe the wolves movement patterns by distinguishing different movement modes (resident versus dispersal versus floating) and quantify their spatial extent, 2) investigate possible seasonal fluctuations in HR size, and 3) describe the wolves habitat preferences in terms of both second and third-order selection.

Methods

Study area

As central Europe is at the crossroads of the present expansion in wolf populations, we established six widely spaced study areas covering the main areas of occurrence (Fig. 1, Table 1). While most of these study areas were sited in two countries, Czechia and Austria, tracking indicated that the activity of individuals often overlapped into the neighbouring countries of Germany, Poland and Slovakia. Each study area included different types of human-altered landscape, and all study areas were Natura 2000 sites and had at least one level of national protection or restricted status, e.g. Military training areas (MTA) with specific management, National Parks (NP) or Protected landscape areas (PLA). Wolves had occupied each area for at least five years before the trapping campaigns began and all packs showed regular evidence of reproduction. Colonisation phase, however, differed in each study area, with the Czech and Saxony Switzerland NPs (CSS) and Beskydy and Kysuce PLAs (BES) populations lying on the borders of large expanding populations. While the Hradiste MTA (HRA), Sumava and Bayerischer Wald NPs (SBW), Allentsteig MTA (ALE) and Jeseníky PLA and Równina Opolska (JER) occupations all represent 'islands' of initial occupation isolated from continuous wolf populations (Fig. 1, Table 1); it means that for (HRA and JER) wolves established here the first permanent occupation.

Previous central European studies have demonstrated that wolves tend to prey on the most common ungulates (Wagner et al. 2012), i.e. red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*, and only occasionally on the less common fallow deer *Dama dama*. At present, these ungulates occur in the study areas at higher abundances than was common in the past (Valente et al. 2020). Of the non-ungulates, the European hare *Lepus europaeus*, also found in high numbers in the study areas, is also often preyed upon by wolves. All areas except HRA have Eurasian beavers

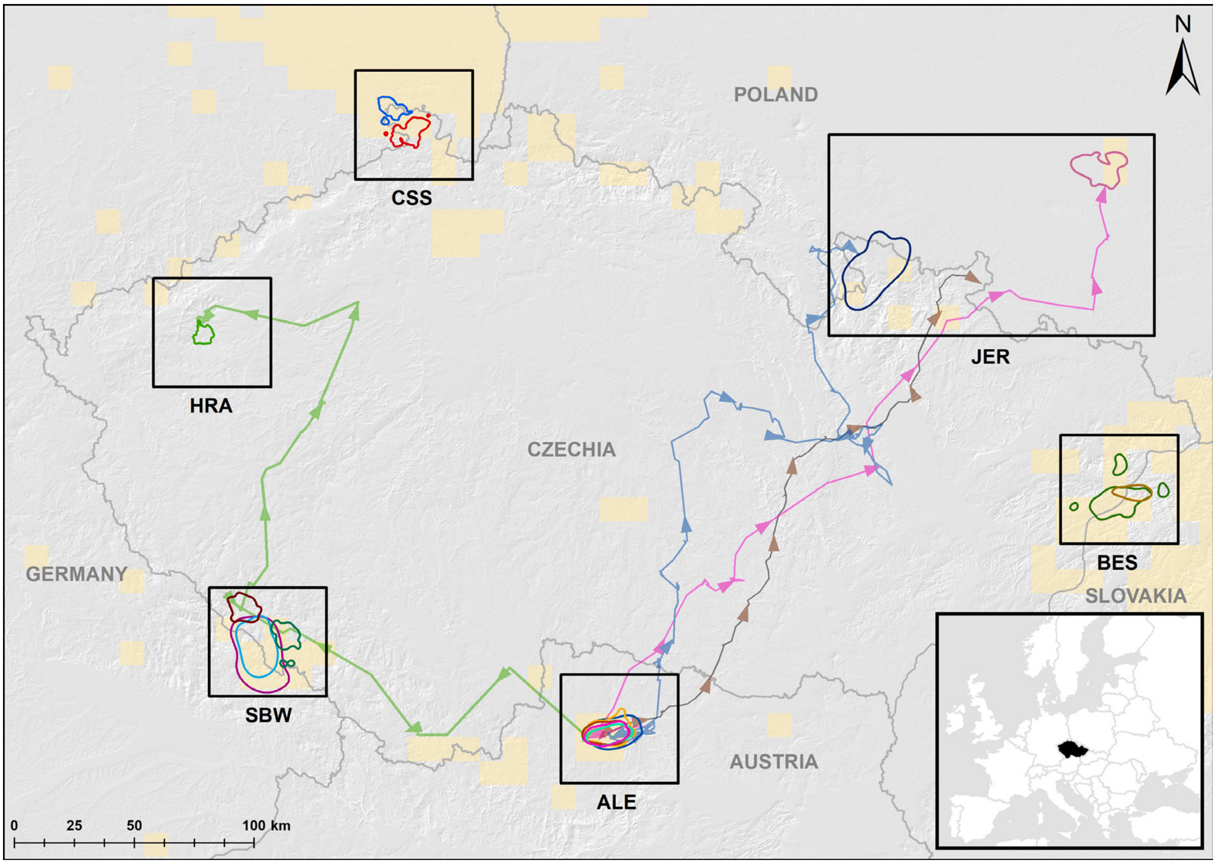

Figure 1. Overview map showing the six distinct regions where wolves were recorded. Wolves were trapped and collared at study sites CSS, SBW, ALE and BES, whereas sites HRA and JER were recolonised via dispersal. Lines indicate successful dispersals recorded during the study period; f29456_AUT (green), m30778_AUT (pink), m46090 (brown), m46088 (blue). Beige areas represents recent wolves distribution according to Kaczensky et al. (2021). For abbreviations and codes, see Table 1, 2 and 3.

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1. Description of the six areas in which the study was conducted. Four of the areas (CSS, SBW, ALE and BES) already had wolf populations and were selected to conduct the trapping campaigns, while wolves dispersed into two areas during the telemetry survey (HRA, JER) and established here the new occupation. [a]Names refer to those areas where wolves conducted either full or partial activity. [b]Coordinates roughly indicate centroids of wolf activity in the given study area. [c]Human population density (pers. km^{-2}).

Area dode	Study area[a]	Country	Y and X coordinates[b]	NATURA 2000 site	Altitude range (m a.s.l.)	Prevailing forest type	Wolves pack since	Population density[c]
CSS	Czech and Saxony Switzerland NPs	CZE/GER	50°57′01.07N″, 14°25′06.38E″	CZ0424031 and DE5050301	250–600	spruces and pines	2011/2012	135.1
HRA	Hradiste MTA	CZE	50°13′01.16N″, 13°07′ 35.47E″	CZ0414127	500–950	spruce	2019/2020	88.5
SBW	Sumava and Bayerischer Wald NPs	CZE/GER	49°01′10.2N″, 13°27′03.5E″	CZ0314024 and DE6946401	800–1350	spruce	2017/2018	70.6
BES	Beskydy and Kysuce PLAs	CZE/SLO	49°19′23.2N″, 18°19′42.1E″	CZ0724089 and SKUEV0642	400–1050	spruce	2019/2020	146.1
JER	Jeseníky PLA and Równina Opolska	CZE/POL	50°17′27.6N″, 17°44′06.4E″	CZ0711016 and PLH160008	250–1150	spruce	2020/2021	160.1
ALE	Allentsteig MTA	AUT	48°39′46.4″, 15°21′19.3″	AT1221V00	500–600	spruce	2016/2017	47.1

Castor fiber at high population densities, and these have also been documented as wolf prey (Vorel et al. unpubl.). There is a large stable population of Eurasian lynx *Lynx lynx* in area CSS, and this large carnivore is also common in areas BES and JER. A permanent presence of brown bear *Ursus arctos* was also recorded in BES (Kutal et al. 2016, 2017).

Data collection

Wolves were captured using Belisle 8″ or Victor soft-catch leg-hold traps set along trails or at marking places identified by trained dogs, camera traps or snow tracking. During trapping, each site was permanently controlled via a satellite transmitter (Telonics Inc.), a GSM Live Trap Alarm (UOVision) and a GPRS camera trap (Spromise) that instantly transmitted footage once triggered, allowing researchers to be on site within 30 minutes up to two hours of wolf capture. On arrival, the wolf was immobilised with a medetomidine–butorphanol–ketamine mixture administered by a trained veterinarian and blood samples collected for subsequent mSAT DNA analysis to reveal relationships between the trapped animals (Szewczyk et al. 2021). After determining sex and approximate age based on teethdevelopment, month of trapping and body mass, a GPS Plus collar (Vectronic Aerospace) was fitted that allowing telemetry data to be sent GSM service. After a short recovery period, the wolf was released at the site of capture. Three modes of wolf activity monitoring were usually employed, each changed remotely. Immediately following release, the GPS schedule was programmed to collect telemetry positions every 0.5 hours (mode 1), after which fixes were obtained every three hours throughout the regular monitoring period (mode 2). Finally, detailed documentation of feeding activity was obtained by taking fixes every 0.5 h between 18:00 and 08:00 (mode 3), i.e. overnight. This regime was used for one month in summer and one in winter to conserve collar battery lifespan.

Data analysis

Behavioural movement modes

The telemetry data was first filtered by excluding animals with < 30 tracking days to ensure enough data for reliable HR estimates and to enable the study of seasonal (monthly) HR dynamics. Next, we filtered out months in which the animal was observed for < 10 days (Supporting information). Finally, fixes with missing values (NA) were removed. To ensure sufficient accuracy, we also removed fixes with a DOP (dilution of precision) value > 6 (Langley 1999). Subsequently, the net squared displacement (NSD) was calculated for each individual using centroids created for each day of tracking prior to calculating the NSD and the most appropriate movement mode determined, using the Akaike information criterion (AIC) for each individual, in the 'MigrateR' software package (Spitz 2019). In each case, fixes were divided into resident or non-resident movement modes (equivalent to dispersal or floating), with resident individuals and resident periods only then used to estimate HRs (Spitz 2017). The resident period was determined first

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

by visually estimating the day on which the resident phase began or ended from the resulting graph, and then determining the best-fitting movement model for that interval of days. We always tried to obtain the longest possible interval for which the resident model was selected as the most appropriate model. The length of dispersal trips (when recognised) was calculated as the Euclidean distance from the centre of the original and new HR. Finally, outliers were visualised and then filtered out. Descriptions of the animals used in the analysis, together with summary data of the pre- and post-filtering dataset, are presented in Table 2 and 3.

Home range quantification

Three different methods were used to estimate wolf 95% and 50% HRs. The autocorrelated kernel density estimation (AKDE; Fleming et al. 2015, Calabrese et al. 2016), implemented in the R package 'ctmm' (www.r-project.org, Fleming and Calabrese 2022), was used as our primary estimation method as the GPS telemetry locations were expected to be highly temporally autocorrelated. This method not only accounts for autocorrelation in GPS locations but also provides an optimal estimate of kernel bandwidth and confidence bands for the HR estimate. To ensure comparability of our results with previous studies, we also used the traditional, and still commonly used, kernel density estimation (KDE) method, by setting the movement model in the AKDE method to IDD, and also computed 95% and 50% minimum convex polygons (MCP), after excluding 5% and 50% of outlying locations, respectively, using the R package 'adehabitatHR' (Calenge and Fortmann-Roe 2023).

The AKDE method first requires that a movement model is fitted to the data. The initial starting values of the model parameters were first obtained using the R function 'ctmm.guess', after which the best fitting model of the possible candidate movement models was selected using the R function *ctmm.select*. We then used the maximum likelihood estimation (MLE) method with the small sample corrected AIC (AICc) criterion to select the best fitting model. We considered the following candidate movement models described in Calabrese et al. (2016): 1) the Independent identically distributed (IDD) model, a 'null' movement model corresponding to the classic KDE method in which both position and velocity are independently distributed variables (i.e. they have no autocorrelation); 2) the Brownian motion model (BM), in which velocities are not autocorrelated but positions are, and space usage is unconstrained; 3) the Ornstein–Uhlenbeck model (OU), a BM with restricted space usage due to a tendency to move back towards a central location; 4) the integrated OU process (IOU), which has unconstrained space usage and both position and velocity are autocorrelated; and 5) the Ornstein–Uhlenbeck foraging model (OUF), which combines restricted space usage with autocorrelated positions and velocities. After selecting the best fitting movement model, we calculated the appropriate bandwidth given the data and then estimated the utilisation distribution (UD). Finally, we delineated the 95% and 50% HRs as the corresponding UD contour and calculated its area.

Table 2. Descriptive parameters for wolves tracked in this study. These individuals exhibited only residential or floater movement modes. Area code = study area labels defined in Table 1 and Fig. 1. Trapped status and Age at capture = both estimated based on teethdevelopment and physical appearance. No. cleared fixes = number of fixes that remained after data cleaning, fixes used in the analyses. [a] calculated human population densities inside each HR, measured in pers. km^2

Individual (collar ID)	Area code	Trapped status	Status type	Sex	Age at capture [year]	Weight [kg]	Capture date	Tracking days	No. fixes	No. cleared fixes	Movement mode	Population density[a]
f30776	ALE	subadult	non-breeding	f	~1	na	31.05.2019	98	336	316	residential	8.8
f30779	ALE	subadult	non-breeding	f	~1.5	na	09.11.2020	199	1169	1104	residential	16.8
f36930	SBW	subadult	non-breeding	f	~ 1.5	30.5	29.11.2020	221	2303	2179	residential	4.1
f36931	SBW	subadult	non-breeding	f	~ 1.5	29.0	24.10.2021	85	1294	1237	residential	23.4
f36927	SBW	subadult	breeding	f	~ 1.5	29.7	02.11.2021	320	4610	4405	residential	6.0
f36928	CSS	adult, mating	breeding	f	~ 4	35.2	02.05.2022	225	2857	2740	residential	41.0
m36932	CSS	adult, mating	breeding	m	~ 4	35.5	09.05.2022	557	6586	6314	residential	45.0
m35302	SBW	juvenile	-	m	~ 0.5	30.0	18.10.2022	4	352	348	na	–
f47016	BES	adult, mating	breeding	f	~ 4	30.0	20.10.2022	272	3235	2135	residential	23.9
f30777	ALE	juvenile	non-breeding	f	<1	35.0	06.01.2023	184	1303	-	floating	19.5
m47015	-	juvenile	-	m	<1	26.0	11.01.2023	28	391	361	na	–
m36893	SBW	adult, mating	breeding	m	~3	34.0	10.10.2023	84	1040	989	residential	12
m35301	SBW	adult, floater	non-breeding	m	~5	39.2	11.10.2023	82	1634	1538	floating	–
f46974	BES	subadult	non-breeding	f	~ 2.5	na	25.10.2023	69	820	487	residential	5.7
m48013	-	adult, mating	breeding	m	~2	35.7	15.11.2023	19	334	312	na	–

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 3. Descriptive parameters for wolves that were tracked in this study; all these individuals showed long dispersal movement mode (except for the residential movement mode either before or/and after conducting the dispersal). Area code = study area labels defined in Table 1 and Fig. 1. Trapped status and Age at capture = both estimated based on teeth-development and physical appearance. No. cleared fixes = number of fixes that remained after data cleaning, fixes used in the analyses. a calculated human population densities inside each HR, measured in pers. km^2

Individual (collar ID)	Area code	Trapped status	Status type	Sex	Age [year]	Weight [kg]	Trap day	Tracking days	No. fixes	No. cleared fixes	Movement mode	Population density[a]
f29456_AUT	ALE	subadult	non-breeding	f	~1.5	na	09.05.2019	224	782	754	residential	10.6
f29456_disp							22.12.2019	29	69	69	dispersal	–
f29456_CZE	HRA	adult, mating	breeding	f	~ 2	32.0	20.01.2020	514	2606	2502	residential	0.1
m30778_AUT	ALE	subadult	non-breeding	m	~1	36.0	24.04.2021	6	57	57	na	–
m30778_disp							30.04.2021	21	107	103	dispersal	–
m30778_POL	JER	adult	breeding	m	~1	36.0	21.05.2021	574	2694	2561	residential	58.2
m46090_AUT	ALE	juvenile	non-breeding	m	<1	35.0	10.01.2023	278	2165	2095	residential	17.6
m46090_disp							14.10.2023	80	1794	1725	dispersal	–
m46088_AUT	ALE	subadult	non-breeding	m	~2	36.0	21.01.2023	93	887	878	residential	11.9
m46088_disp							24.04.2023	174	2997	2838	dispersal	–
m46088_CZE	JER	subadult	non-breeding	m	~2	36.0	15.10.2023	80	1734	1613	residential	34.5
f36933	SBW	subadult	non-breeding	f	~3	31.3	09.10.2023	85	1606	1502	dispersal	–

To analyse HR spatiotemporal dynamics, we first divided the data for each wolf into monthly intervals and calculated the area of each monthly 95% HR using the AKDE method, then replotted these values against months to assess HR seasonal dynamics. As variation in the original HR sizes made them difficult to compare in a single plot, we decided to transform HR area into 'HR radius', defined as the radius of a circle with an equivalent area to the HR, calculated by defining HR area divided by PI first and then taking the square root. The HR radius can be interpreted as the typical 'radius of action' of the animal. HR spatiotemporal dynamics were also visualised as videos using the R package 'gganimate' (Pedersen and Robinson 2022).

Habitat selection

Wolf habitat selection was assessed in two ways. First, we assessed second-order selection by calculating landscape composition inside the HR, along with the human population density in the regions selected by wolves. Landscape composition was assessed using 10 m resolution ESA WorldCover 2022 data, a detailed landcover dataset based on Sentinel-1 and Sentinel-2 satellite data containing 11 classes with an overall accuracy of 76.7% (Zanaga et al. 2022). For each individual, we clipped the land cover raster using the 95% HR polygon and calculated the relative frequency of each land cover class within the polygon. To assess habitat preference in relation to human presence, we compared both local (i.e. for each individual's HR) and regional (i.e. over the larger spatial context of each study region) mean human population density (ind. km^{-2}), estimated using the 1 km spatial resolution population density raster developed as part of the WorldPop program (WorldPop 2018). For local estimates, we overlaid this raster with each 95% HR estimated using the AKDE method and determined averages using zonal statistics. For regional estimates, we did the same using the corresponding NUTS3 (Nomenclature of Territorial Units for Statistics) polygons (Eurostat 2021).

Second, we assessed the resident wolf's third-order selection, i.e. preferences within their HR, by 1) quantifying their occurrence in different land cover classes, and 2) using step selection analysis (Thurfjell et al. 2014, Fieberg et al. 2021). The former was achieved by overlaying the UD raster over the land cover raster and summing the values over each land cover class (i.e. zonal statistics). For the latter, we first generated ten hypothetical random steps for each observation of each individual, simulated from the fitted step length and turning angle distributions. We then fitted the conditional logistic regression model, with presence/pseudo-absence as response ('pseudo-absence' representing an occurrence from the simulated random step) and the following habitat selection predictors: distance to roads, distance to built-up areas, distance to permanent water bodies, habitat type (three levels: forest, grassland and crops), elevation and terrain slope (The data sources and processing of these predictors are summarised in greater detail in the Supporting information). To obtain unbiased coefficient estimates, we also included step length, logarithm of step length and cosine of turning angle

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

among the habitat selection predictors (Fieberg et al. 2021). Before fitting the models, we always checked for multi-collinearity by calculating variance inflection factors and sequentially removing the predictor with the highest value until all values were < 5. After fitting the models, we used backward stepwise model selection based on minimising AIC. From the final models, we used exponentiated coefficients to express the 'relative selection strength' (RSS), representing the ratio between estimated occurrence frequency of two sites that only differ by one unit in the value of a given predictor but are identical in all other predictors (Fieberg et al. 2021). To enhance interpretability of the model coefficients, we used a unit of 500 m for all distance-based predictors, 100 m for elevation and 5° for terrain slope. For habitat type, we set 'Forest' as the base level, with RSS values for the remaining habitat types expressed as use relative to that of the base category. Both R (www.r-project.org) and RStudio (RStudio Team 2020) were used for data analysis, using the package 'amt' (Signer et al. 2019) for step selection analysis, the 'tidyverse' metapackage (Wickham et al. 2019) for data manipulation and graphics, and the packages 'terra' (Hijmans 2023), 'sf' (Pebesma 2018) and 'stars' (Pebesma and Bivand 2023) for spatial data handling.

Results

Over the five years of trapping, we collared 20 wolves, of which eleven were females and nine males (Table 2–3). Most animals were subadults (n = 10) or juveniles (n = 4), with just six being full adults. During tracking, however, the status of some animals changed, with confirmed reproduction indicating that three subadults had become breeding adults over the following spring. Using mSAT analysis, we were able to confirm relatedness between some of the trapped animals, with all wolves from ALE being full siblings (i.e. members of one pack with the same parents) and the breeding male (m36983) from SBW being associated with his two daughters (f36931, f36933).

Behavioural movement modes

Three animals (m35302, m47015, m48013) were excluded from further analysis due to insufficient tracking days. NSD analysis for the remaining 17 wolves indicated a range of movement modes, with some animals displaying more than one mode (Table 2–3, Supporting information). Overall, the NSD residential mode was most common (n = 10), followed by either complete or incomplete dispersal (n = 5) and floaters (n = 2) (Table 2–3).

Four of the five dispersing animals undertook long dispersal trips, with animals f29456 and m30778 displaying HRs at both their sites of origin and successfully established HRs after completing dispersal, while animals m46090 and m46088 left their originating pack but had yet to establish a new HR at the end of the study (classified as unfinished dispersal in NSD). For these four animals, we were able to calculate a mean length for their dispersal trips of 252.6 km (with extremes: min = 222.6, max = 309.5 km; Fig. 1). For one subadult animal (f36933), while NSD selected the dispersion movement mode, ongoing behavioural patterns indicated a series of shorter, unfinished dispersal attempts with no new HR established. The two animals classified as floaters (f30777, m35301) displayed neither residential nor dispersal behaviour (compare NSD analysis in the Supporting information).

Home range quantification

HR sizes could be quantified for 14 individuals (five males, nine females) originally belonging to seven independent packs (Fig. 2). Owing to their subsequent dispersion, however, some animals established additional HRs during collar functionality, resulting in a total of 16 HRs. Of these 16 HRs, nine belonged to non-breeding individuals (i.e. subadults) and seven to breeding (adult) animals. The final average tracking length for non-breeding wolves (± SD) was 149.7 (± 79.8) days, with a mean of 1184.8 (± 664.4) cleared fixes (number of fixes that remained after data cleaning, fixes used in the analyses) per focal animal, while the final average tracking length for breeding wolves was 363.7 (± 188.0) days, with a mean of 3092.3 (± 1741.5) cleared fixes per focal animal.

For most individuals, HR values were roughly similar across the three methods used (i.e. MCP, KDE, AKDE; Fig. 3, Supporting information). Nevertheless, three individuals (f36931, m36983, m46088_CZE) had relatively large HRs with two (f36931, m36983) displaying relatively large differences between the methods. Note, however, that all three of these wolves had some of the lowest numbers of tracking days (n = 83; SD = ±2.6; Table 2–3). As the AKDE method is considered optimal for GPS telemetry data (Fleming et al. 2015, Silva et al. 2022), we only used AKDE-based results for all further analysis. For all but one individual, the OUF model was the best-fitting movement model using the AKDE method, the only exception being individual m30778_POL, for which the best-fitting model was OU. Both models are conceptually very similar, and the OUF model was the second-best model for this individual, with a minimal difference in AICc.

The average 95% (± SD) HR estimated by the AKDE method for all wolves in our dataset was 213.3 (± 158.2) km^2, while the average 50% HR was 38.6 (± 37.9) km^2. For non-breeding wolves it was 241.5 (± 178.4) km^2 and the average 50% HR 47.0 (± 43.2) km^2. The average 95% HR for adult wolves was 166.2 (± 116.5 km^2) and 50% HR 24.4 (± 23.5) km^2 (Fig. 3, Supporting information). The smallest 95% HR was recorded for wolf f29456_CZE at 51.3 km^2. All HRs were relatively compact, though there were occasional single or multiple small 'satellite' HRs, i.e. areas of high use separate from, but close to, the main HR (Fig. 2). Core areas (estimated as the 50% HR and depicted as beige areas in Fig. 2) were roughly situated in the centre of each HR. In study areas CSS, SBW and JER, where individuals from

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

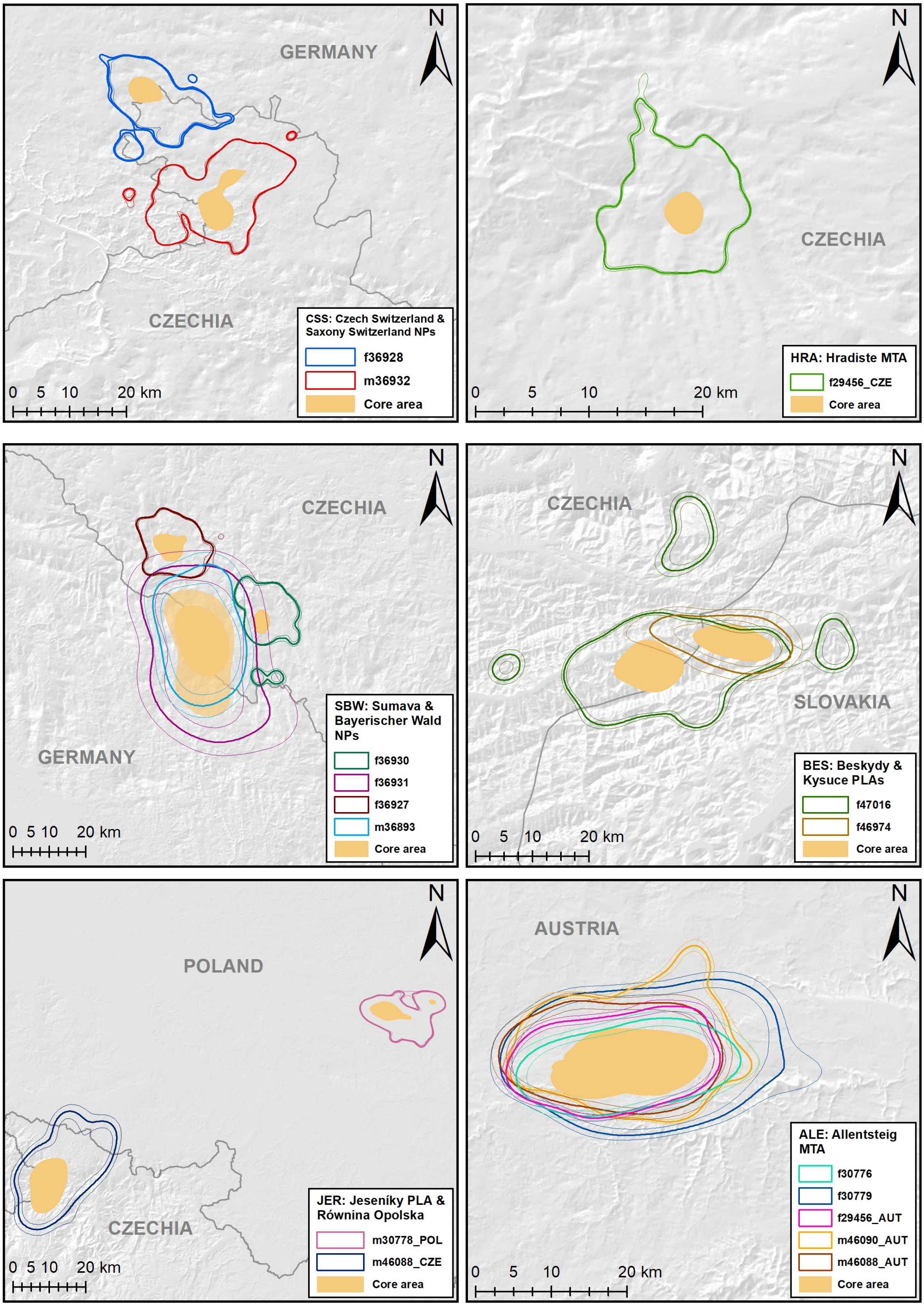

Figure 2. Individual home ranges in each study region, estimated using the AKDE method. The 95% home ranges are depicted by coloured lines, with thinner lines indicating the 95% confidence bands for the estimates. The smaller beige-shaded areas inside the home ranges depict their 'core areas', estimated as 50% of home ranges. For abbreviations and codes, see Table 1, 2 and 3.

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

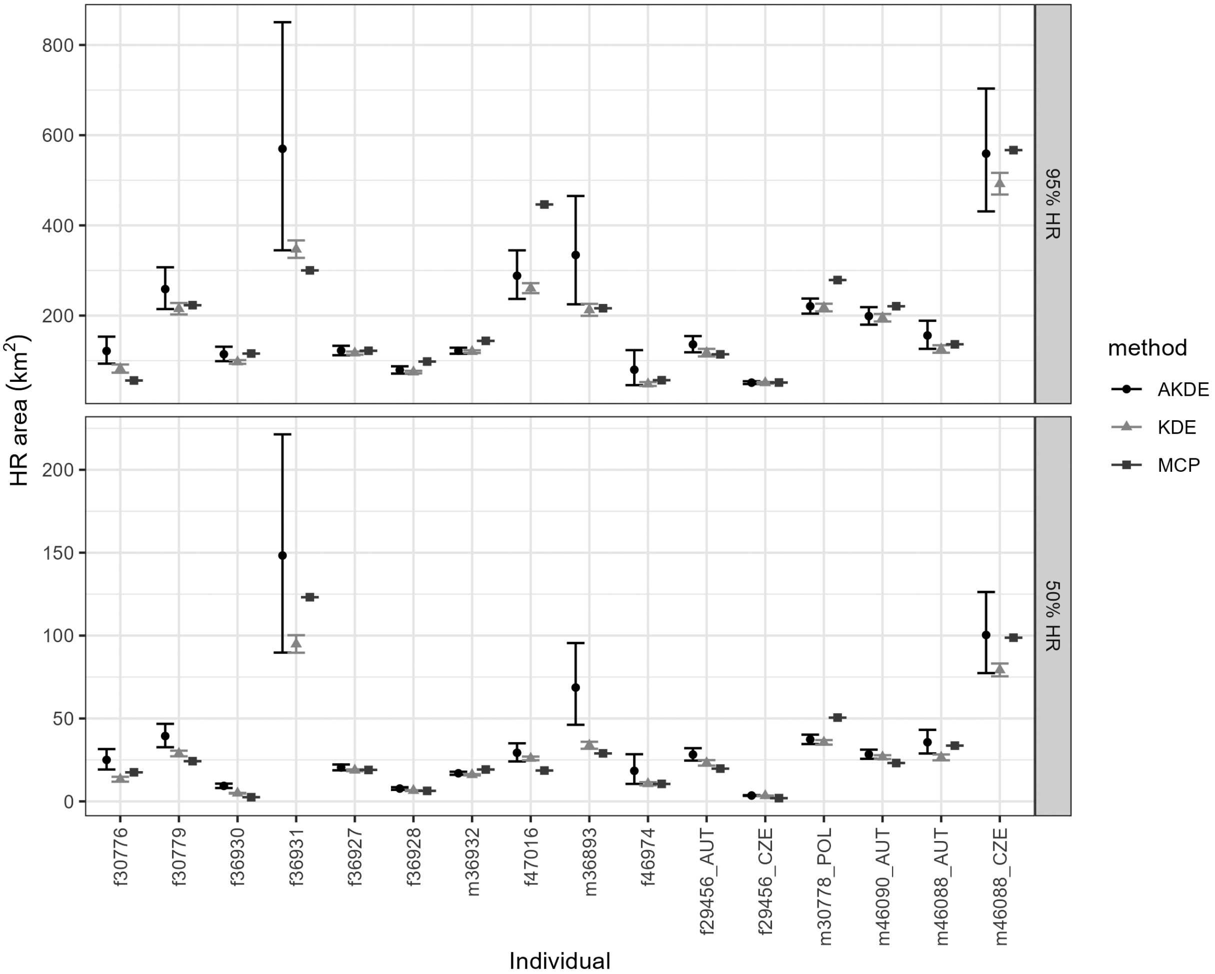

Figure 3. Home range sizes (upper panel = 95%, lower panel = 50%) for individual wolves, estimated using the AKDE, KDE and MCP methods, with 95% confidence intervals included for AKDE and KDE. Wolves are sorted according to increasing number of tracking days. For abbreviations and codes, see Table 1, 2 and 3.

multiple packs were recorded, the neighbouring HRs were normally non-overlapping, except for that of wolf f36931 (study area SBW), whose HR partly overlapped with two others. Owing to the relatively low number of GPS fixes for this individual, however, its HR shape is probably oversimplified and subject to high uncertainty (Fig. 2, area SBW). The high level of overlap between all wolves from the ALE study area and two individuals from SBW (f36931, f36933) was due to the confirmed relatedness of the animals and the same pack membership. Although wolves from BES overlapped their HRs in Fig. 2, they did not necessarily share this HR simultaneously.

All breeding females showed similar seasonal HR dynamics, characterised by a notable minimum in May or June when they had their pups (upper panel Fig. 4). The two breeding males recorded (m36932, m30778) also occupied smallest HRs in April or May, though the fluctuations in their HR size were rather small (mean = 103.2 km^2, SD = 30.5 km^2) compared to those of female breeders (SD = 124.6 km^2). Non-breeding individuals, on the other hand, showed no clear pattern, with some having very stable HRs and others showing an increasing trend with the onset of winter (lower panel Fig. 4).

Habitat selection

Wolf second-order selection (Fig. 5 left) was dominated by forest ([mean ± SD] 62.1 ± 16.0% cover proportion), grassland (24.8 ± 8.1%) and cropland (11.3 ± 11.4%), with the fourth most represented element being built-up areas (1.3 ± 0.8%) and the remaining land cover types all occurring at < 1%. The relatively high mean percentage of cropland was almost certainly due to the high overlap between the HR area of wolves in study area ALE, where cropland represented almost 40% of total cover (Fig. 5 left). The mean (± SD) estimated human population density inside the HRs was 19.9 ± 16.1 ind. /km^{-2} (Table 2–3), whereas the density over the region as a whole was 107.9 ± 45.6 ind. km^{-2} (Table 1).

Habitat use inside the HRs (i.e. third-order selection; Fig. 5 right) was consistent between individuals from the

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

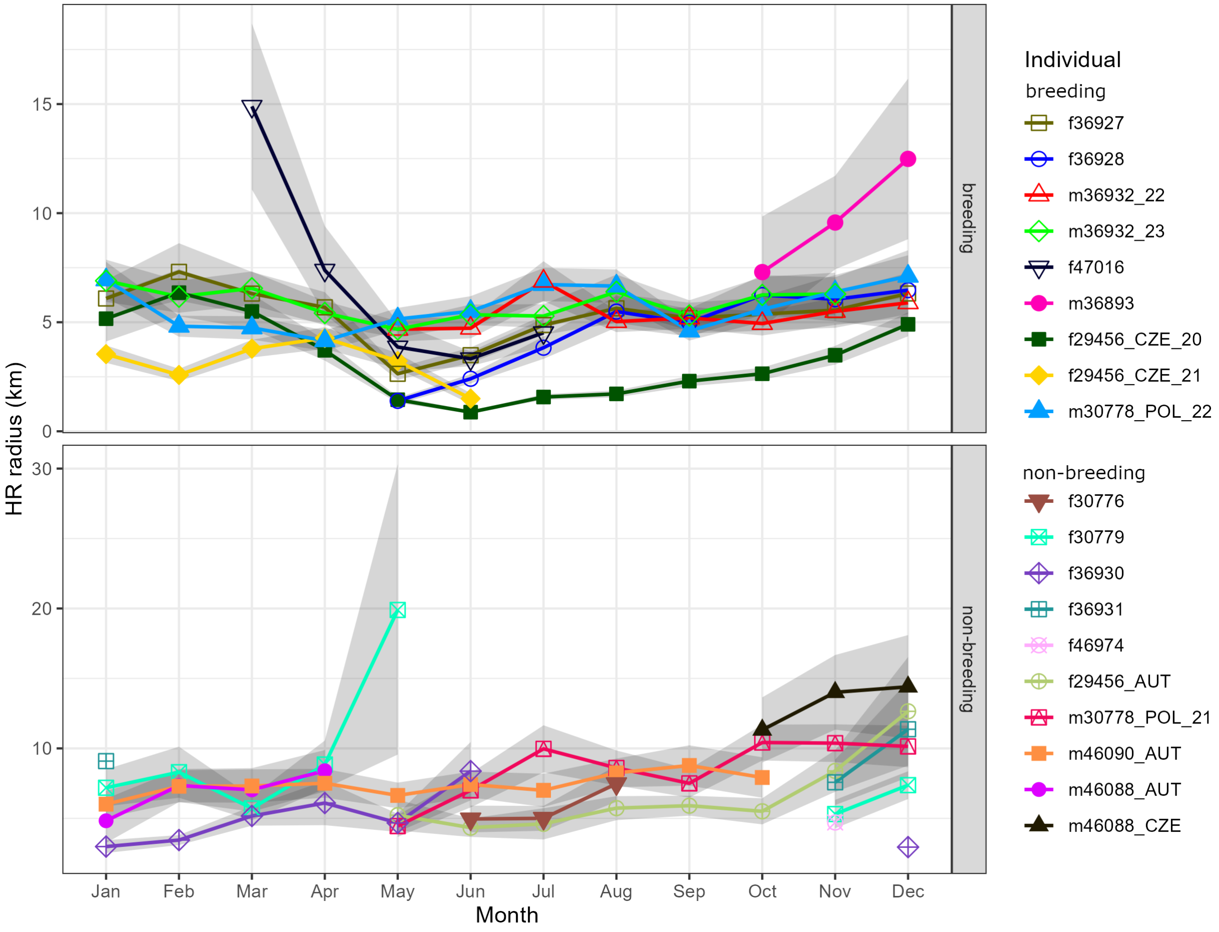

Figure 4. Seasonal dynamics in home range radius for breeding (upper panel) and non-breeding (lower panel) individuals. Monthly home range radii were estimated by extracting GPS fixes for a given month and year and calculating the 95% home range area using the AKDE method, then dividing by PI and applying the square-root. To emphasise seasonal patterns, data for individuals recorded over multiple years are displayed separately for each year (f29456, m30778, m36932). Shaded areas represent the 95% confidence bands around the area estimates, after dividing by PI and applying the square-root. For abbreviations and codes, see Table 1, 2 and 3.

same study area, and mostly mirrored the available landscape composition (Fig. 5 left). However, in study areas CSS and JER, wolves displayed a preference for forests of ca 20 percentage points more than would be expected from actual forest cover. In study area ALE, wolves also showed a preference for grassland of ca eight percentage points over availability. Practically all wolves tended to avoid cropland and built-up areas, though the occurrence rate in these classes rarely dropped to zero.

The RSS (Fig. 6, Supporting information) was significantly influenced by habitat predictors, though the predictor effects were largely inconsistent between individual wolves. Relatively similar patterns, however, were followed by individuals from the same study region (Fig. 6). All conditional logistic models were highly significant, though they showed relatively low predictive power, with concordance indices ranging between 0.55 and 0.76 (Supporting information). Compared to their occurrence in forest, six individuals showed a relative preference for grassland (RSS 1.58 ± 0.31 [mean ± SD]) and four relative avoidance (RSS 0.74 ± 0.05). Use of cropland was more like that of forests, with only two individuals showing a preference (RSS 1.51 ± 0.12) and two avoidance (RSS 0.61 ± 0.02). Ten individuals exhibited moderate avoidance of built-up areas (i.e. occurrence frequency increased 1.25 (± 0.22) times with each 500 m distance), with just one wolf (f36930) exhibiting a preference (RSS 0.74). Similar behaviour was exhibited with respect to roads, with eight animals showing an increase in occurrence further from roads (RSS 1.26 ± 0.16) and only one (f36928) showing the opposite (RSS 0.89). Six individuals showed an increasing occurrence (RSS 2.09 ± 0.70), and two decreasing occurrence (RSS 0.44 ± 0.08), with increasing distance to water bodies, this response being considerably stronger than distance to built-up areas or roads (Fig. 6). In terms of terrain, eight animals tended to select higher elevation, with occurrence increasing 1.65 (± 0.78) times with every 100 m increase in elevation (see especially wolf f36928, with an RSS reaching 3.50), while just one wolf (f30776) showed the opposite tendency (RSS 0.33). Finally, four individuals significantly

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

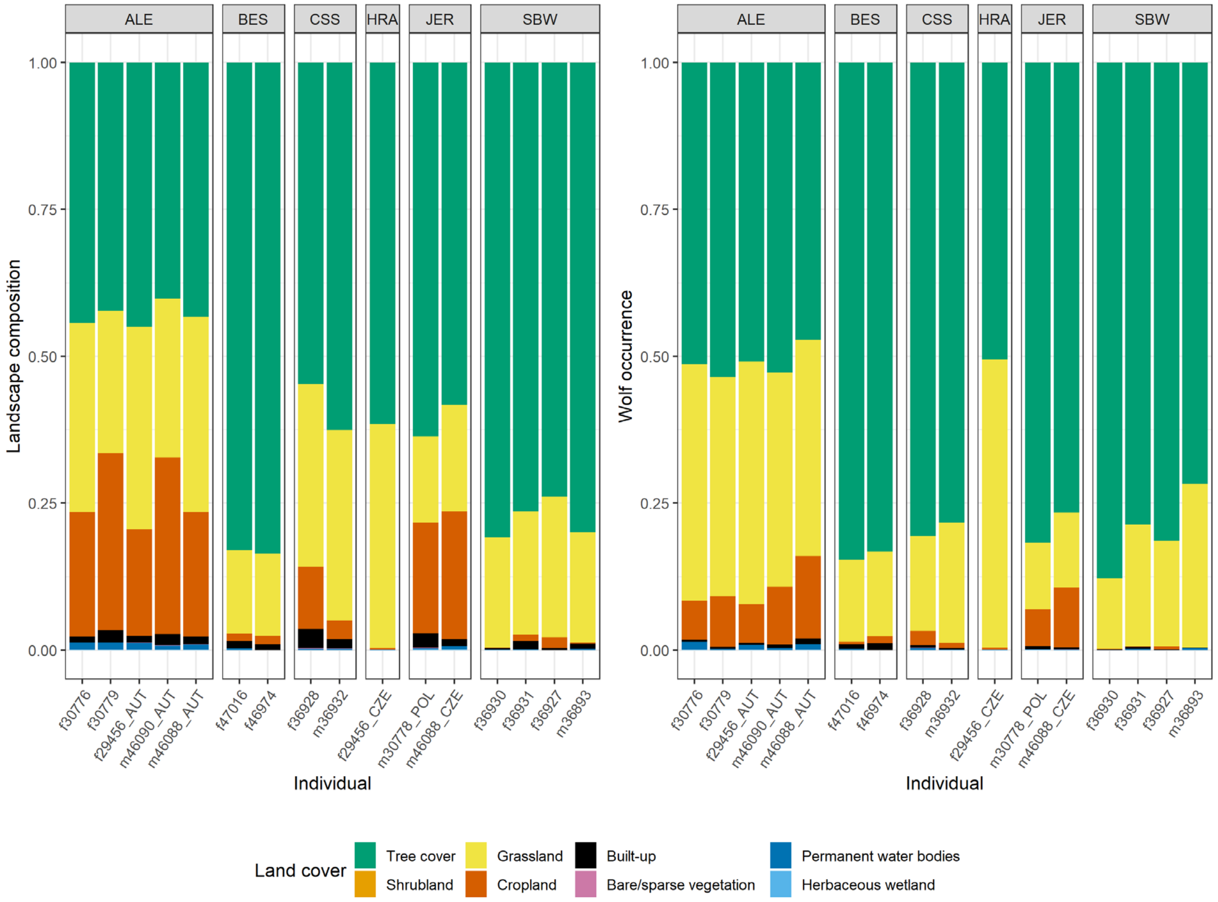

Figure 5. Landscape composition within each wolfs home range (left), and the relative use of different land cover classes by wolves, calculated by overlying their utilisation distributions over the land cover raster. Based on ESA WorldCover 2020 (Zanaga et al. 2022). Each panel corresponds to a different study region. For abbreviations and codes, see Table 1, 2 and 3.

increased their occurrence with each 5° increase in terrain slope (1.16 times ± 0.10), while six decreased their occurrence (0.81 times ± 0.06).

Discussion

The wolves tracked in this study occupied HRs of variable size, ranging from ca 50 to 570 km^2, with the majority being within a range of 100 to 220 km^2 (AKDE estimates). Breeding females followed a common seasonal pattern, with a noticeable reduction in HR to around 3 to 50 km^2 during the May/June breeding period. Two collared breeding males followed a similar pattern, though to a lesser extent, while some non-breeders showed a recognisable tendency to increase HR size with the onset of autumn and winter. While the wolves mainly occupied landscapes dominated by forests with around 25% grassland, in some cases (e.g. study areas JER and ALE), they were able to tolerate as much as 20 to 30% cropland, though built-up areas were always generally avoided. Nevertheless, their actual use of the landscape suggested that they always tried to avoid human-altered landcover types, sticking mainly to forest and grassland.

Behavioural movement modes

Using NSD, we divided our wolves into three main categories based on movement modes, i.e. floating, dispersing and resident individuals. The two floaters (f30777, m35301) roamed within their respective study areas with no evidence of any established HR. On the other hand, they often visited HRs of other packs during their roaming, presumably to increase their chances of either joining an established pack or usurping a mate for breeding and forming their own pack, with the subsequent establishment of a new HR (Blanco and Cortés 2007, Mancinelli et al. 2018).

Unlike floaters, some individuals leave their natal pack with the clear intention of forming a breeding pair with a new HR. Some wolves have been documented as displaying clear pre-dispersal forays prior to leaving the natal HR and potentially settling immediately adjacent to their former HRs (Wabakken et al. 2007, Kirilyuk et al. 2020). All the wolves demonstrating dispersal movements in our study, however, showed no evidence of pre-dispersal forays prior to their long-distance dispersals; instead, they began to use the peripheries of their HR more frequently before dispersing, a behaviour also noted by Blanco and Cortés (2007).

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

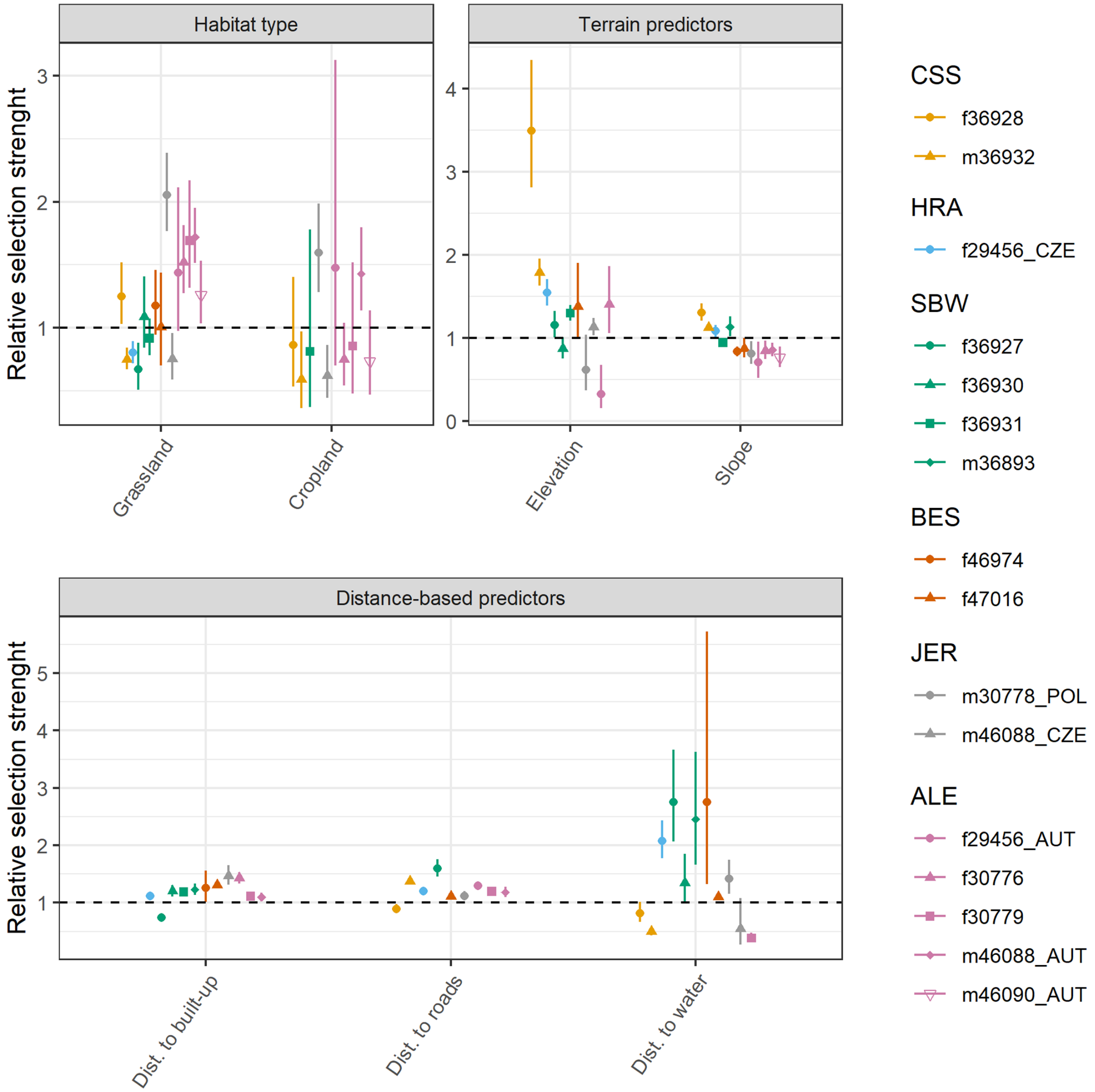

Figure 6. Relative strength of wolf habitat selection depending on different predictors. Values, estimated using a step-selection analysis, represent the relative (i.e. multiplicative) increase/decrease in selection strength per unit increase in the predictor value (i.e. a value of one represents no change in selection strength). Each unit is 500 m for all distance predictors, 100 m for elevation and 5° for terrain slope. For habitat type, values represent the relative increase/decrease in selection strength compared to the base category of forest t (which is not displayed). Error bars represent 95% Wald confidence intervals. For abbreviations and codes, see Table 1, 2 and 3.

Interestingly, three of the four dispersing wolves leaving ALE made a deliberate movement northeast to study area JER, where two of the wolves then established a new HR while the third remained in the area but continued to show dispersal movement without establishing an HR. Unlike areas with low human density, where dispersal after recolonisation tends to lack any clear pattern (Kojola et al. 2006), human dominated landscapes tend to force wolves to preferentially seek places with low human disturbances (Reinhardt et al. 2019). A further condition for a wolf to settle in a new area is the presence of other wolves, which is one of the reasons why dispersing individuals tend to cross through existing wolf territories (Blanco and Cortés 2007, Kirilyuk et al. 2020). This behaviour was clearly observed with the two longer-dispersing wolves in this study, with f29456 passing through SBW and m46088 crossing a territory between ALE and JER formed in 2022 (Vorel et al unpubl.). While these wolves may have been successful in finding a mate in these territories, they apparently decided not to establish a new HR there but continued to their current sites.

The dispersal distances recorded in our study compare well with those of individuals dispersing in an expanding

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

population in Finland (Kojola et al. 2006), though less so with other examples of long-distance dispersal in Europe (Wabakken et al. 2007, Andersen et al. 2015, Ražen et al. 2016), especially those in agricultural land (Blanco and Cortés 2007). However, unlike the uni-directional movements observed for individuals in other studies (Wabakken et al. 2007, Ražen et al. 2016), even our 'shorter' dispersals were likely to result in reconnections between the major European wolf populations on a regular basis. While all our currently dispersing collared wolves (ALE) originate from the central European population, their current whereabouts (JER) could easily be reached by either Carpathian or Baltic wolves. Consequently, our study areas could represent a crossroads for the four major European wolf populations, i.e. the Central European, Carpathian, Alpine and Baltic groups (Chapron et al. 2014, Hulva et al. 2018, Szewczyk et al. 2021).

Home range quantification

The general agreement between methods of HR estimation (i.e. AKDE, KDE and MCP; Fig. 3) suggests that they are, to some extent, interchangeable. However, there are counter examples (i.e. individuals f36931, f47016, m36893 and m46088_CZE) that illustrate situations where method choice proved important. In the case of f47016, the higher HR estimate using the MCP method (compared to AKDE and KDE) was due to the highly non-convex shape of the area occupied (Fig. 2, study area BES), suggesting that this wolf had probably undertaken several dispersal trips into neighbouring areas. Even when we applied NSD to exclude such periods of dispersal behaviour (compare with approach Dickie et al. (2022), some individuals (incl. f47016, but also f36930 and f46974) still exhibited occasional visits outside their main HR area, resulting in spatially fragmented HR estimates (Fig. 2). Enveloping such a non-convex shape using an MCP naturally led to an overestimation of HR area due to the inclusion of unoccupied parts of the landscape. The same effect, but at a lower magnitude, was also clear for many other individuals when MCP HRs were compared with those estimated using KDE (Fig. 3). This is a well-known problem with the MCP method (together with numerous other problems; Powell 2000); nevertheless, we included the method for the sake of comparability with older studies, which frequently use this method (Ciucci et al. 1997, Okarma et al. 1998, Reinhardt and Kluth, 2016, Mysłajek et al. 2018). In the second case (related wolves f36931 and m36893), both exhibited much larger HRs when using the AKDE method (compared to KDE and MCP), probably as these individuals had shorter tracking times (84 and 85 tracking days, respectively) than the other wolves while occupying relatively large areas. At the same time, they had a relatively high number of fixes, which naturally led to a high level of temporal autocorrelation. In such cases, the AKDE method compensates for autocorrelation by creating a larger HR with a regular and obviously oversimplified shape, accompanied with greater uncertainty (Fleming et al. 2015). Though these results may seem inferior to the apparently more precise KDE estimates (Fig. 3), they better reflect the true uncertainty of such data. In this case, the apparent precision of the KDE estimates was due to its ignoring autocorrelation between fixes; thus, the corresponding HR area is likely to be underestimated.

Aside from the four wolves mentioned above, the sizes of individual HRs in our study were comparable with those from previous studies based in central Europe (Okarma et al. 1998, Jedrzejewski et al. 2007, Mysłajek et al. 2018, Reinhardt et al. 2019). This is most likely due to the low variation in latitude compared to other large-scale studies, where HRs varied considerably in response to latitudinal change (Adams et al. 2008, Mattisson et al. 2013).

Our data confirmed a general pattern for breeding individuals, with minimum HR size during reproduction (Jedrzejewski et al. 2007, Roffler and Gregovich 2018) and a subsequent increase in HR as the pups gain mobility. Wolves generally increase their HRs during winter (Jedrzejewski et al. 2007), especially in areas with migratory prey (Mech and Boitani 2003, Middleton et al. 2013). On the contrary, in central Europe, ungulate prey remain overabundant throughout the year (Carpio et al. 2021) and commonly migrate horizontally from the mountains to the valleys in winter to obtain food (Luccarini et al. 2006). As wolves naturally follow their prey species, this could help explain the increased winter HR sizes for some of our wolves in area SBW (e.g. f36931 and m36893, which appeared to avoid mountain ridges, based on visual inspection of telemetry data), though to a much lesser extent than observed with migratory prey at higher latitudes (Middleton et al. 2013). The HRs of non-breeding individuals tended to fluctuate in size with no clear pattern. According to Roffler and Gregovich (2018), non-breeding individuals associated with a den tend to have smaller HRs, which could indicate that some of our non-breeders (e.g. f36930), who decreased their HRs over the reproductive season, were affiliated with a breeding pack.

Habitat selection

Though central Europe is often described as completely human-altered, there are still areas remaining with relatively low anthropogenic pressure. These areas, which tend to be more undisturbed and quieter, such as mountains, hilly landscapes, military training areas or nature protection areas, are commonly the first to be recolonised by wolves (Mysłajek et al. 2018, Reinhardt et al. 2019). Our wolves showed a clear preference for such less disturbed patches within the human-impacted landscape mosaic, with the average human density in the regions selected by wolves much lower than the average human density for the whole region. Our data also showed that wolves almost always settled and used forested areas, regardless of landscape composition or study area type, and showed a general tendency during the early colonisation phase to avoid built-up areas and farmland (Capitani et al. 2006, Bassi et al. 2015). Nevertheless, Zanni et al. (2023) showed that the HRs of wolves in heavily altered landscapes often encompassed settlements, and this was also observed for our

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

wolves, though they appeared to cross through such landscape features predominantly during the night.

While our wolves mainly occupied forests, those in MTAs (HRA and ALE) often also made use of grassland. MTAs typically have frequent patches of open land, resulting from a variety of army operations, and those encourage heavy exploitation by ungulates (Valente et al. 2020). This high density of grazing ungulates in turn attracts wolves; thus, the open grasslands function as regularly attended hunting grounds for wolves (Torretta et al. 2018). The results of our step selection analysis must be interpreted with caution, however, as for each individual, significant effects can easily be caused by specific local landscape configurations instead of actual wolf preferences; consequently, generalising preferences from just six study areas may be unreliable, and therefore it will be necessary to expand the dataset in the future and verify these results again. On the other hand, predictors showing consistent effects between most of the individuals should allow for hypotheses to be formulated. For example, the wolf's apparent tendency to avoid built-up areas (Fig. 6) is in agreement with their general tendency to select quieter locations with low human presence and higher concentrations of prey (Sanz-Pérez et al. 2018). This probably also explains their increasing occurrence at higher elevations, as higher altitudes in these mountainous landscapes are typically forested and unoccupied by humans. Avoidance of roads is also to be expected as human transportation is known to represent a major source of mortality for wildlife species (Barry et al. 2020), however, Raynor et al. (2021) or Dickie et al. (2022) both documented frequent utilization of roads by wolves, therefore road characteristics and traffic frequency should also be taken to consideration.

Conclusion

Our results provide the first detailed insights into wolf spatial ecology and habitat selection during their initial re-colonisation of the continental European landscape. Though GPS telemetry has often been used across Europe, there have been relatively few published results from such projects, which, with a few exceptions (Sanz-Pérez et al. 2018, Dennehy et al. 2021), have mostly been based on small sample sizes, preventing generalisable conclusions. We attempt to fill this gap by tracking a relatively large sample size (n = 17 animals), the results of which provide early insights into wolf recolonisation in human-altered central European environments. This is especially true considering the dataset includes animals of differing pack status (breeding versus non-breeding), both sexes (reproducing males and females) and different life histories (dispersing versus residential). On the other hand, this diversity increases outcome complexity, making it difficult to generalise on behavioural patterns. Consequently, we encourage future studies on wolf HR determination to not only publish their outputs but also to put aside constraints of political borders and combine datasets with studies undertaken in other countries with similar environments, thereby increasing confidence in wolf life history and behavioural and spatial patterns.

Acknowledgements – We would like to express our sincere gratitude to all contributors in the field, namely to: Andreas Berger, Michal Bojda, Christian Eder, Šárka Frýbová, Jiří Labuda and Simon Zauner. We are thankful for the assistance of Hana Horáková, Vladimír Piaček and other veterinarians during the trapping. We would especially like to thank Ashley McLaren, Bryce Olson, Ilka Reinhardt and Steve K. Windels for sharing their experience, advice and training in wolf trapping. We are also grateful to the Austrian Ministry of Defense, Šumava NP and Czech Switzerland NP, the Nature Conservation Agency of the Czech Republic Beskydy PLA Administration, the Ministry of the Environment of the Czech Republic, Lesy České Republiky for their cooperation and support. Finally, we would like to thank Kevin Roche for his fruitful comments to the manuscript and language corrections.

Funding – Our research was founded with the support of the Interreg Czech-Saxony Programme 2014-2021: 100400831 and 100322836, Interreg Czech-Bayern 2021-2027: BYCZ01-001 and the Operational Programme Environment (no. CZ.05.4.27/0.0/0.0/20_139/0012815). The government of Lower Austria financially supported the Austrian part of the research. Interreg Central Europe LECA - Supporting the coexistence and conservation of Carpathian LargE CArnivores , ID: CE0100170

Permits – The trapping of live animals was authorised by local nature protection authorities and followed the ethical standards set by collaborating universities and governments, i.e. Czech University of Life Sciences: MZP/2018/630/2582, MZP/2022/630/929, SZ NPS 08816/2020/4, SZ SNPCS 00118/2022, KUUK/049576/2022; Mendel University: SR/0012/US/2021-5; MZP/2022/630/735; and the Government of Lower Austria: LF1-TVG-59/001-2018.

Author contributions

Aleš Vorel: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Validation (lead); Writing – original draft (equal); Writing – review and editing (lead). **Ivo Kadlec**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (supporting); Resources (supporting); Software (supporting); Visualization (equal); Writing – original draft (equal). **Tadeáš Toulec**: Conceptualization (supporting); Formal analysis (supporting); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Aldin Selimovic**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Resources (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Jan Horníček**: Conceptualization (supporting); Data curation (lead); Formal analysis (supporting); Investigation (supporting); Methodology (supporting). **Oldřich Vojtěch**: Data curation (supporting); Formal analysis (supporting); Methodology (supporting). **Jan Mokrý**: Conceptualization (supporting); Data curation (equal); Funding acquisition (equal); Methodology (supporting); Project administration (equal); Supervision (supporting). **Lukáš Pavlačík**: Conceptualization (supporting); Data curation (supporting); Methodology (supporting); Resources (supporting). **Walter Arnold**: Data curation (supporting);

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Formal analysis (supporting). **Jessica Cornils**: Data curation (supporting); Formal analysis (supporting). **Miroslav Kutal**: Conceptualization (supporting); Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (supporting); Writing – review and editing (supporting). **Martin Duľa**: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Funding acquisition (supporting); Methodology (supporting); Resources (supporting); Writing – review and editing (supporting). **Lukáš Žák**: Data curation (supporting); Methodology (supporting). **Vojta Barták**: Conceptualization (equal); Formal analysis (equal); Investigation (lead); Methodology (equal); Supervision (supporting); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal)

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cz8w9gjbt (Vorel et al. 2024). Due to the protection status of wolves some of the data are blurred; the original data is possible to reach after contacting of one of contact persons.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Adams, L. G., Stephenson, R. O., Dale, B. W., Ahgook, R. T. and Demma, D. J. 2008. Population dynamics and harvest characteristics of wolves in the central Brooks Range, Alaska. – Wildl. Monogr. 170: 1–25.

Andersen, L. W., Harms, V., Caniglia, R., Czarnomska, S. D., Fabbri, E., Jędrzejewska, B., Kluth, G., Madsen, A. B., Nowak, C., Pertoldi, C., Randi, E., Reinhardt, I. and Stronen, A. V. 2015. Long-distance dispersal of a wolf, *Canis lupus*, in northwestern Europe. – Mamm. Res. 60: 163–168.

Barry, T., Gurarie, E., Cheraghi, F., Kojola, I. and Fagan, W. F. 2020. Does dispersal make the heart grow bolder? Avoidance of anthropogenic habitat elements across wolf life history. – Anim. Behav. 166: 219–231.

Bassi, E., Willis, S. G., Passilongo, D., Mattioli, L. and Apollonio, M. 2015. Predicting the spatial distribution of wolf (*Canis lupus*) breeding areas in a mountainous region of central Italy. – PLoS One 10: e0124698.

Benson, J. F. and Patterson, B. R. 2015. Spatial overlap, proximity, and habitat use of individual wolves within the same packs. – Wildl. Soc. Bull. 39: 31–40.

Blanco, J. C. and Cortés, Y. 2007. Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. – J. Zool. 273: 114–124.

Boitani, L. 2000. Action Plan for the conservation of the wolves (*Canis lupus*) in Europe. – In: Convention on the Conservation of European Wildlife and Natural Habitats. Council of Europe Strasbourg.

Borkowski, J., Banul, R., Jurkiewicz, J., Hołdyński, C., Świeczkowska, J., Nasiadko, M. and Załuski, D. 2019. High density of keystone herbivore vs conservation of natural resources: factors affecting red deer distribution and impact on vegetation in Słowiński National Park, Poland. – For. Ecol. Manage. 450: 117503.

Breitenmoser, U. 1998. Large predators in the Alps: the fall and rise of man's competitors. – Biol. Conserv. 83: 279–289.

Calabrese, J. M., Fleming, C. H. and Gurarie, E. 2016. Ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. – Methods Ecol. Evol. 7: 1124–1132.

Calenge, C. and Fortmann-Roe, S. 2023. _adehabitatHR: Home Range Estimation_. – R package ver. 0.4.21. https://CRAN.R-project.org/package=adehabitatHR.

Capitani, C., Mattioli, L., Avanzinelli, E., Gazzola, A., Lamberti, P., Mauri, L., Scandura, M., Viviani, A. and Apollonio, M. 2006. Selection of rendezvous sites and reuse of pup raising areas among wolves *Canis lupus* of north-eastern Apennines, Italy. – Acta Theriol. (Warsz) 51: 395–404.

Carpio, A. J., Apollonio, M. and Acevedo, P. 2021. Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. – Mamm. Rev. 51: 95–108.

Chapron, G. et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. – Science 346: 1517–1519.

Ciucci, P., Boitani, L., Francisci, F. and Andreoli, G. 1997. Home range, activity and movements of a wolf pack in central Italy. – J. Zool. 243: 803–819.

Dennehy, E., Llaneza, L. and López-Bao, J. V. 2021. Contrasting wolf responses to different paved roads and traffic volume levels. – Biodivers. Conserv. 30: 3133–3150.

Dickie, M., Serrouya, R., Avgar, T., McLoughlin, P., McNay, R. S., DeMars, C., Boutin, S. and Ford, A. T. 2022. Resource exploitation efficiency collapses the home range of an apex predator. – Ecology 103: e3642.

Dressel, S., Sandström, C. and Ericsson, G. 2015. A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976–2012. – Conserv. Biol. 29: 565–574.

Eggermann, J., da Costa, G. F., Guerra, A. M., Kirchner, W. H. and Petrucci-Fonseca, F. 2011. Presence of Iberian wolf (*Canis lupus signatus*) in relation to land cover, livestock and human influence in Portugal. – Mamm. Biol. 76: 217–221.

Eurostat 2021. NUTS - Nomenclature of territorial units for statistics [data set]. – https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/nuts.

Fabbri, E., Caniglia, R., Kusak, J., Galov, A., Gomerčić, T., Arbanasić, H., Huber, D. and Randi, E. 2014. Genetic structure of expanding wolf (*Canis lupus*) populations in Italy and Croatia, and the early steps of the recolonization of the Eastern Alps. – Mamm. Biol. 79: 138–148.

Fabbri, E., Miquel, C., Lucchini, V., Santini, A., Caniglia, R., Duchamp, C., Weber, J. M., Lequette, B., Marucco, F., Boitani, L., Fumagalli, L., Taberlet, P. and Randi, E. 2007. From the Apennines to the Alps: colonization genetics of the naturally expanding Italian wolf (*Canis lupus*) population. – Mol. Ecol. 16: 1661–1671.

Fieberg, J., Signer, J., Smith, B. and Avgar, T. 2021. A "How to" guide for interpreting parameters in habitat-selection analyses. – J. Anim. Ecol. 90: 1027–1043.

Fleming, C. H. and Calabrese, J. M. 2022. _ctmm: continuous-time movement modeling_. – R package ver. 1.1.0, https://CRAN.R-project.org/package=ctmm.

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P. and Calabrese, J. M. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. – Ecology 96: 1182–1188.

Fritts, S. H., Stephenson, R. O., Hayes, R. D. and Boitani, L. 2003. Wolves and humans. – In: Mech, L. D. and Boitani, L. (eds), Wolves: behavior, ecology and conservation. Univ. of Chicago Press, pp. 289–317.

Fuller, T. K., Mech, L. D. and Cochrane, J. F. 2003. Wolf Population dynamics. – In: Mech, L. D. and Boitani, L. (eds), Wolves: behavior, ecology and conservation. Univ. of Chicago Press, pp. 161–191.

Gese, E. M. and Mech, L. D. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. – Can. J. Zool. 69: 2946–2955.

Glikman, J. A., Vaske, J. J., Bath, A. J., Ciucci, P. and Boitani, L. 2012. Residents' support for wolf and bear conservation: the moderating influence of knowledge. – Eur. J. Wildl. Res. 58: 295–302.

Hijmans, J. R. 2023. terra: spatial data analysis. – R package ver. 1.7-23, https://CRAN.R-project.org/package=terra.

Hulva, P., Černá Bolfíková, B., Woznicová, V., Jindřichová, M., Benešová, M., Mysłajek, R. W., Nowak, S., Szewczyk, M., Niedźwiecka, N., Figura, M., Hájková, A., Sándor, A. D., Zyka, V., Romportl, D., Kutal, M., Finďo, S. and Antal, V. 2018. Wolves at the crossroad: fission–fusion range biogeography in the western Carpathians and central Europe. – Divers. Distrib. 24: 179–192.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B. and Kowalczyk, R. 2007. Territory size of wolves *Canis lupus*: linking local (Białowieża Primeval Forest, Poland) and Holarctic-scale patterns. – Ecography 30: 66–76.

Jędrzejewski, W., Jedrzejewska, B., Zawadzka, B., Borowik, T., Nowak, S. and Mysłajek, R. W. 2008. Habitat suitability model for Polish wolves based on long-term national census. – Anim. Conserv. 11: 377–390.

Kaartinen, S., Kojola, I. and Colpaert, A. 2005. Finnish wolves avoid roads and settlements. – Ann. Zool. Fenn. 42: 523–532.

Kaczensky, P., Linnell, J., Huber, D., Von Arx, M., Andren, H., Breitenmoser, U. and Boitani, L. 2021. Distribution of large carnivores in Europe 2012–2016: distribution maps for brown bear, Eurasian lynx, grey wolf, and wolverine [Dataset]. – Dryad, https://doi.org/10.5061/dryad.pc866t1p3.

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R. and Boyce, M. S. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. – Ecol. Lett. 10: 690–700.

Khorozyan, I. and Heurich, M. 2022. Large-scale sheep losses to wolves (*Canis lupus*) in Germany are related to the expansion of the wolf population but not to increasing wolf numbers. – Front. Ecol. Evol. 10: 778917.

Kirilyuk, A. V., Kirilyuk, V. E. and Ke, R. 2020. Long-distance dispersal of wolves in the Dauria ecoregion. – Mamm. Res. 65: 639–646.

Kittle, A. M., Anderson, M., Avgar, T., Baker, J. A., Brown, G. S., Hagens, J., Iwachewski, E., Moffatt, S., Mosser, A., Patterson, B. R., Reid, D. E. B., Rodgers, A. R., Shuter, J., Street, G. M., Thompson, I. D., Vander Vennen, L. M. and Fryxell, J. M. 2015. Wolves adapt territory size, not pack size to local habitat quality. – J. Anim. Ecol. 84: 1177–1186.

Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C. and Ronkainen, S. 2006. Dispersal in an expanding wolf population in Finland. – J. Mammal. 87: 281–286.

Kuijper, D. P. J., Churski, M., Trouwborst, A., Heurich, M., Smit, C., Kerley, G. I. H. and Cromsigt, J. P. G. M. 2019. Keep the wolf from the door: how to conserve wolves in Europe's human-dominated landscapes? – Biol. Conserv. 235: 102–111.

Kusak, J., Skrbinšek, A. M. and Huber, D. 2005. Home ranges, movements, and activity of wolves (*Canis lupus*) in the dalmatian part of Dinarids, Croatia. – Eur. J. Wildl. Res. 51: 254–262.

Kutal, M., Belotti, E., Volfová, J., Mináriková, T., Bufka, L., Poledník, L., Krojerová, J., Bojda, M., Váňa, M., Kafka, P., Poledníková, K., Pospíšková, J., Dekar, P., Machciník, B., Koubek, P., & Dul'a, M. 2017. Occurrence of large carnivores – *Lynx lynx, Canis lupus* and *Ursus arctos* – and of *Felis silvestris* in the Czech Republic and western Slovakia in 2012–2016 (Carnivora). – Lynx 48: 93–107.

Kutal, M., Váňa, M., Suchomel, J., Chapron, G. and López-Bao, J. V. 2016. Trans-boundary edge effects in the western Carpathians: the influence of hunting on large carnivore occupancy. – PLoS One 11: e0168292.

Langley, R. B. 1999. Dilution of precision. – G.P.S. World 10: 52–59.

Linnell, J. D. C., Swenson, J. E. and Anderson, R. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. – Anim. Conserv. 4: 345–349.

Luccarini, S., Mauri, L., Ciuti, S., Lamberti, P. and Apollonio, M. 2006. Red deer (*Cervus elaphus*) spatial use in the Italian alps: home range patterns, seasonal migrations, and effects of snow and winter feeding. – Ethol. Ecol. Evol. 18: 127–145.

Mancinelli, S., Boitani, L. and Ciucci, P. 2018. Determinants of home range size and space use patterns in a protected wolf (*Canis lupus*) population in the central Apennines, Italy. – Can. J. Zool. 96: 828–838.

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J. D. C., Rauset, G. R. and Pedersen, H. C. 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. – Oecologia 173: 813–825.

Mech, L. D. 1994. Buffer zones of territories of gray wolves as regions of intraspecific strife. – J. Mammal. 75: 199–202.

Mech, L. D. 2017. Where can wolves live and how can we live with them? – Biol. Conserv. 210: 310–317.

Mech, L. D. and Boitani, L. 2003. Wolf social ecology. – In: Mech, L. D. and Boitani, L. (eds), Wolves behavior, ecology and conservation Univ. of Chicago Press, pp. 1–34.

Middleton, A. D., Kauffman, M. J., Mcwhirter, D. E., Jimenez, M. D., Cook, R. C., Cook, J. G., Albeke, S. E., Sawyer, H. and White, P. J. 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. – Ecol. Lett. 16: 1023–1030.

Morales-González, A., Fernández-Gil, A., Quevedo, M. and Revilla, E. 2022. Patterns and determinants of dispersal in grey wolves (*Canis lupus*). – Biol. Rev. 97: 466–480.

Mysłajek, R. W., Tracz, M., Tracz, M., Tomczak, P., Szewczyk, M., Niedźwiecka, N. and Nowak, S. 2018. Spatial organization in wolves *Canis lupus* recolonizing north-west Poland: large territories at low population density. – Mamm. Biol. 92: 37–44.

Newsome, T. M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C. R., Dellinger, J. A., López-Bao, J. V., Peterson, R. O., Shores, C. R., Wirsing, A. J. and Ripple, W. J. 2016. Food habits of the world's grey wolves. – Mamm. Rev. 46: 255–269.

Nowak, S. and Mysłajek, R. W. 2016. Wolf recovery and population dynamics in western Poland, 2001–2012. – Mamm. Res. 61: 83–98.

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Okarma, H., Jędrzejewski, W., Schmidt, K., Śniezko, S., Bunevich, A. N. and Jędrzejewska, B. 1998. Home ranges of wolves in Białowieza Primeval Forest, Poland, compared with other Eurasian populations. – J. Mammal. 79: 842–852.

Packard, J. M. 2003. Wolf behavior: reproductive, social, and intelligent. – In: Mech, L. D. and Boitani, L. (eds), Wolves behavior, ecology and conservation. Univ. of Chicago Press, pp. 35–65.

Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data. – R J. 10: 439–446.

Pebesma, E. and Bivand, R. 2023. Spatial data science: with applications in R. – Chapman and Hall/CRC, https://r-spatial.org/book/.

Pedersen, T. and Robinson, D. 2022. _gganimate: a grammar of animated graphics_. – R package ver. 1.0.8, https://CRAN.R-project.org/package=gganimate.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. – In: Boitani, L. and Fuller, T. (eds), Research techniques in animal ecology: controversies and consequences. Columbia Univ. Press.

Rauer, G. and Blaschka, A. 2021. Situation des Wolfs in Österreich. Verein Österreichzentrum Bär, Wolf, Luchs. – https://baer-wolf-luchs.at/wp-content/uploads/2022/05/OeZ_Wolfsmanagement_Empfehlungen_2021.pdf.

Raynor, J. L., Grainger, C. A. and Parker, D. P. 2021. Wolves make roadways safer, generating large economic returns to predator conservation. – Proc. Natl Acad. Sci. USA 118: 1–10.

Ražen, N., Brugnoli, A., Castagna, C., Groff, C., Kaczensky, P., Kljun, F., Knauer, F., Kos, I., Krofel, M., Luštrik, R., Majić, A., Rauer, G., Righetti, D. and Potočnik, H. 2016. Long-distance dispersal connects Dinaric-Balkan and Alpine grey wolf (*Canis lupus*) populations. – Eur. J. Wildl. Res. 62: 137–142.

Reinhardt, I. and Kluth, G. 2016. Abwanderungs und Raumnutzungsverhalten von Wölfen (*Canis lupus*) in Deutschland.- Natur und Landschaft 91. 262-271. 10.17433/6.2016.50153396.262-271.

Reinhardt, I., Kluth, G., Nowak, C., Szentiks, C. A., Krone, O., Ansorge, H. and Mueller, T. 2019. Military training areas facilitate the recolonization of wolves in Germany. – Conserv. Lett. 12: e12635.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D. and Wirsing, A. J. 2014. Status and ecological effects of the world's largest carnivores. – Science 343: 1241484.

Roffler, G. H. and Gregovich, D. P. 2018. Wolf space use during denning season on Prince of Wales Island, Alaska. – Wildl. Biol. 2018: 1–18.

Ronnenberg, K., Habbe, B., Gräber, R., Strauß, E. and Siebert, U. 2017. Coexistence of wolves and humans in a densely populated region (Lower Saxony, Germany). – Basic Appl. Ecol. 25: 1–14.

RStudio Team 2020. RStudio: integrated development for R. – RStudio, PBC.

Sanz-Pérez, A., Ordiz, A., Sand, H., Swenson, J. E., Wabakken, P., Wikenros, C., Zimmermann, B., Åkesson, M. and Milleret, C. 2018. No place like home? A test of the natal habitat-biased dispersal hypothesis in Scandinavian wolves. – R. Soc. Open Sci. 5: 181379.

Signer, J., Fieberg, J. and Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. – Ecol. Evol. 9: 880–890.

Silva, I., Fleming, C. H., Noonan, M. J., Alston, J., Folta, C., Fagan, W. F. and Calabrese, J. M. 2022. Autocorrelation-informed home range estimation: a review and practical guide. – Methods Ecol. Evol. 13: 534–544.

Spitz, D. 2019. migrateR: animal movement classification. – R package ver. 1.0.9, https://github.com/dbspitz/migrateR.

Spitz, D. B., Hebblewhite, M. and Stephenson, T. R. 2017. "MigrateR": extending model-driven methods for classifying and quantifying animal movement behavior. – Ecography 40: 788–799.

Szewczyk, M. et al. 2021. Genetic support for the current discrete conservation unit of the central European wolf population. – Wildl. Biol. 2021: wlb.00809.

Thurfjell, H., Ciuti, S. and Boyce, M. S. 2014. Applications of step-selection functions in ecology and conservation. – Mov. Ecol. 2: 1–12.

Torretta, E., Caviglia, L., Serafini, M. and Meriggi, A. 2018. Wolf predation on wild ungulates: how slope and habitat cover influence the localization of kill sites. – Curr. Zool. 64: 271–275.

Valente, A. M., Acevedo, P., Figueiredo, A. M., Fonseca, C. and Torres, R. T. 2020. Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. – Mamm. Rev. 50: 353–366.

Vorel, A., Kadlec, I., Toulec, T., Selimovic, A., Horníček, J., Vojtěch, O., Mokrý, J., Pavlačík, L., Arnold, W., Cornils, J., Kutal, M., Duľa, M., Žák, L. and Bartak, V. 2024. Data from: Home range and habitat selection of wolves recolonising central European human-dominated landscapes. – Dryad Digital Repository, https://doi.org/10.5061/dryad.cz8w9gjbt.

Wabakken, P., Sand, H., Kojola, I., Zimmermann, B., Arnemo, J. M., Pedersen, H. C. and Liberg, O. 2007. Multistage, long-range natal dispersal by a global positioning system-collared Scandinavian wolf. – J. Wildl. Manage. 71: 1631–1634.

Wabakken, P., Sand, H., Liberg, O. and Bjärvall, A. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian Peninsula, 1978–1998. – Can. J. Zool. 79: 710–725.

Wagner, C., Holzapfel, M., Kluth, G., Reinhardt, I. and Ansorge, H. 2012. Wolf (*Canis lupus*) feeding habits during the first eight years of its occurrence in Germany. – Mamm. Biol. 77: 196–203.

Walton, L. R., Cluff, H. D., Paquet, P. C. and Ramsay, M. A. 2001. Movement patterns of barren-ground wolves in the central Canadian Arctic. – J. Mammal. 82: 867–876.

Wickham, H. et al. 2019. Welcome to the Tidyverse. – J. Open Source Softw. 4: 1686.

WorldPop (www.worldpop.org - School of Geography and Environmental Science, University of Southampton, Department of Geography and Geosciences, University of Louisville, Departement de Geographie, Universite de Namur) and Center for International Earth Science Information Network (CIESIN), Columbia University. 2018. Global high resolution population denominators project - Funded by The Bill and Melinda Gates Foundation (OPP1134076). – https://doi.org/10.5258/SOTON/WP00674.

Zanaga, D., Van De Kerchove, R., Daems, D., De Keersmaecker, W., Brockmann, C., Kirches, G., Wevers, J., Cartus, O., Santoro, M., Fritz, S., Lesiv, M., Herold, M., Tsendbazar, N. E., Xu, P., Ramoino, F. and Arino, O. 2022. ESA WorldCover 10 m 2021 v200. – https://doi.org/10.5281/zenodo.7254221.

Zanni, M., Brogi, R., Merli, E. and Apollonio, M. 2023. The wolf and the city: insights on wolves conservation in the Anthropocene. – Anim. Conserv. 26: 766–780.

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01245 by Veterinärmedizinische Universität Wien, Wiley Online Library on [05/07/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License