



# First-year dispersal in white-tailed eagles *Haliaeetus albicilla*

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## Abstract

Dispersal is a key process affecting the dynamic and genetic structure of populations. To increase our knowledge on first-year dispersal in the white-tailed eagle (WTE), 35 nestlings in the Czech Republic, Hungary, and Austria were equipped with GPS/GSM loggers while on the nest between 2016 and 2019. Twenty-nine individuals surviving until March 31 were used to assess post-fledging areas, first-year dispersal distance and direction, temporary settlement areas, and habitat selection. The first flight from the nest was observed between May 19 and July 8. Start of dispersal from post-fledging areas occurred between July 1 and November 14. Post-fledging areas were significantly larger in males ( $p = 0.001$ , median 1236 km<sup>2</sup>,  $n = 15$ ) than females (median 139 km<sup>2</sup>,  $n = 12$ ). Maximal dispersal distance ranged from 93 to 433 km from the native nest (median = 187 km) and did not correlate with Simpson's Diversity Index computed for habitats in individual 100% minimum convex polygons (MCP). Median sizes of minimum convex polygons were 26,888 km<sup>2</sup> for 100% MCP and 13,376 km<sup>2</sup> for 95% MCP ( $n = 29$ ). Median sizes of kernel density estimates (KDE) were 3393 km<sup>2</sup> for 80% KDE and 1137 km<sup>2</sup> for 50% KDE. After start of dispersal, young WTEs returned to the proximity of the parental nest for night roosting sporadically. No sex-specific differences in dispersal distance were recorded. While young individuals from the three subpopulations are likely to occur in the same area during the first year of life, future nesting site identification will enable us to assess real gene flow and the connectivity level among them. As this study has illustrated, future conservation efforts to protect young WTEs will require cross-border cooperation.

**Keywords** Telemetry · Raptor · Home range · Compositional analysis · Habitat · TSA · PFA · Temporary settlement area · Post-fledging area · GPS · GSM

## Introduction

Dispersal behaviour is an important process shaping population structure of species through its effect on population size, dynamics, and genetics (Prugnolle and de Meeus 2002). An

understanding of dispersal rules, especially in long-lived species with delayed maturity, can markedly contribute to effective conservation of endangered species. The dispersal patterns of raptors over a large spatial scale (as with migration patterns) remained hidden to biologists until the development

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of appropriate individual marking methods. Use of conspicuous tags, such as coloured rings or wing tags, with a unique code has enabled researchers to concentrate on raptor dispersal at an individual level, covering subjects such as adult breeding dispersal and also juvenile dispersal (Whitfield et al. 2009a; Forero et al. 2002). From many perspectives, the development of animal-borne telemetry devices has revolutionised our ability to study animals in the wild (Cagnacci et al. 2010; Kays et al. 2015; Hooten et al. 2017). Radio-tracking methods have increased the efficiency of finding of the same individual in time and space, enabling us to collect large datasets for individuals. One drawback from such studies, however, was the fact that signals from radio-tracked birds of prey sometimes ‘disappeared’ from the study area due to the bird having an unexpectedly large action radius, especially in the case of non-nesters (Nygård et al. 2000; Penteriani et al. 2011). Current telemetry methods give us opportunity to obtain detailed information also on young individuals during the process of achieving independence from parents, including the most distant locations of their first-year dispersal. Technological improvements in telemetry, such as the development of GPS/GSM loggers, now provide volumes of data previously considered inconceivable (López-López 2016), and the current challenge facing biologists is how best to analyse the large amounts of data received from GPS/GSM loggers.

The classic concept of animal home ranges is based on minimum convex polygons (MCP) and kernel density estimates (KDE) computed from all the locations obtained for an individual; however, this may not be the most appropriate method to describe the spatio-temporal activities of juvenile, subadult, and non-breeding adult eagles. Initially, fledglings occur in a post-fledging area (PFA) that surrounds the nesting area of the parental pair, defined as the area used by the family group from the time the young fledge until they are no longer dependent on the adults for food (Tapia and Zuberogoitia 2018). This may be a sensitive period for induction of natal habitat preference (Davis and Stamps 2004). Later, young birds perform long-distance movements and occupy one or more temporary settlement areas (TSA; del Mar Delgado et al. 2009; Nemček et al. 2016; Morandini et al. 2020), also called dispersal areas (Cadahía et al. 2010) or staging areas (Mellone et al. 2011). These sites are used repeatedly by the individuals and are used for the longest period throughout the dispersal process (Cadahía et al. 2010). To date, however, there is no unified definition of how best to identify and delineate TSAs, though species-specific differences can be expected.

The white-tailed eagle (WTE; *Haliaeetus albicilla*) is a non-migratory species that, aside from some northern European and Asian populations (Helander and Stjernberg 2002), does not regularly overwinter outside of its breeding distribution range. As such, it is an ideal species for studying

the effects of resource availability (e.g. habitat, food, supply of free mates) on settlement behaviour in young individuals. In WTEs, natal dispersal, defined as the movement of wandering individuals from birthplace to first breeding location (Greenwood 1980; Ronce 2007; Penteriani and del Mar Delgado 2009), has a greater effect on gene flow and population demography than breeding dispersal (Whitfield et al. 2009b). WTEs usually breed for the first time at 5 years of age (Cramp and Simmons 1982), though earlier successful nestings (e.g. at 3 years) have also been recorded (Struwe-Juhl and Grünkorn 2007; Tihanyi et al. 2009; Škorpiková and Tunka 2013; Nygård and Mee 2017). Dispersal movements generally comprise three stages: (1) departure or emigration, (2) a vagrant stage, and (3) settling or immigration (Ronce 2007). Note, however, that the beginning of dispersal has been understood differently in different studies on WTEs (Nygård et al. 2000; Balotari-Chiebao et al. 2016; Tikkanen et al. 2018). The wandering phase can be relatively long in WTEs, as with other similar species with delayed sexual maturity. Though reproduction is presumed not to occur in the second and third calendar year of life in WTEs, Whitfield et al. (2009a) found a significant positive relationship between maximum juvenile dispersal distance in the first 2 years of life and natal dispersal distance, suggesting that first-year dispersal data could be sufficient to predict natal dispersal distance in young WTEs.

A number of previous studies have examined the genetic structure of WTEs from a range of European subpopulations to verify the origin of individuals recolonising Central Europe (e.g. Literák et al. 2007; Nemesházi et al. 2016). Nemesházi et al. (2016) recognised at least three genetic clusters in Central European countries: (1) a ‘northern cluster’ corresponding to genetic signatures for northern European WTEs from Finland and Lithuania; (2) a ‘central cluster’ mainly containing WTEs originating from Germany, Poland, and northern Austria; and (3) a ‘southern cluster’ unifying WTEs from the Pannonian Basin (e.g. from Hungary, Slovakia, Serbia) with north-eastern Austria. As individuals from all three clusters occur in the Czech Republic and Hungary, with individuals from two of the clusters in Austria (Nemesházi et al. 2016), these three countries may represent an interesting study area for further telemetry research aimed at WTE natal dispersal. Following the population bottleneck that persisted until the 1970s, WTEs began recolonising the Czech Republic in the 1980s, with breeding occurring in two core areas in the southwestern (South Bohemia) and southeastern parts (South Moravia) of the Czech Republic (Bělka and Horal 2009). By 2016, the population size had reached 116 pairs (Bělka 2017), and by 2019 it was estimated at ca 130–140 pairs (Bělka pers. comm.). Despite a large decline in numbers reported between the 1950s and 1970s, the species probably never became extinct in Hungary, and following a conservation programme launched in 1987, population numbers have increased

substantially (Horváth 2009), with as many as 360–380 territorial pairs estimated in 2017 (Szelényi in Demeter et al. 2017). In Austria, the WTE has gone extinct twice, the first time in the 19th century and again in the late 1950s (Probst and Peter 2009). In 1999, the species started to breed in Austria once again (Probst 2009), and by 2017, its population size had risen to 30 pairs (Probst and Pichler 2017), increasing to ca. 40 pairs in 2019 (Probst pers. comm.). At present, there is a general lack of data on levels of connectivity between these three subpopulations of the European metapopulation and on the dispersal of young WTEs from the natal nests. For example, it is not known whether a more homogenous environment will result in longer dispersal distances in WTEs and whether fledged individuals return for night roosting to the vicinity of the parental nest.

The main aim of this study was to answer a series of questions concerning the dispersal of young WTEs during their first year of life. These cover five main areas: (1) How large are PFAs, when exactly does dispersal begin, and how frequently does the individual return to the nest? (2) How far do fledglings disperse from the hatching site, which direction do they take (azimuth), and how large is their total action radius over one year? (3) Are there any sex-specific differences in dispersal distance, dispersal direction, or PFA size? (4) What habitats do individuals prefer and does habitat diversity affect maximal dispersal distance? (5) What areas are occupied by birds originating from different subpopulations?

## Material and methods

### Tagging of individuals

Between 2016 and 2019, a total of 35 WTE nestlings (7–8 weeks old) were tagged with a GPS/GSM/GPRS logger in nests in the Czech Republic, Hungary, and Austria (Table 1). GPS/GSM tags were fixed to the bird's back (as a backpack) using a harness consisting of two 6 mm Teflon ribbons encircling the body (one loop around the base of each wing, both loops joined in front of the breastbone). Between 2016 and 2017, 23 individuals were fitted with SKUA-H LF =

**Table 1** Number white-tailed eagle nestlings tagged with a GPS/GSM logger over the 4 years covered by this study

Year	Czech Republic	Hungary	Austria
2016	0	0	2
2017	14	6	1
2018	4	1	0
2019	5	2	0
Total	23	9	3

KITE-H LF Ecotone loggers (Poland), while 12 individuals were fitted with OT-E50B-3GC Ornitela loggers (Lithuania) between 2018 and 2019. All Ecotone loggers were set to collect one location each 3 h from midnight to 21 PM (UTC), while one location per hour was used from Ornitela loggers.

### Sex determination

Nestling tarsus thickness (cut-off point 14.15 mm) and weight (cut-off point 4300 g) were measured using a digital calliper and digital hanging scale, the measurements subsequently being used for sex identification based on the methods of Helander (1981) and Helander et al. (2007). Feather samples were also taken from Czech nestlings (stored in 96% ethanol) in order to confirm sex determination genetically, based on PCR using the primers CHD1-i16F and CHD1-i16R (Suh et al. 2011) and visualisation using horizontal agarose gel electrophoresis illuminated with a UV-transilluminator (Rymešová et al. 2020). DNA was first isolated using the Tissue Genomic DNA Mini Kit (Geneaid Biotech, Taiwan), following the manufacturer's protocol. Conditions for PCR were set as follows: (1) 2 min at 94°C; (2) 35 cycles: (a) 30 s at 94°C, (b) 30 s at 56°C, and (c) 80 s at 72°C; (3) 5 min at 72°C; and (4) 10°C. Sex was determined based upon the occurrence of CHD-genes (CHD-Z and CHD-W) after PCR reaction (PPP Master Mix (Top-Bio, CZ) 10 µL, PCR water 4 µL, primer CHD1-i16F 2 µL, primer CHD1-i16R 2 µL, DNA 2 µL). Molecular sex determination confirmed that all but one male nestling from Czech nests could be successfully sexed on the basis of weight and tarsus thickness measurement at the thinnest point alone. Two nestlings tagged in 2016 (BS0041, BS0042) were not measured or sampled for DNA, and their sex is unknown.

### GIS analysis and dispersal definitions

CSV files containing individual locations and sampling dates and times were downloaded onto a personalised provider's website and further analysed in ArcMap 10.1 with Spatial Analyst extension (ESRI, USA). The data were first checked for possible errors (e.g. points with longitude = 0 and latitude = 0 simultaneously), and these outliers were removed from the dataset. Night roosting sites were selected in a separate layer as a list of first locations from each day (close to 0:00 UTC). Trajectories from successive points were created and home range sizes calculated using the free extension ArcMET 10.1.1. and Home Range Tools for ArcGIS 10.1 (HRT) in the Projected Coordinate System (WGS 1984 UTM Zone 33 N). Home range areas were calculated from all obtained locations (including night locations) from the tagging day to March 31 of the next calendar year (1-year-old birds in their second calendar year of life; 2CY) for 29 individuals (in six cases to an earlier date; Table 2). Occupied areas were defined

**Table 2** List of white-tailed eagle nestlings tracked by satellite telemetry, with number of locations obtained, number of tracking days, mean number of locations per day, date of first flight, and start of dispersal date (individuals not surviving until March 31 are marked in italic; \* = proven

death of an individual, otherwise loss of signal before March 31). Sex: M males, F females, - = undetermined; country/location of native nest: A Austria, CZ Czech Republic, HU Hungary

Tagging day	End of data collection	Ring	Sex	Country	No. of locations	No. of days tracked	Locations per day	First flight	Dispersal date
21.05.2016	31.03.2017	BS0041	-	A	2037	314	6.5	23.06.	01.07.
21.05.2016	31.03.2017	BS0042	-	A	2432	314	7.7	04.06.	16.10.
05.05.2017	31.03.2018	LX493	M	CZ	1689	330	5.1	28.05.	18.08.
05.05.2017	31.03.2018	LX494	F	CZ	1678	330	5.1	19.05.	20.08.
05.05.2017	31.03.2018	LX495	M	CZ	1922	330	5.8	02.06.	01.10.
05.05.2017	31.03.2018	LX496	M	CZ	2026	330	6.1	21.05.	14.09.
16.05.2017	31.03.2018	LX472	F	CZ	2101	319	6.6	10.06.	24.08.
16.05.2017	31.03.2018	LX473	F	CZ	1935	319	6.1	02.06.	18.08.
16.05.2017	31.03.2018	LX475	M	CZ	1959	319	6.1	22.06.	24.08.
17.05.2017	31.03.2018	H0581	F	HU	1789	318	5.6	28.06.	14.09.
17.05.2017	31.03.2018	H0582	M	HU	1938	318	6.1	26.05.	08.09.
17.05.2017	31.03.2018	H0584	F	HU	2191	318	6.9	19.05.	05.08.
21.05.2017	31.03.2018	LX460	M	CZ	1689	314	5.4	16.06.	02.10.
21.05.2017	31.03.2018	LX462	F	CZ	1974	314	6.3	20.06.	05.09.
26.05.2017	31.03.2018	H0585	F	HU	2018	309	6.5	02.06.	14.11.
28.05.2017	31.03.2018	LX305	F	CZ	1903	307	6.2	01.07.	06.09.
28.05.2017	31.03.2018	LX465	M	CZ	1877	307	6.1	22.06.	14.08.
28.05.2017	31.03.2018	LX463	M	CZ	1488	307	4.8	31.05.	30.08.
31.05.2017	31.03.2018	no ring	F	HU	1694	304	5.6	02.06.	28.09.
18.05.2018	31.03.2019	H0624	F	HU	4838	316	15.3	26.05.	11.09.
24.05.2018	31.03.2019	LX628	M	CZ	4484	311	14.4	21.06.	17.08.
24.05.2018	31.03.2019	LX629	M	CZ	4155	311	13.4	26.06.	15.08.
24.05.2018	31.03.2019	LX621	F	CZ	4887	311	15.7	30.05.	27.08.
24.05.2018	31.03.2019	LX622	F	CZ	5333	311	17.1	22.06.	16.09.
16.05.2019	31.03.2020	LX744	F	CZ	5579	320	17.4	05.06.	16.09.
16.05.2019	31.03.2020	LX742	M	CZ	5879	320	18.4	14.06.	23.08.
28.05.2019	31.03.2020	LX852	M	CZ	5330	308	17.3	27.06.	19.09.
28.05.2019	31.03.2020	LX853	M	CZ	5327	308	17.3	25.06.	15.09.
17.05.2019	31.03.2020	H0349	M	HU	5527	319	17.3	03.06.	24.07.
<i>01.06.2017</i>	<i>27.09.2017*</i>	<i>BS0044</i>	<i>M</i>	<i>A</i>	<i>751</i>	<i>118</i>	<i>6.4</i>	<i>08.07.</i>	<i>30.08.</i>
<i>16.05.2017</i>	<i>08.02.2018*</i>	<i>LX471</i>	<i>F</i>	<i>CZ</i>	<i>1578</i>	<i>268</i>	<i>5.9</i>	<i>23.05.</i>	<i>22.08.</i>
<i>16.05.2017</i>	<i>04.01.2018</i>	<i>LX193</i>	<i>F</i>	<i>CZ</i>	<i>1426</i>	<i>233</i>	<i>6.1</i>	<i>24.06.</i>	<i>26.08.</i>
<i>17.05.2017</i>	<i>28.11.2017</i>	<i>H0583</i>	<i>M</i>	<i>HU</i>	<i>1382</i>	<i>195</i>	<i>7.1</i>	<i>17.06.</i>	<i>31.08.</i>
<i>16.05.2019</i>	<i>23.03.2020</i>	<i>LX743</i>	<i>F</i>	<i>CZ</i>	<i>5448</i>	<i>312</i>	<i>17.5</i>	<i>19.05.</i>	<i>01.09.</i>
<i>24.05.2019</i>	<i>07.12.2019</i>	<i>H0588</i>	<i>F</i>	<i>HU</i>	<i>3735</i>	<i>197</i>	<i>19.0</i>	<i>26.05.</i>	<i>05.08.</i>

from several points of view: (1) overall area used, defined as *100% minimum convex polygon (MCP)*; (2) overall area used without the most extreme exploratory flights (*95% MCP*); (3) core area of occurrence *sensu lato (80% Kernel Density Estimate = KDE)*; (4) core area of occurrence *sensu stricto (50% KDE)*; and (5) *temporary settlement areas (TSAs)*, representing the most 'important' or 'preferred' areas with repeated occurrence of an individual. Each MCP was created with the floating mean method. The fixed kernel method with

a reference bandwidth was used for KDE creation. TSAs were defined for each individual on the basis of a subsample of points selected according to the following criteria. First, we only worked with the layer that contained the earliest night roosting location for every day (close to 0:00 UTC). We then looked for clusters of points where night locations were maximally 10 km distant from each other (using the ArcGIS Buffer tool to create borders with a 5 km radius from each point and analysing any overlaps) and, simultaneously, where

individuals occurred on at least ten nights. After identifying these point clusters, all daily locations with the same dates were added to the selected night roosting location, and the 95% MCP of these points was taken to represent a TSA. The first TSA containing the native nest was termed the *post-fledging area* (PFA).

*Maximal dispersal distance* was measured as a line between the most distant location and the native nest. *Dispersal direction* was measured in three ways. First, the azimuth to north between the natal nest and the most distant location (in degrees) was measured using the ArcGIS COGO tool. Second, the azimuth was measured between the natal nest and the centroid of the 50% KDE polygon (using the ArcGIS Feature to Point tool). Third, the azimuth was measured between the natal nest and the centroid of the 100% MCP from March locations. Similarly, distance between this March centroid and natal nest was measured to assess final occurrence of each individual. We computed the ratio of 100% MCP area from March locations to overall area used as an individual measure of final sedentarity at the end of observation. The *date of first flight* from the nest was determined as the first day when distance of the individual from the nest exceeded 200 m. Dispersal date was based on the definition of Balotari-Chiebao et al. (2016). When an individual occurred more than 5 km from the nest on at least eleven consecutive days, the first day of reaching of this distance was regarded as the *beginning of dispersal* (i.e. *dispersal date*) from the parental nest. This date simultaneously corresponded to the date, following which there was no subsequent return to the nest (closer than 200 m) in most individuals (77%). March 31 was used as the universal limit representing the end of the first year of life in all individuals studied, based on the common nesting cycle of WTE in the Czech Republic where eggs are most often laid during February and March (Kloubec et al. 2015). The last dates of occurrence closer than 200 m and closer than 5 km from the nest were recorded too.

### Habitat classification and analysis

Habitat preferences were analysed through compositional analysis (Aebischer et al. 1993) using the AdehabitatHS package in R 3.6.2 (R Core Team 2019), based on a dataset comprising all 35 individuals. The percentage of different habitat areas (measured in km<sup>2</sup>) inside individual 100% MCPs represented the *available habitat*, and the percentage of individual locations in the habitats of 100% MCPs was regarded as the *used habitat*. Unique values were obtained for each individual studied. Preliminary classification of habitats in individual 100% MCPs and in individual locations was based on the 2018 CORINE land cover layer (<https://land.copernicus.eu/pan-european/corine-land-cover>). Thirty-three CORINE

habitat categories were found in all 100% MCPs (categories no. 111, 112, 121-124, 131-133, 141, 142, 211, 212, 213, 221, 222, 231, 242, 243, 311-313, 321, 322, 324, 331-334, 411, 412, 511, 512; Bossard et al. 2000; Büttner and Kosztra 2017). Next, we reclassified the original categories into eight groups in order to obtain the most frequent habitats across all individuals (Table 3). Five habitat categories were not included in the compositional analysis (322, moors and heathland; 331, beaches, dunes, and sand plains; 332, bare rocks; 333, sparsely vegetated areas; 334, burnt areas) due to their low representation in MCPs and locations (medians equal to zero). Finally, compositional analysis was also undertaken on datasets of males and females separately ( $n = 33$ : 17 females, 16 males, sex undetermined in two cases; later reclassified as 27 individuals surviving the whole year: 13 females, 14 males).

### Statistical analysis

As a first step, all datasets were checked for normal distribution of values with Shapiro-Wilk tests in Unistat 6.5. As normal distribution was not confirmed (variables were maximal dispersal distance, number of locations (overall and per day), number of tracking days, areas of 50% and 80% KDEs and 100% and 95% MCPs), non-parametric statistics were used for further dataset analysis. We computed basic descriptive statistics (median, min, max, standard error) for 29 individuals surviving until March 31. Dispersal date and date of first flight were computed for the whole dataset ( $n = 35$  individuals) as both events occurred before eventual signal loss. The Mann-Whitney  $U$  test was used to compare home range sizes, dispersal dates, maximal dispersal distances, and azimuths between sexes, while the Spearman correlation was used to test the relationship between maximal dispersal distance and 100% MCP, 95% MCP, 80% KDE, 50% KDE, and Simpson's Diversity Index. The 'compana' function in R was used for testing random or non-random utilisation of habitats by WTEs, based on the following settings: test = c('randomisation'), rnv = 0.01, nrep = 500, and alpha = 0.05. Simpson's Diversity Index (1-D) was computed for each individual on the basis of available habitat percentage (Index value ranges between 0 and 1; the higher the value, the greater the habitat diversity in each 100% MCP).

## Results

### Beginning of dispersal and PFA size

After excluding six individuals with signal loss before March 31, we obtained 1488–5879 locations per individual (median = 2026 locations) over 304–330 tracking days (median = 314 days; Table 2). Individual frequency of localisation ranged from five to 18 locations per day, with a

**Table 3** Habitat types used for compositional analysis, created on the basis of original CORINE land use categories

Habitat	CORINE codes	CORINE categories
Urban areas	111, 112, 121, 122, 123, 124, 131, 132, 133, 141, 142	Continuous urban fabric, discontinuous urban fabric, industrial or commercial units, road and rail networks and associated land, port areas, airports, mineral extraction sites, dump sites, construction sites, green urban areas, sport and leisure facilities
Fields	211, 212, 213	Non-irrigated arable land, permanently irrigated land, rice fields
Vineyards and orchards	221, 222	Vineyards, fruit trees, and berry plantations
Meadows	231, 321	Pastures, natural grassland
Gardens and small fields	242, 243	Complex cultivation patterns, land principally occupied by agriculture, with significant areas of natural vegetation
Forests	311, 312, 313	Broad-leaved forest, coniferous forest, mixed forest
Shrubs	324	Transitional woodland/shrub
Water areas	411, 412, 511, 512	Inland marshes, peatbogs, water courses, water bodies

median of seven locations per day. First flight from the nest was performed between May 19 and July 8, with a median date of June 5 ( $n = 35$  individuals). Dispersal began between July 1 and November 14, with a median date of August 30 (Table 2). No sex-specific differences were found in both these variables (Mann-Whitney  $U$  test:  $p > 0.05$ ). The length of the period between first flight from the nest and the beginning of dispersal was 8–165 days (median 82 days). After the beginning of dispersal, young WTEs only sporadically returned to the proximity of the parental nest for night roosting. This behaviour was only observed in eight of 35 tracked individuals and most of them (six individuals) spent only one night inside the 200 m radius from the native nest (twice in August, twice in September, once in December, once in February). Only one female and one male were recorded for two nights inside this distance, the female on two consecutive nights in October, and the male in October and March. Post-fledging area size was 0.4–2963 km<sup>2</sup>, with a median of 383 km<sup>2</sup> ( $n = 29$  individuals; Table 4). There was a significant difference in post-fledging area size between sexes (Mann-Whitney  $U$  test:  $U = 26$ ,  $p = 0.001$ ;  $n = 27$  individuals), being significantly larger in males (median 1151 km<sup>2</sup>;  $n = 14$ ) than females (median 149 km<sup>2</sup>;  $n = 13$ ).

### Dispersal distance and direction and action radius

Maximal dispersal distance ranged from 93 to 433 km from the native nest, with a median of 187 km ( $n = 29$  individuals; Fig. 1). Individuals occurred in the most distant point between July 6 and March 31 (median January 30, Table 4). Azimuth directions between the native nest and the furthest location appeared to be random (Table 4 - Azimuth 1). The highest number of individuals moved to the south (6 of 29 individuals, 20.7%), followed by the southwest (5 individuals, 17.2%) or northwest (5

individuals, 17.2%) for the furthest exploratory flights. Other directions were also recorded, though less frequently (Fig. 1; 4 x southeast, 4 x west, 3 x east, 1 x north, 1 x northeast). Though these azimuths appear to represent random exploratory flight directions rather than a shift in the core area of all locations obtained, a final summarisation for azimuths between the native nest and the centroid of the 50% KDE provided very similar results (Table 4 - Azimuth 2; 7 x south, 6 x west, 5 x northwest, 4 x southwest, 3 x east, 3 x southeast, 1 x north).

Overall area used (100% MCP) during the first year of life ranged from 2777 to 111249 km<sup>2</sup> (median = 26888 km<sup>2</sup>,  $n = 29$ ; Table 4). The median of the 95% MCP (100% MCP excluding the most extreme exploratory flights) was 13,376 km<sup>2</sup> (min-max: 2178–103,497 km<sup>2</sup>), while that of the core area *sensu lato* (80% KDE) was 3393 km<sup>2</sup> (min-max: 447–47,802 km<sup>2</sup>) and that of the core area *sensu stricto* (50% KDE) was 1137 km<sup>2</sup> (min-max: 138–15,825 km<sup>2</sup>). There was no significant difference between males and females for maximal dispersal distance, azimuth to north and MCP or KDE size ( $n = 27$ , i.e. 29 minus two individuals of unknown sex, Mann-Whitney  $U$  test:  $p > 0.05$ ). Excluding PFA, each individual occurred in 0–7 TSAs (median = 2 TSAs; Table 4) with mean sizes from 97 to 2277 km<sup>2</sup>, with a median of 514 km<sup>2</sup>.

### Habitat selection

Compositional analysis with 35 individuals and eight habitat types confirmed significantly non-random utilisation of habitats by young WTEs during their first year of life (Lambda = 0.030;  $p < 0.002$ ). Water areas were identified as the most preferred habitat type, followed by forests and shrubs and meadows (Table 5). While there was a non-significant preference

**Table 4** Dispersal characteristics of 35 young white-tailed eagles tracked during the first year of life (individuals with a lost signal or that died before March 31 are marked in italic). *Max. dist* maximal dispersal distance from the native nest (km) *Max. dist. date* date of the most distant location from the native nest *MCP / KDE* size of minimum convex polygon / kernel density estimate computed from given % of locations

(km<sup>2</sup>) *No. of TSAs* number of individual temporary settlement areas *Mean TSA area* mean size computed from all TSAs (km<sup>2</sup>) *PFA area* post-fledging area size (km<sup>2</sup>) *Azimuth 1* azimuth to North between the most distant location and the native nest (in degrees) *Azimuth 2* azimuth to North between the centroid of KDE50 polygon and the native nest)

Ring	Max dist.	Max dist. date	MCP100	MCP95	KDE80	KDE50	No. of TSAs	Mean TSA area	PFA area	Azimuth 1	Azimuth 2
BS0041	346	06.07.	106720	102980	47802	15825	7	170	254	94	8
BS0042	233	28.10.	27226	2797	1137	357	2	507	318	120	84
LX493	179	29.03.	25622	13376	2196	865	2	134	332	70	311
LX494	185	25.03.	40159	12775	1537	565	1	132	269	315	312
LX495	160	30.01.	20028	4503	911	295	1	1318	865	126	206
LX496	163	06.03.	17177	14337	5142	1723	2	2277	1316	150	168
LX472	239	29.12.	20836	18842	6695	2630	2	276	26	111	103
LX473	347	25.02.	85561	55003	25500	8747	4	300	18	270	299
LX475	123	18.08.	15014	2980	963	318	0	-	1963	184	315
H0581	107	31.08.	15962	2178	754	264	1	1737	1238	39	255
H0582	176	30.12.	12359	10719	5437	1739	3	419	560	236	227
H0584	111	24.12.	14645	14104	5877	2304	3	1029	1294	215	162
LX460	433	30.03.	70533	24067	6961	2143	1	735	2383	301	264
LX462	204	13.10.	59991	43856	6572	2148	3	663	61	226	258
H0585	93	31.03.	2777	2205	447	138	2	471	149	183	332
LX305	110	21.01.	9494	6247	2327	947	1	1263	383	120	120
LX465	126	28.02.	12829	2213	812	253	1	947	5	236	189
LX463	373	21.03.	37419	5733	3846	1288	1	846	2645	249	79
no ring	324	23.11.	63507	59177	23322	6378	3	330	128	173	182
H0624	193	24.03.	24488	21240	7956	2963	3	521	0.4	170	182
LX628	293	14.08.	44779	12524	2576	1001	3	442	426	305	182
LX629	187	30.03.	39135	24635	3753	1137	2	2120	2963	298	186
LX621	366	31.03.	61681	40489	4307	1594	1	2208	357	173	138
LX622	214	21.03.	41495	19036	3393	1375	1	456	14	283	275
LX744	113	17.12.	17457	16945	2094	625	4	330	150	173	155
LX742	159	15.02.	35115	3969	852	284	1	418	627	267	286
LX852	123	11.03.	10282	3077	1012	299	1	791	2289	3	269
LX853	216	12.09.	26888	9474	1150	393	1	97	1537	299	216
H0349	339	24.12.	111249	103497	32427	10648	5	1325	986	219	222
<i>BS0044</i>	<i>236</i>	<i>31.08.</i>	<i>17421</i>	<i>3065</i>	<i>1315</i>	<i>469</i>	<i>0</i>	<i>-</i>	<i>331</i>	<i>340</i>	<i>183</i>
<i>LX471</i>	<i>249</i>	<i>30.08.</i>	<i>28457</i>	<i>23297</i>	<i>13098</i>	<i>5408</i>	<i>1</i>	<i>108</i>	<i>415</i>	<i>282</i>	<i>286</i>
<i>LX193</i>	<i>183</i>	<i>26.09.</i>	<i>16621</i>	<i>12279</i>	<i>3788</i>	<i>1216</i>	<i>2</i>	<i>676</i>	<i>1648</i>	<i>281</i>	<i>272</i>
<i>H0583</i>	<i>90</i>	<i>22.09.</i>	<i>8284</i>	<i>4497</i>	<i>1190</i>	<i>410</i>	<i>0</i>	<i>-</i>	<i>2886</i>	<i>228</i>	<i>121</i>
<i>LX743</i>	<i>413</i>	<i>05.09.</i>	<i>34713</i>	<i>33310</i>	<i>15458</i>	<i>6554</i>	<i>1</i>	<i>2070</i>	<i>0.2</i>	<i>349</i>	<i>2</i>
<i>H0588</i>	<i>327</i>	<i>14.10.</i>	<i>62852</i>	<i>60807</i>	<i>20875</i>	<i>7627</i>	<i>3</i>	<i>359</i>	<i>13</i>	<i>97</i>	<i>85</i>

for forests over shrubs ( $p > 0.05$ ), differences in preference or avoidance in all other habitats were significant ( $p < 0.05$ ). Sex-specific compositional analysis showed no difference in the final rank of selected habitats (Table 5). Simpson's Diversity Index ranged from 0.46 to 0.75 (median 0.68), with no correlation observed with maximal dispersal distance ( $r_S = 0.21$ ;  $p > 0.05$ ).

### Final occurrence and connectivity between subpopulations

The last occurrence of individuals closer than 200 m from the native nest was observed between July 1 (of the first calendar year of life: 1CY) and March 5 of the second calendar year of life (2CY; median September 5; Table 6). The last occurrence

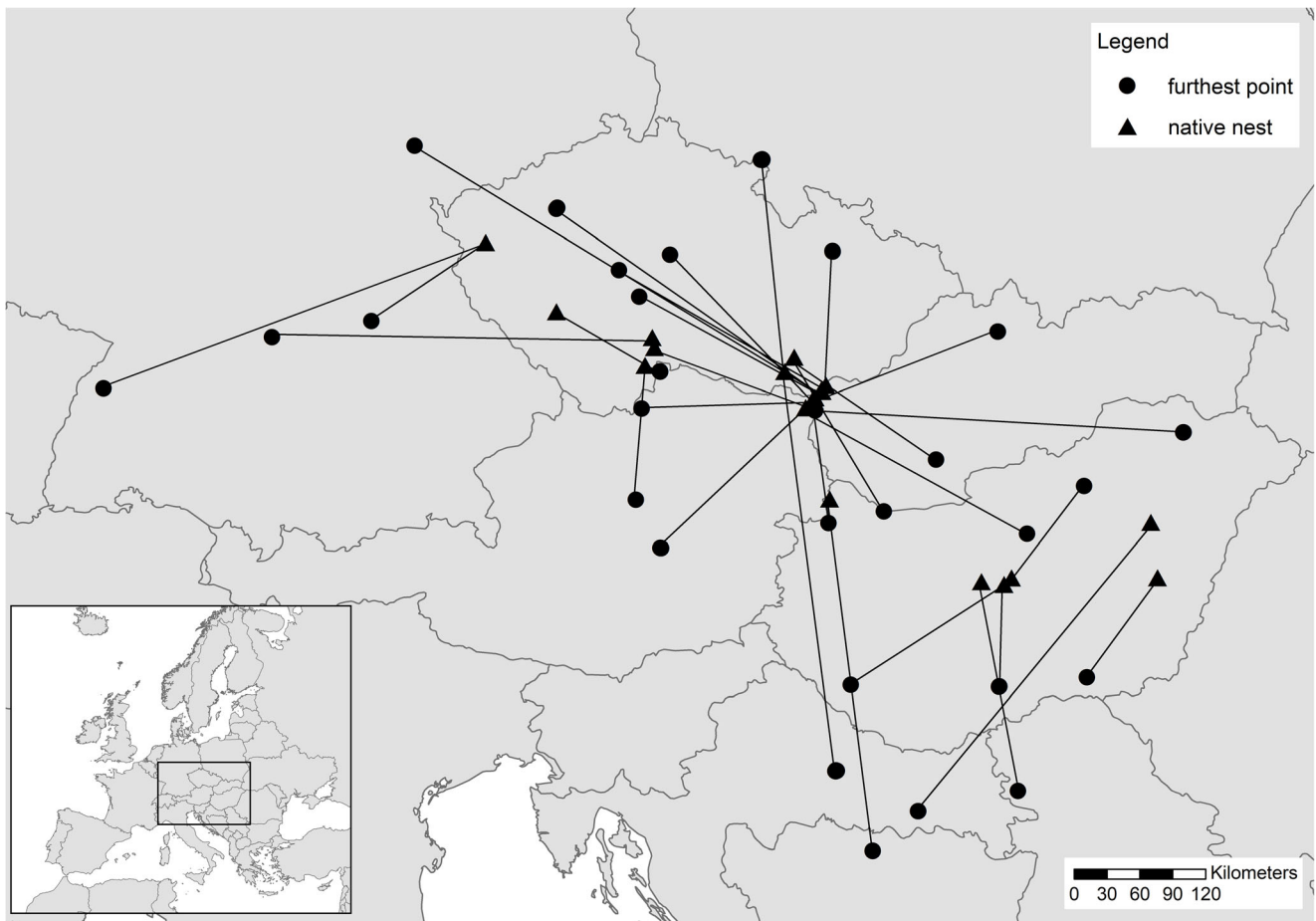


Fig. 1 Furthest locations from the nest of 29 white-tailed eagles surviving until March 31

**Table 5** Percentage of locations (habitats used) and percentage of habitat area sizes (available habitats) in 100% minimum convex polygons and final rank of habitat preference. Data are stated for all individuals ( $n = 35$ ) and for males and females surviving until March 31 (13 females, 14 males). The final rank of preferences was the same for all groups (most preferred habitat = 7; most avoided habitat = 0; CA compositional analysis; habitats: *WAT* water areas, *FOR* forests, *SHR* shrubs, *MEA* meadows, *GAR* gardens and small fields, *FIE* fields, *VIN* vineyards and orchards, *URB* urban areas)

Habitats (%)			WAT	FOR	SHR	MEA	GAR	FIE	VIN	URB
Available	All	Median	1.51	28.34	1.37	7.49	6.9	47.8	1.69	7.54
		Minimum	0.4	3.47	0.68	1.52	1.72	22.08	0.08	3.54
		Maximum	6.53	43.17	5.48	20.41	14.71	74.9	4.97	10.74
Used	All	Median	7.93	68.02	3.46	3.4	2.65	11.19	0.08	0.07
		Minimum	0.8	12.5	0.19	0.27	0.05	0.63	0.01	0.01
		Maximum	23.63	80.71	34.71	70.12	7.28	58.5	0.78	0.59
Available	Females	Median	2.32	28.38	1.41	7.86	6.98	45.19	1.91	5.58
		Minimum	0.79	3.47	0.68	2.15	2.39	29.22	0.16	3.54
		Maximum	6.53	37.62	5.48	20.41	11.26	71.05	4.97	10.74
Available	Males	Median	1.31	27.89	1.17	4.43	6.73	48.76	1.62	7.68
		Minimum	0.40	17.57	0.86	1.52	1.72	27.56	0.09	4.34
		Maximum	2.32	41.52	4.06	17.72	14.71	56.21	3.18	10.47
Used	Females	Median	9.04	71.11	3.81	3.15	1.56	7.66	0.05	0.05
		Minimum	3.52	12.50	0.19	0.91	0.05	1.80	0.01	0.01
		Maximum	18.81	79.07	34.71	70.12	6.90	58.50	0.10	0.21
Used	Males	Median	7.30	67.28	3.66	2.76	3.55	14.49	0.16	0.22
		Minimum	3.14	26.66	0.47	1.04	0.78	3.85	0.01	0.01
		Maximum	23.63	77.48	32.45	26.36	7.16	21.60	0.54	0.59
Rank of preference	CA results		7	6	5	4	3	2	1	0



**Table 6** Final occurrence characteristics of tagged white-tailed eagles based on all March locations. (Individuals not surviving until March 31 are marked in italic, and most their values could not be computed). *March centroid direction* azimuth to North between the centroid of March MCP100 and the native nest, *March centroid distance* distance between the centroid of March MCP100 and the native nest, *March MCP100 / total MCP100* individual proportion of March MCP100 out of total MCP100 computed from all obtained locations, *March MCP100 size* of the 100% minimum convex polygon computed from March locations, *Last return < 200 m / < 5 km* date of the last occurrence closer than 200 m / 5 km from the native nest

Ring	March centroid direction (°)	March centroid distance (km)	March MCP / total MCP100 (%)	March MCP100 (km <sup>2</sup> )	Last return < 200m	Last return < 5km
BS0041	142	72	18.7	19985	01.07.	31.03.
BS0042	304	36	16.0	4354	01.12.	11.03.
LX493	76	67	82.0	21016	06.07.	24.03.
LX494	306	85	66.2	26593	05.07.	05.03.
LX495	124	23	14.2	2854	05.03.	07.03.
LX496	155	61	22.1	3799	28.09.	10.03.
LX472	139	15	68.2	14209	21.07.	22.09.
LX473	292	179	2.4	2024	17.08.	18.08.
LX475	340	10	5.1	760	24.08.	31.03.
H0581	358	19	47.0	7505	12.10.	11.03.
H0582	0	0	7.9	976	07.02.	30.03.
H0584	108	29	16.1	2362	17.07.	31.03.
LX460	266	89	88.1	62128	01.10.	02.10.
LX462	132	47	19.2	11548	05.09.	05.09.
H0585	185	66	28.2	782	31.10.	15.02.
LX305	115	82	5.1	482	06.09.	06.09.
LX465	208	30	45.8	5872	14.08.	14.08.
LX463	241	179	83.4	31225	13.08.	05.03.
no ring	155	166	42.2	26831	27.09.	28.09.
H0624	180	116	30.3	7424	11.09.	11.09.
LX628	173	63	9.1	4074	16.08.	10.11.
LX629	301	100	49.7	19464	15.08.	05.02.
LX621	167	178	35.6	21964	27.08.	08.03.
LX622	280	157	6.6	2745	05.09.	15.09.
LX744	323	39	23.9	4169	02.09.	24.03.
LX742	104	49	59.3	20818	10.09.	28.03.
LX852	349	39	64.4	6619	18.09.	13.03.
LX853	284	59	60.3	16218	10.09.	23.03.
H0349	127	109	30.1	33513	23.08.	31.03.
<i>BS0044</i>	-	-	-	-	<i>10.07.</i>	<i>13.09.</i>
<i>LX471</i>	-	-	-	-	<i>07.08.</i>	<i>22.08.</i>
<i>LX193</i>	-	-	-	-	<i>10.08.</i>	<i>12.12.</i>
<i>H0583</i>	-	-	-	-	<i>17.07.</i>	<i>10.10.</i>
<i>LX743</i>	-	-	-	-	<i>31.08.</i>	<i>31.08.</i>
<i>H0588</i>	-	-	-	-	<i>24.06.</i>	<i>05.08.</i>

closer than 5 km from the native nest was between August 14 (1CY) and March 31 (2CY; median March 7). Concerning the level of sedentarity at the end of observation, 100% MCP computed from March locations ranged from 482 to 62128 km<sup>2</sup> (median 7424 km<sup>2</sup>), representing 2.4–88.1% of the overall area used (median 30.1%). Distance between the native nest and the centroid of March 100% MCP ranged from 0 to 179 km (median 63 km).

We recorded high connectivity between subpopulations of 1-year old WTEs from the Czech Republic, Austria, and Hungary (Fig. 2), although we do not know their future nest sites yet. Austrian WTEs were also recorded in Slovakia and Poland during their first year of life (Fig. 2b), while young WTEs from Czech nests were also recorded in Slovakia, Poland, and Germany (Fig. 2c). In addition to Austria, the Czech Republic, and Slovakia, Hungarian birds were also tracked in Croatia, Serbia, Romania, and Bosnia and Herzegovina (Fig. 2d).

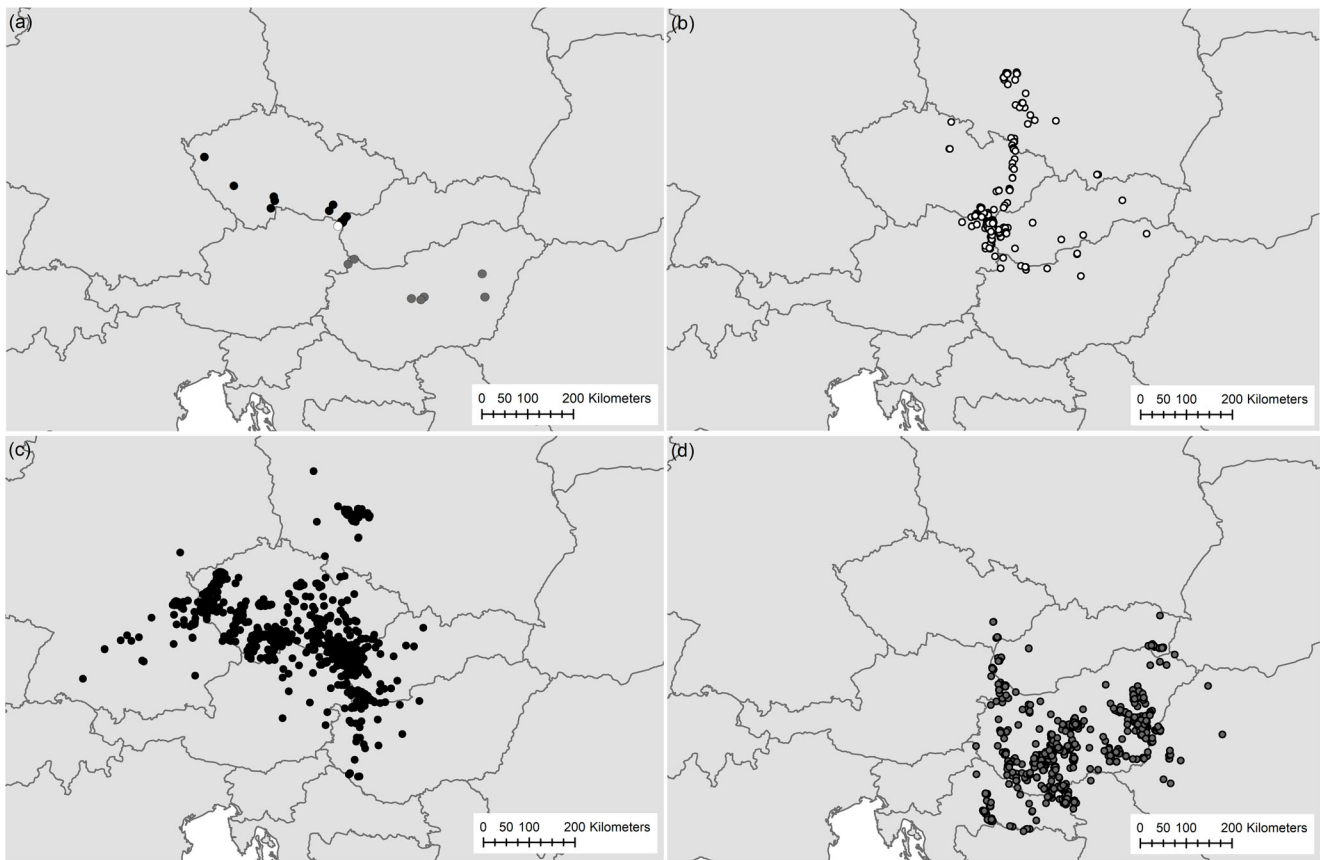
## Discussion

### Sex-specific size of PFA

As far as we know, this is the first study revealing sex-specific PFA sizes in WTEs. From a parental point of view, providing longer post-fledging periods increases offspring survival and thereby parental fitness (López-Idiáquez et al. 2018). In this study, however, larger post-fledging areas in males could not be explained by different timing of dispersal from the natal nest site as no sex-specific differences in dispersal date were found. Reversed sexual size dimorphism is typical for most birds of prey, including WTEs. Thus, we believe that smaller males may be competitively forced to displace by their larger female siblings or conspecifics. A further explanation could be connected with different foraging strategies in comparison with females. Males usually catch smaller and more agile prey, which may require prolonged gathering of more prey items over a larger area compared to females in order to cover their daily energetic costs. We also cannot exclude an active role of parents in the differing feeding efforts of different sexed siblings.

### No sex-specific dispersal

In most birds, natal dispersal distance is greater for females than males (Clarke et al. 1997; Kingma et al. 2017; Végvári et al. 2018). This sex-biased dispersal is usually explained by the ‘inbreeding avoidance’ or ‘resource-holding potential’ hypotheses (Greenwood 1980; Kingma et al. 2017).



**Fig. 2** Native nests of the 35 white-tailed eagle nestlings tagged in this study (a) and night roosting locations of individuals originating from Austria (b, white points), the Czech Republic (c, black points), and Hungary (d, grey points). One night location per day is shown for each individual

Surprisingly, maximal dispersal distance of WTE females and males did not differ in this study. In raptors (Accipitriformes), both female-biased (e.g. Eurasian sparrowhawk *Accipiter nisus*) and male-biased (e.g. northern goshawk *Accipiter gentilis*) natal dispersals have previously been described; however, there have also been previous cases where no effect of sex has been observed on natal dispersal, e.g. hen harrier *Circus cyaneus* (Clarke et al. 1997). No significant sex-specific differences in maximal dispersal distance have also been recorded in the Spanish Imperial Eagle *Aquila adalberti* (Ferrer 1993).

It is possible that a longer period or more detailed time measurements may be necessary to assess the role of sex in dispersal in WTEs. Whitfield et al. (2009a, 2009b), who studied WTE juvenile dispersal (up to age 48 months) and natal dispersal using coloured rings and patagium wing tags rather than telemetry, recorded significantly shorter natal dispersal distances in males than females in a reintroduced population of WTE in Scotland (Whitfield et al. 2009b) when measuring the distance between release site and the first breeding site of wing-tagged individuals. Whitfield et al. (2009a) stated that males initially dispersed farther than females in the first year

of life, but that females occurred farther from the natal site in their second year. As breeding age approached, males were found closer to the natal site than females (Whitfield et al. 2009a). In a radio telemetry study, Nygård et al. (2000) observed females farther away from their natal site than males in winter. We cannot confirm these sex-specific findings on the basis of our dataset using molecular sexing. Maximal dispersal distances, used as a measure of dispersal in this study, were computed until March 31 of the second calendar year of life, and these need not correspond to the future nesting site, though Whitfield et al. (2009a) found a significant positive relationship between maximum juvenile dispersal distance in the first 2 years of life and natal dispersal distance. A longer tracking period than that described in this study may yet confirm their observations. According to Whitfield et al. (2009a), maximum juvenile dispersal distance was not affected by individual fledging date, body size, or native brood size, and we also observed no effect of fledging date on dispersal distance in this study. Similarly, dispersal distance in the Spanish Imperial Eagle was also not related to the date of departure from the natal population (Ferrer 1993).

## Timing of dispersal

With improvements in molecular biology methods (Nemesházi et al. 2018; Rymešová et al. 2020) and animal tracking technologies, the importance of non-nesting WTEs (juvenile, subadult, and non-nesting adults) for intraspecific interactions and the dynamics of breeding population has been reassessed (Penteriani and del Mar Delgado 2009). Though dispersal is an essential process in population biology, with three natal dispersal phases usually recognised (emigration, transfer, and immigration), the beginning of the emigration phase has been defined differently by different authors (e.g. Cadahía et al. 2008; Soutullo et al. 2006a). A post hoc examination of locations is most frequently used for determining the end of the post-fledging period, which represents the first limit for the emigration phase (Cadahía et al. 2008). Due to different definitions and methods used by authors, or poor descriptions of the methods used, it is often not possible to compare the results of previously published studies on the same species. Similar inconsistencies also arise in definitions of home range size or TSAs. In this study, we used the same definition for the beginning of dispersal as Balotari-Chiebao et al. (2016), who, along with Tikkanen et al. (2018), stated that departure of young WTEs from their natal areas was indicated when individuals spent more than 10 consecutive days farther than 5 km from their natal nest. Similarly, Nygård et al. (2000, 2003) radio tracked 41 young WTEs in Norway and defined the beginning of dispersal as occurring with locations more than 4 km away from the nest with no subsequent return that season. Nygård et al. (2003) recorded permanent departure from the natal area on a median date of 1 October for males (estimated age 161 days) and 22 October for females (age 181 days), with non-significant differences between the sexes. Similarly, in Poland, Mirski et al. (2017) recorded young WTEs as finally leaving the parental territory at the end of October. Another contribution mentions September 29 as average date of leaving (July 27–January 20; Mirski 2017). We recorded a lower median for the beginning of dispersal (August 30), indicating an earlier departure of young WTEs from the PFA (July 1–November 14).

## WTE dispersal distance in the first year

In this study, the median maximal dispersal distance was 187 km (93–433 km). Whitfield et al. (2009a) recorded a maximum juvenile dispersal distance ranging from 18 to 200 km, while Struwe-Juhl and Grünkorn (2007) recorded a median natal dispersal distance (on the basis of ringing) of 89 km, with a maximum of 450 km. This maximum recorded distance is similar to that observed in this study, at 433 km. On the other hand, a young WTE female from Russia spent her first winter 1100–1330 km away from the natal nest (Babushkin et al. 2017). Previous studies based on satellite telemetry

usually have a very low sample size (e.g. three individuals: Mirski et al. 2017, Bekmansurov et al. 2018). Mirski et al. (2017), for example, tracked three young WTEs in Poland from fledging to November and recorded a female moving 723 km from the natal nest to Hungary, whereas a male moved only about 100 km. Mirski et al. (2017) stated that juveniles moved on average up to 367 km from nest (143–785 km). Bekmansurov et al. (2018) studied dispersal distances over a 2-month period after tagging on the nest and recorded distances from the native nest of 505 km and 260 km (without sex determination). Young WTEs from Schleswig-Holstein in Germany ( $n = 328$  ringed nestlings) dispersed in all directions, with birds in the first, second, and third calendar year wandering widely (mostly alone) and returning to the natal location only occasionally (Struwe-Juhl and Grünkorn 2007), while older birds in their fourth and fifth calendar year occurred closer to their natal site, apparently searching for a breeding territory. Finally, in Norway, two young WTEs evidently did not leave the natal area at all during their first winter (Nygård et al. 2000, 2003). The same was also observed in some individuals in Finland (Saurola 2017).

## Overall area used and TSAs

Bekmansurov et al. (2018) estimated the natal areas of three young WTEs tagged on the nest and tracked between May and August as ranging from 2.6 to 19.5 km<sup>2</sup> (95% MCP). Balotari-Chiebao et al. (2016) tracked 14 WTE from fledging until the onset of dispersal from the natal area (up until December of the first calendar year) and described mean natal home range sizes as 0.67 km<sup>2</sup> (50% KDE) and 7.83 km<sup>2</sup> (95% KDE). The home range size of WTE was assessed for the first time by GPS telemetry by Krone et al. (2009), in a study tracking a 12-year-old female. Using a sample regime of three locations per day enabled them to obtain 475 positions for the female from July to January, which corresponded to a home range size of 4.53 km<sup>2</sup> by 95% KDE, or 8.22 km<sup>2</sup> by 95% MCP (Krone et al. 2009). In comparison to our own results for juveniles, adult nesting females appear to have a very limited action radius. Similarly, GPS data loggers placed on four adult WTEs (> 5 years old) in Germany (Krone et al. 2013) indicated a 100% MCP size of up to 669.7 km<sup>2</sup> and a 50% fixed KDE of 2.97 km<sup>2</sup>. However, in this case, Krone et al. (2013) removed all outlying positions at a distance larger than six times the mean to the activity centre prior to MCP and KDE construction. Soutullo et al. (2006b) observed no statistical difference between the sexes in total area explored (MCP) of golden eagles (*Aquila chrysaetos*) during their first year of life.

Bragin et al. (2018) described three periods on the basis of different movement patterns of young WTEs after fledging: (1) the nest period, (2) the transitory period, and (3) the

stopover period (defined as movements within a 30 km radius between transitory periods). Similarly, Cadahía et al. (2010) distinguished three phases of dispersal in young Bonelli's eagles *Aquila fasciata*: (1) a dependence period, (2) departure from the parental territory, and (3) settlement in dispersal areas. For the first time, we attempted to define TSAs of WTEs in their first year of life as the most important stopover area for juveniles, with the aim of encouraging conservation of these sites. We suggest that future long-term studies should further assess the applicability of the TSA definition used in this study for WTE conservation management. While the method used in this study satisfactorily delimited the main clusters of individual locations, the resultant TSA sizes were not comparable between individuals due to differing numbers of night roosting sites and different numbers and dates of included tracking days. Nevertheless, the number of TSAs appears to be a good measure of individual sedentarity. Our data indicated that the TSAs of all the individuals studied showed a particular overlap around the nesting sites. Cadahía et al. (2010) found great individual variation in dispersal areas for Bonelli's eagles, which only seldom overlapped, and recommended that conservation efforts should focus on the whole landscape matrix or preferred habitats rather than on a few clearly delimited geographical areas (Cadahía et al. 2010).

### Habitat selection

Individual variation in habitat preference can play a role in WTE metapopulation dynamics (Davis and Stamps 2004). Bragin et al. (2018) used satellite telemetry and recorded highest habitat preference in WTEs for water areas, and this was confirmed by our own results. This preference fully corresponds with the WTE foraging strategy, which is based on prey consisting mainly of waterfowl and other birds, fishes, and smaller mammals (Sulkava et al. 1997; Sándor et al. 2015). Tikkanen et al. (2018) stated that subadult WTEs preferred the coastline and archipelagos along the Finnish coast close to their natal sites and avoided the open sea, urban areas, other constructed areas, and agricultural fields. Evans et al. (2010) examined nesting habitats of WTEs. Davis and Stamps (2004) noted that environmental heterogeneity may play an important role in the maintenance of genetic variation as different genotypes are likely to be favoured in different environment types. Tucker et al. (2019) revealed that environmental heterogeneity could affect dispersal distances. In this study, however, habitat diversity in 100% MCPs had no apparent effect on maximal dispersal distance in young WTEs. We suggest that detailed data on the habitat requirements of WTEs during their first year of life could be used together with future data from later years in a study exploring whether natal habitat preference induction plays a role in this species.

### Final occurrence and future research

Ferrer (1993) noted that natal and breeding dispersal influences gene flow between populations or subpopulations. Unfortunately, the data obtained in this study were limited to a short period covering the first year of life and, as such, should be treated with caution as sites explored during the first year of life need not coincide with the final settlement and nesting area chosen over the next 4 years. Though young individuals from the three subpopulations studied occurred in the same areas during the first year of life, future nesting site identification will enable us to assess real gene flow and connectivity levels between subpopulations. Despite the above mentioned limitations, our study brought new data about post-fledging areas, overall area used, maximal dispersal distances, and returns to the native nest in WTEs during their first year of life. Obtained results are unique, at least for three countries, where the tagging was conducted. Data will be used in conservation of species.

Based on our results, we are of the opinion that an international approach is necessary for effective conservation of WTEs on a European-wide scale. The attachment of GPS/GSM loggers to WTE nestlings gave us a unique opportunity to study movements and behaviour of future nesting and non-nesting individuals, thereby enabling us to reliably estimate the floater-to-breeder ratio in the breeding age. Where floaters and dispersers constitute a substantial part of an endangered population, then it becomes essential that they are taken into account in conservation biology. Any future conservation efforts on endangered species with small population sizes such as the WTE should aim to protect not only traditional nesting sites but also the most important TSAs, which could attract many non-nesting individuals.

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**Code availability** Not applicable

**Author contribution** RR and IL designed the study and provided legislative permissions. RR, IL, PS, DR, and DH participated in the tagging of nestlings and regular checks of locations recorded and individual fates. DR, with VM, DD, and LR, analysed the data in GIS. DR contributed most to the writing of the paper, which was reviewed and approved by the other co-authors.

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**Data availability** The datasets used and analysed during the current study are available from the corresponding author upon reasonable request.

## Declarations

**Ethics approval** All animal manipulation and tagging were consistent with the laws of the Czech Republic, Austria, and Hungary. Tagging was allowed on the basis of the following permissions: (1) Czech Republic: JMK 48995/2017 (S-JMK 25358/2017 OŽP/Ško), JMK 18112/2018 (S-JMK 176395/2017 OŽP/Ško), KUCJK 40400/2017 (OZZL 25808/2017); (2) Austria: GFL2-J-107/014; (3) Hungary: tagging was performed by the ringer Péter Spakovszky under general deliverance PE-KTF/97-13/2017 of the Hungarian Bird Ringing Centre (MME/BirdLife).

**Consent to participate** Not applicable

**Consent for publication** Not applicable

**Conflict of interest** The authors declare no competing interests.

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