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RESEARCH PAPER

Dispersal of eastern imperial eagles from the Czech Republic

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Abstract. The first successful breeding of eastern imperial eagles (*Aquila heliaca*) in the Czech Republic, which lies at the north-western edge of its world breeding range, was confirmed in 1998. Here we summarise the dispersal, overwintering and expansion of the Czech population based on observational, ringing and telemetry data. The Czech breeding population had increased to at least 14 breeding pairs and 18 territorial pairs by 2022. Between 2017 and 2021, 19 nestlings were equipped with GPS/GSM devices. Two of the 16 surviving individuals (12.5%) spent their first winter in the Mediterranean (1,460 km and 1,671 km from natal nest), but did not repeat this migration pattern again. The other 14 tracked individuals wintered close to their natal areas. Maximal recorded distances from the natal nest and total area occupied (100% minimal convex polygons) were significantly lower in the first calendar year than the second. Signs of settlement prior to the first nesting attempt were already apparent by the third or fourth calendar year. Excluding exploratory trips during the floater period, final natal dispersals for two of the breeding males were 46 km and 92 km, respectively. Further spreading of the species' Czech breeding range is expected in the future.

Key words: *Aquila heliaca*, breeding, dispersal, GPS/GSM, bird ringing, telemetry, overwintering

Introduction

Humans have always been fascinated by the large-scale movements of birds. Traditionally, bird species were labelled as strictly resident or migratory (Schwarz & Bairlein 2004). However, while this sorting may be valid for many species, especially passerines, different tagging methods have revealed that, in some species, only part of the population may migrate (partial migrants), or that different components of the population migrate to different extents (differential migrants) (Schwarz & Bairlein 2004). Without accurate and frequent telemetry data, distinguishing between natal and breeding dispersal, or migration and short-term individual exploratory trips, can be difficult. This is particularly true of eagle species with delayed sexual maturity, where the "floater period" typically takes several years (Penteriani & del Mar Delgado 2009). Bird migration can be defined as a regular seasonal movement

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along a flyway between breeding and wintering grounds, where individuals then spend several months, while natal dispersal is the movement of wandering individuals from their birthplace to their first breeding location (Soutullo et al. 2006, Penteriani & del Mar Delgado 2009), and breeding dispersal is the movement between successive breeding sites (Cadahía et al. 2010). Exploratory trips can be made in various directions from the central occupied area, usually lasting only 1-5 nights before returning. Finally, movements undertaken by juveniles once they become independent of their parents are termed juvenile dispersals (Soutullo et al. 2006).

The eastern imperial eagle (*Aquila heliaca*) is a monotypic species (after taxonomic separation of the Spanish imperial eagle (*Aquila adalberti*)) distributed across the central and western Palearctic region (Cepák et al. 2008, Birdlife International 2019), where it shows a preference for open steppe habitats and plains with isolated trees due to its habit of hunting over open ground (Cramp & Simmons 1980, Huntley et al. 2007). Over the 20th century, strong anthropogenic pressure has caused a drastic decline in the Central and Southeastern European population (Demerdzhiev et al. 2011), with estimated mature population numbers now less than 10,000 individuals with a decreasing population trend; consequently, the species is now regarded as vulnerable on a global scale (Birdlife International 2019).

Surprisingly, the sources are not consistent regarding the migration and wintering strategy of the eastern imperial eagle. Birdlife International (2019) states that the species is a full migrant, though it is traditionally assessed as resident or partially migratory (Cramp & Simmons 1980, Keller et al. 2020). While Huntley et al. (2007) also classify the species as migratory, they described it as a partial migrant in Central Europe, with young and immature individuals moving south to the Mediterranean region (Cepák et al. 2008, Bragin et al. 2021), while adult territorial birds are mainly resident in Central and Southeastern Europe, spending winter in their breeding territories (Bagyura et al. 2002, Stoychev et al. 2004, Demerdzhiev et al. 2011). Bragin et al. (2021) states that the species is partially-migratory or non-migratory, breeding in forest-steppe regions of Eurasia and wintering in Northern Africa, the Middle East or South Asia, while Horváth et al. (2018b) states that while the large eastern populations in Russia and Kazakhstan are migratory, the western populations in Central Europe, the Balkans, Anatolia and Caucasus are thought to be resident.

Owing to the longevity of the species (more than 28 years in the wild; Danko & Mihók 2020), its natal dispersal period lasts several years, with birds in the first calendar year (1st CY) appearing to have the lowest survival rate (59%; Stoychev et al. 2014). Eastern imperial eagles in Kazakhstan had an estimated annual adult survival rate of 84%, based on molecular analysis of moulted feathers found in nesting territories (Rudnick et al. 2005). Eastern imperial eagles gain their final adult plumage after four or five annual moults, i.e. around the 6th CY (Clark 2004, Bragin et al. 2021). Nevertheless, the eagles regularly breed between the 3rd and 5th CY, before they obtain their dark brown adult plumage (Horváth et al. 2014).

The Pannonian basin population began to increase in numbers and range during the 1990s (Bagyura et al. 2002), with a ca. 250% increase since 2000 (Keller et al. 2020) and, presently, the Czech Republic and Austria represent the north-westerly limit of the birds breeding range (Schmidt & Horal 2018). The first successful breeding of the species was confirmed in the Czech Republic in 1998 (Horák 1998), though nest building had already been observed on the Czech side of the River Dyje (Thaya; Czech-Austrian border) in 1997, and the number of nesting pairs has increased slowly ever since (Horal 2014, Schmidt & Horal 2018). Horal (2014) has since summarised the number of breeding pairs and number of fledglings up to 2013, with Schmidt & Horal (2018) compiling more recent results up to 2018. Schmidt & Horal (2018) noted that the eagles' breeding grounds in the Czech Republic include floodplain forests and lines of trees in intensively used farmland, and that successful breeding can take place as early as the 3rd CY.

Eastern imperial eagles appear to have diverse migratory strategies with regard to age and origin (Bragin et al. 2021); thus, their seasonal distribution may have to be studied on different levels, i.e. through indirect count data without individual recognition, uniquely tagged individuals with random resighting and/or individuals tracked by telemetry on a long-term basis (Thorup et al. 2014). While bird ringing has a long tradition and is still important, radio telemetry using GPS/GSM loggers charged with solar batteries tends to be more favoured nowadays as it allows for the study of spatial behaviour in large bird species that regularly move in sunlight (Urios et al. 2015). Nevertheless, rings are still used as they serve as a primary identifier of individuals, even when GPS or radio transmitters fail, are lost or their battery is temporarily or permanently discharged. Despite the possibilities of data transmission outage in winter, or some regions still having low GSM coverage, GPS telemetry now allows for the collection of formerly inconceivable volumes of individual data (López-López 2016).

The linkages between the northern breeding areas of eastern imperial eagles and their southern wintering areas are not well known (Bragin et al. 2021). Further, there is a lack of data on stopover behaviour, daily distances travelled and the frequency and repeatability of migration journeys in juveniles, sub-adults and adults from different parts of its distribution range. The aim of this study, therefore, was to 1) provide an overview of breeding pairs in the Czech Republic, and 2) to detect wintering sites and possible migration routes of individuals tagged with rings and telemetry loggers. In doing so, we focused on the connectivity of birds originating in the Czech Republic and the core Pannonian population via migratory flyways, juvenile dispersal (hereafter "dispersal") and natal dispersal. Dispersal is here understood as the maximal dispersal distance, i.e. distance between the natal nest and the most distant night location in a given year, which is comparable with the sporadic random distance obtained from ringing recoveries. In addition, we determined habitat preferences for night roosting sites and compared differences in yearly distance and direction of the farthest location from the natal nest and the total area occupied in each calendar year and by different sexes.

Material and Methods

Breeding characteristics

To describe the Czech breeding population size in each year, we assessed the number of territorial pairs, nesting pairs, breeding pairs, pairs with chicks, successful pairs and number of fledglings. Territorial pairs were counted as the minimum number of territories where territorial behaviour of a pair was observed, while number of nesting pairs was defined on the basis of territories where at least one new nest was built, or an older nest was renovated, by a pair. Breeding pairs were represented by the number of territories where eggs were laid and incubation was started, while the number of territories with hatched chicks is stated as pairs with chicks. Finally, the number of territories with at least one recorded fledgling was used to calculate the number of successful pairs.

Ringing data

The Czech Bird Ringing Centre (National Museum, Prague) provided data on ringing of eastern imperial eagles and the number of ringing recoveries up to 31st December 2021. In addition, data on the number of nestlings ringed in 2022 was provided by Hynek Matušík. The final dataset included information on 95 wild imperial eagles ringed as nestlings in the Czech Republic between 1998 and 2022, along with recovery data for eagles ringed in the Czech Republic and found in foreign countries (n = 7), and for those ringed abroad (as *pulli*) and found in the Czech Republic (n = 12).

Telemetry

Between 2017 and 2021, 19 ca. eight-week-old nestlings were equipped with a GPS/GSM device in the Czech Republic (Table S1; all tagged between June 30th and July 12th; mean July 6th, median July 3rd). The total comprised seven females and twelve males, with sex determination confirmed through molecular analysis of pin feathers (PCR and gel electrophoresis with primers CHD1-i16F (5′-GTCCTGATTTTCTCACAGATGG-3′), CHD1-i16R (5′-ATGATCCAGTGCTTGTTTCC-3′; Suh et al. 2011). Seven individuals were equipped with Ecotone (Poland) devices in 2017 and 2018, and 12 individuals with Ornitela (Lithuania) devices between 2019 and 2021. The GPS/GSM backpack tags were fixed to the bird's back 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). The Ecotone devices weighed ca. 30 g, while the Ornitela devices used in 2019-2020 weighed 50 g and those in 2021 25 g. All 19 eagles were ringed by the same person (H. Matušík), while P. Spakovszky, and R. Raab, accompanied by either I. Literák or D. Rymešová, tagged 17 of the eagles in 2017 and 2019-2021. The five tags from 2017 were provided by TB Raab, the three tags from 2019 by the LIFE Great Bustard Project (LIFE15 NAT/AT/000834), and the nine tags used in 2020 and 2021 by the LIFE EUROKITE Project (LIFE18 NAT/AT/000048). Two eagles from 2018 were ringed by H. Matušík and tagged by L. Peške, the tags being provided by the PannonEagle Project (LIFE15 NAT/HU/000902).

Data analysis in GIS

Individual locations and trajectories were analysed in ArcMap 10.1 (ESRI, USA) with Spatial Analyst, HRT and ArcMET extensions. Regardless of individual settings, the first location after midnight (UTC) was selected every day for each individual in the source CSV files. A 200 m distance criterion was used to exclude initial locations in the natal nest using the Point Distance Tool, the first night location further than 200 m from the nest being used to start the dataset. In all cases, data collection ended on 31st December 2021. The number of locations obtained occasionally differed from the number of days tracked due to device failures, particularly where temporary problems with battery charging occurred due to lack of sunshine in winter (Table S1).

Azimuth to north (in degrees) between the most distant location (whole dataset) and the natal nest was measured using the "COGO" tool. Owing to different migration strategies and differing survival between tracked individuals, 100% minimum convex polygons (MCP) of night locations only were created for each calendar year, these representing the assumed total area occupied by each individual that year. In addition, 100% MCPs were created for December locations only to visualise the overwintering area (for eagles with adequate survival). For two individuals (LX535, LX536), January locations were used instead due to a lack or absence of December locations.

In addition to the individual analyses, the "Merge" tool was used to join all midnight points of all individuals into one layer to highlight hot spots of eagle occurrence over an equidistant 10 × 10 km grid projected in ETRS 1989 LAEA (https://www.eea.europa.eu/data-and-maps/data/eea-reference-grids-2). The number of points in each grid square was then counted and a raster created using geometrical intervals and five density categories. To describe preferred night roosting sites, regardless of age, sex and season, the area of habitat used in each square was assessed (km^2, %) using the 2018 Corine land cover dataset (https://land.copernicus.eu/pan-european/corine-land-cover), this being used to represent "available habitats" during compositional analysis (Aebischer et al. 1993). "Used habitats" were determined on the basis of locations recorded in Corine habitats in each square (n = 855 squares with at least one location). Nine squares laid outside the European CLC 2018 layers were excluded.

Statistical analysis

The following data were obtained and tested for normality (Shapiro-Wilk normality test): 1) maximal distances of a night roosting site from the natal nest in each calendar year (1st CY and 2nd CY) or 2) over the whole tracking period, 3) number of locations, 4) maximal number of tracking days and 5) number of tracking days starting from the 200 m limit from the natal nest, 6) azimuth to north, 7) yearly 100% MCP. The azimuths were normally distributed and so a two-sample t-test was used to test for differences between sexes or different age cohorts (with an alternative chosen after the F-test). The same procedure was used for the size of the yearly 100% MCP after

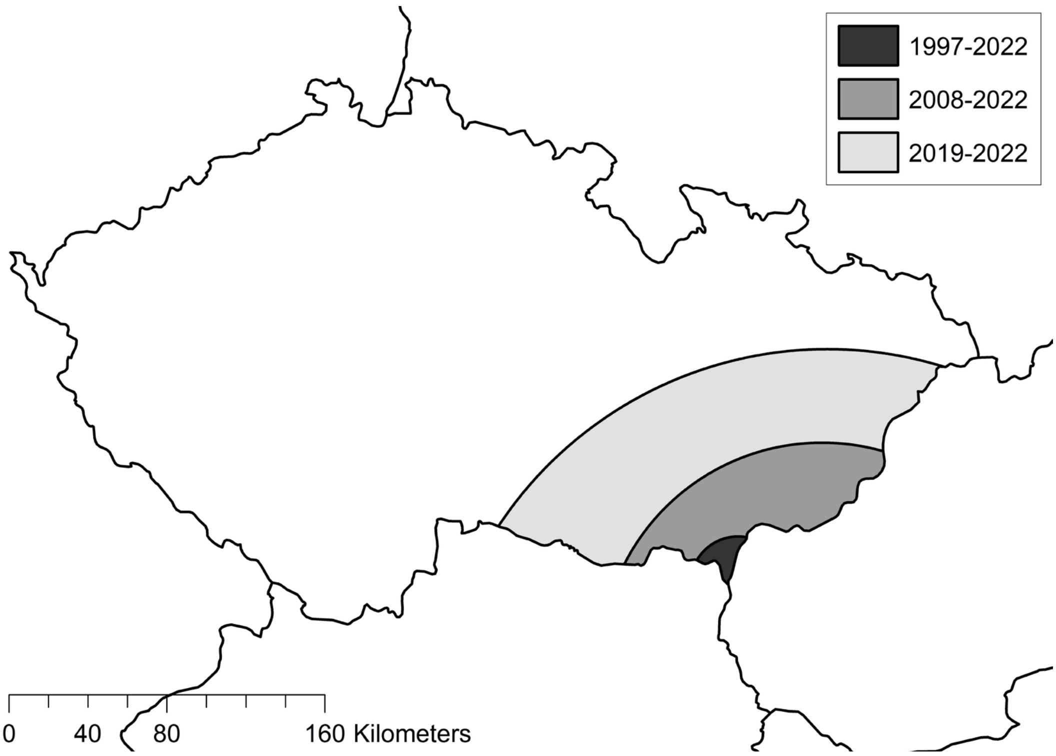

Fig. 1. Limits of eastern imperial eagle spread in the Czech Republic (as observed for territorial pairs) since the first confirmed breeding attempt in 1997 (based on 138 observed breeding attempts; detailed locations not published for conservation reasons).

logarithmic transformation (ln). Individual LX532 was excluded from all statistical analyses owing to the low number of locations obtained before death (Table S1). Testing of differences in maximal distances (after square root transformation) or MCP sizes (after ln transformation) during 1st CY and 2nd CY were performed using the paired t-test for both years with data of individuals with minimal survival until the end of the 2nd CY (n = 7). The Mann-Whitney U test was used to test for differences between males and females for all other variables that were not normally distributed even after transformation. All statistical computations were performed in R v. 3.6.2 (R Core Team 2013).

For habitat analysis, the percentage of locations and habitats in squares with at least 50 locations (n = 25 squares) was assessed using the "compana" function in the Adehabitat HS package in R. Seven Corine habitat types were not detected in the occupied squares (habitat nos. 241, 244, 335, 422, 423, 522, 999, Bossard et al. 2000, Büttner & Kosztra 2017), while a further nine habitats were excluded because of their absence in the analysed squares (habitat nos. 123, 132, 212, 213, 322, 331, 332, 421, 521); thus, primary compositional analysis was performed on 29 habitat categories. These 29 habitat categories were then combined into eight pooled categories, i.e. 1) urban areas (111, 112, 121, 122, 124, 131, 133, 141, 142), 2) fields (211), 3) vineyards and orchards (221, 222, 223), 4) meadows (231, 321), 5) gardens and small fields (242, 243), 6) forests (311, 312, 313), 7) shrubs and sparsely vegetated areas (323, 324, 333, 334) and 8) water areas (411, 412, 511, 512, 523). For night roosting locations, these categories represent trees or perching sites inside or near the defined habitat.

Results

Breeding population in the Czech Republic

The size of the Czech breeding population has increased slowly since the first successful breeding attempt in 1998 (Table S2, Fig. 1). In 2022, incubation had started in 14 nests, with 11 pairs nesting successfully and 19 fledglings recorded in total that year. In addition, observations of nesting attempts by imperial eagles with immature plumage have also increased, with four cases including males

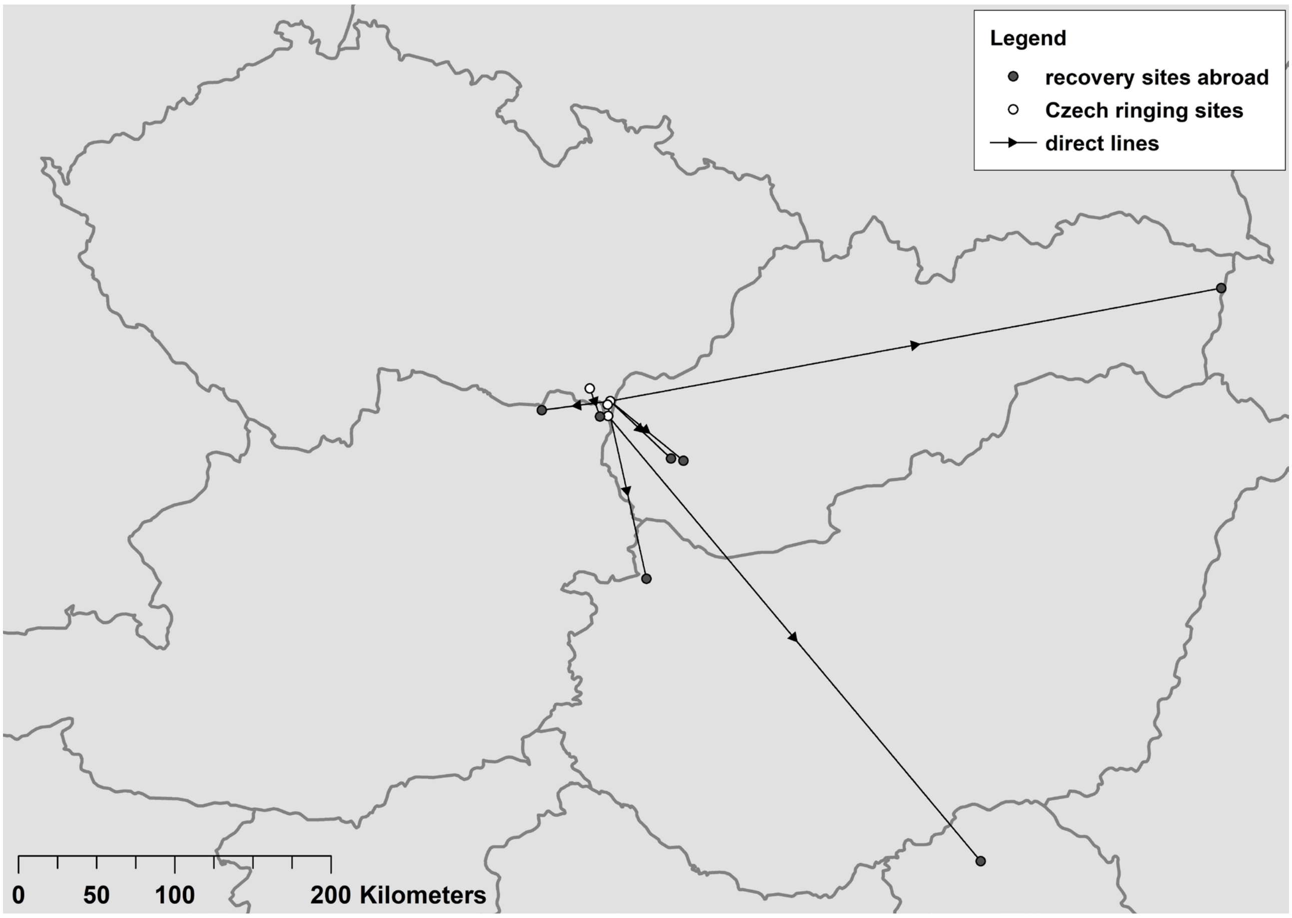

Fig. 2. Eastern imperial eagles ringed in the Czech Republic and found abroad (data from The Czech Bird Ringing Centre (National Museum, Prague); data valid to 31st December 2021).

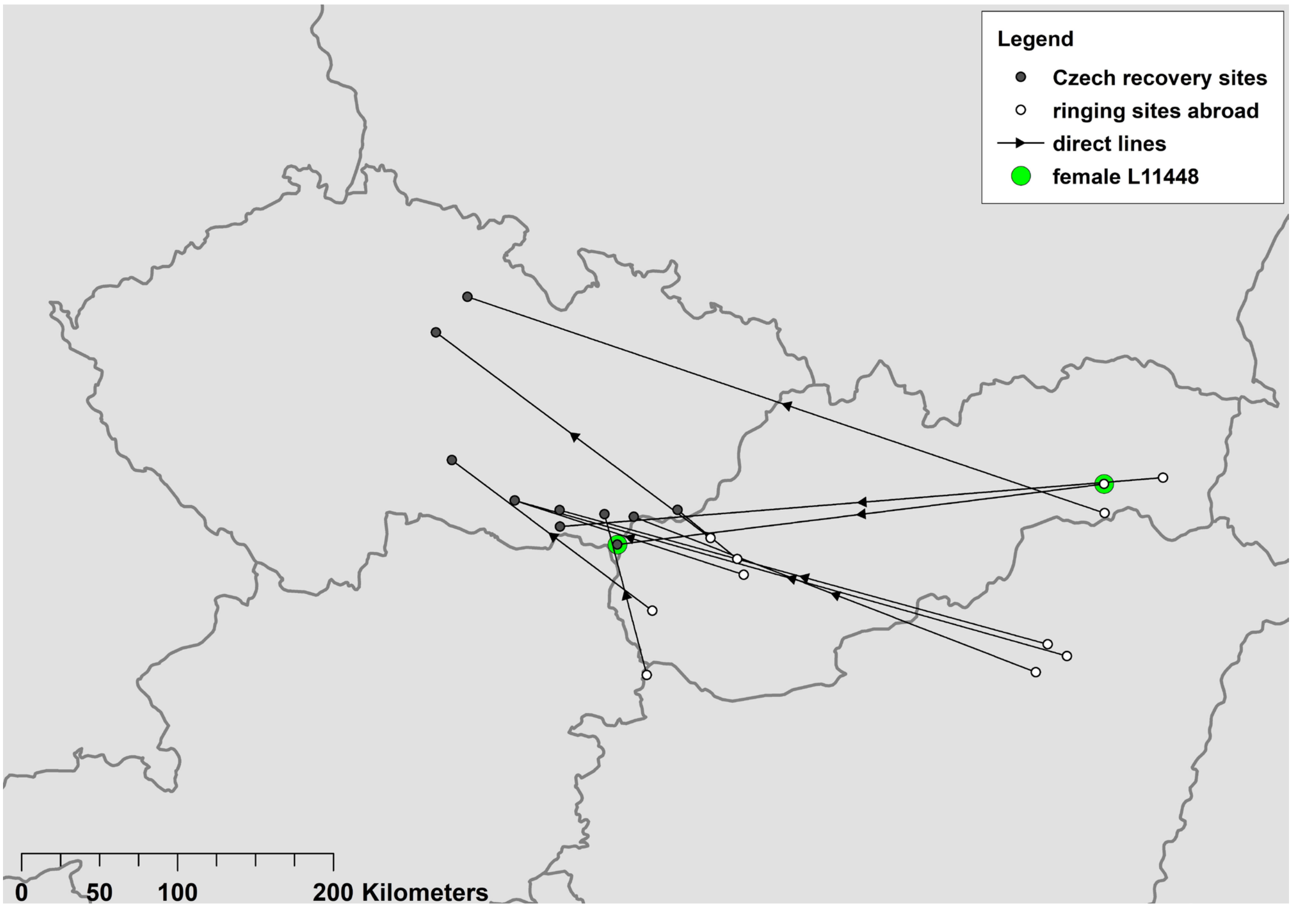

Fig. 3. Eastern imperial eagles ringed abroad and found in the Czech Republic (data from The Czech Bird Ringing Centre (National Museum, Prague); data valid to 31st December 2021. Ringing recovery of the female in her 28th CY marked with green circles).

(× 2) and females (× 2) linked to the Czech Republic by origin or nest location. Both these males were tagged with a GPS/GSM device in 2017 and their breeding had already been confirmed at 4th CY. One male (ring LX522, alias Auki 69) was frequently observed near a successfully reared nest close to Czech-Austrian border as early as 2019. A change of male in a local breeding pair was observed between the end of February and the beginning of March 2019. Though paternity of male LX522 was possible, but unsure, in 2019, it certainly nested at the site between 2020 and 2022. Another male of Czech origin (ring no. LX034, alias Auki 72) nested successfully in Austria in 2020 and 2021, while a female (ring no. SK463) hatched in western Slovakia in 2019 built a nest in the Czech Republic in 2021, and also nested there successfully in 2022. Finally, in 2022 (3rd CY), an unsuccessful breeding attempt in the Czech Republic (Central Moravia) was recorded for a female (ring no. BS0093) hatched in Lower Austria in 2020.

Dispersal based on ringing data

Seven ringed Czech eagles were recovered from abroad, three in Slovakia, two in Austria, one in Serbia and one in Hungary (Fig. 2). The two most distant ringing recoveries from the natal nest were 397 km after 87 days (azimuth 79.4° from N, LX56) and 372 km after 284 days (azimuth 140.0°, LX538) in Slovakia and Serbia, respectively. Aside from bird LX536, all other findings of this type were found at distances shorter than 70 km, though after a longer period than one year. The ringing recovery of individual LX57 after 1,728 days (found dead at 5th CY, 54 km from natal nest) represents the longest monitoring period for an eastern imperial eagle ringed in the Czech Republic. The most recent ringing recovery of a dead imperial eagle of Czech origin was from Hungary (114 km after 279 days) for bird LX536, one of the birds equipped with a GPS/GSM device (Table S1).

Eleven eastern imperial eagles ringed abroad were checked at least once in the Czech Republic (Fig. 3), seven having been ringed in Slovakia and four in Hungary. Those of Slovak origin were 50-431 km from their ringing site after 79 to 6,948 days. The two most distant ringing recoveries from non-Czech ringing sites were 431 km after 675 days (azimuth 288.8°; ZM119) and 387 km after 410 days (azimuth 265.4°, A2820). The four eagles ringed as nestlings in

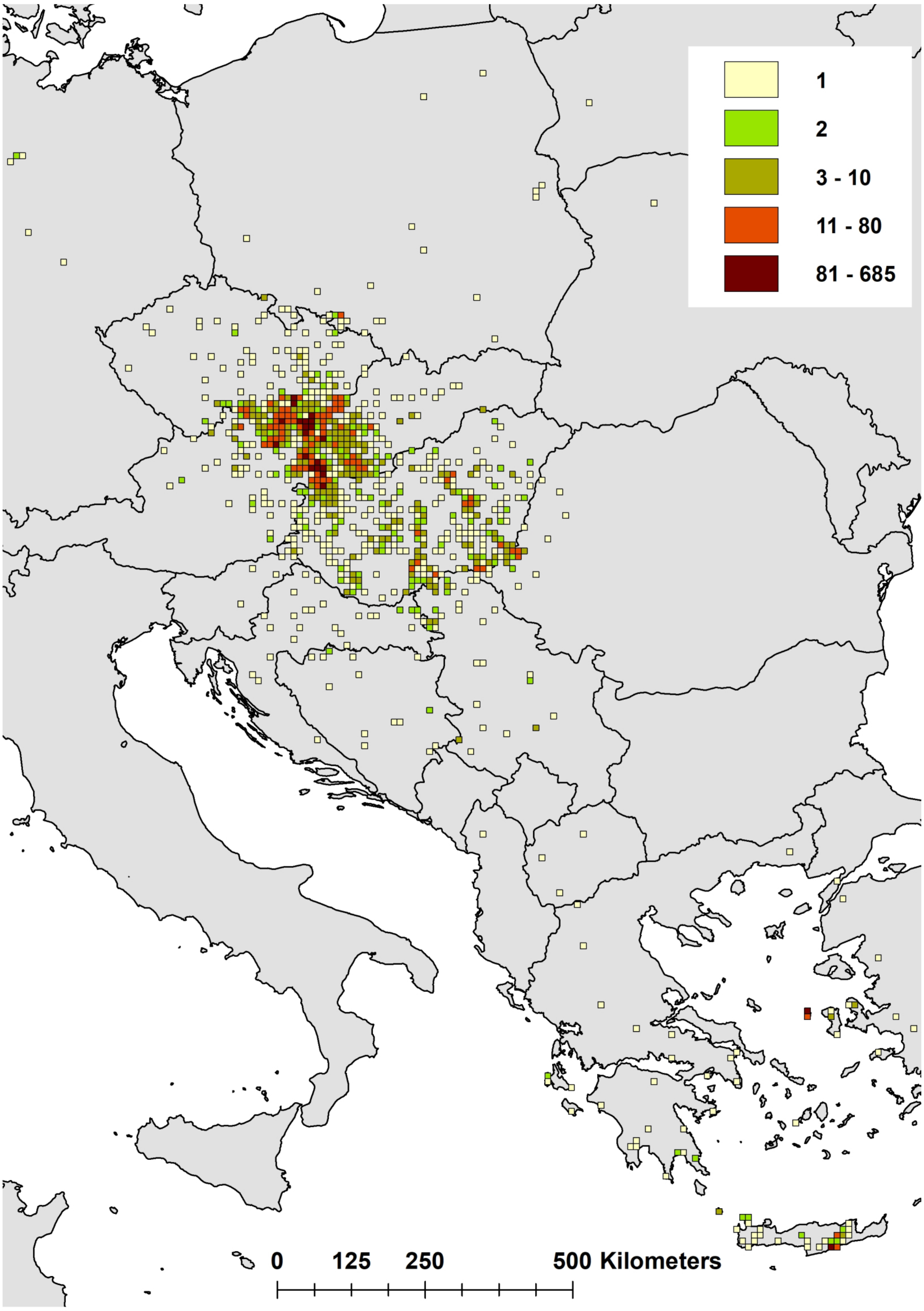

Fig. 4. Categorised number of night locations for all 19 tagged eastern imperial eagles from Czech nests over a 10 × 10 km grid (data valid to 31st December 2021).

Hungary were recovered between 246 and 442 days after ringing at 107-368 km from their ringing site. The ringing recovery of Slovak eagle L11448 at 317 km from its ringing site after 9,856 days (i.e. in its 28th CY; azimuth 262.9° from N, date of ringing 21st June 1994), represents the oldest eastern imperial eagle recorded in the Czech database of ringed birds. Moreover, this recovery concerned a breeding female whose ring had already been reported once before, in its 20th CY (June 2013) and finally 28th CY (June 2021). The female has been recorded at the same nesting site since 2006, having reared 28 young over 17 breeding seasons (up to autumn 2022), with breeding being unsuccessful over just three seasons.

Telemetry results

Summarised results

Individual eagles were tracked for 15 to 1,642 days from tagging up to the end of 2021 (mean 490 days, median 264 days). Concerning the threshold of 200 m, 3 to 1,610 locations were obtained per individual (mean 429, median 215), with first movement > 200 m from the nest occurring between five and 48 days after tagging (mean 24 days, median 23 days), i.e. between July 8th and August 29th (Table S1). In total, 8,148 locations were obtained from tagged individuals up to the end of 2021, though only 58% of tagged individuals were known to be alive at that time. Two mortality cases were definitively confirmed when the carcasses were found at the end of 2021, while the signals of six individuals (32%) disappeared abruptly with no further clarification.

Dispersal based on telemetry

Compared to ringing recoveries, GPS locations of tracked individuals were recorded in many European countries, including the Asian part of Turkey (Fig. 4). Direct maximal distances from the natal nest were 25-1,671 km for the 1st CY (median 197 km, mean 364 km, n = 16), 314-1,380 km for the 2nd CY (median 466 km, mean 616 km, n = 7) and 54-628 km for the 3rd CY (median 489 km, mean 431 km, n = 5; data does not include individuals who survived less than the whole calendar year in each cohort; Table S3). Maximal distances were significantly lower in the 1st CY than the 2nd CY (paired t-test after square root transformation: t = 4.345, df = 6, *P* < 0.01) in individuals with minimal survival until the end of the 2nd CY (Fig. 5). Maximal distances from the natal nest did not differ significantly between males (median 217.5 km, mean 407.3 km, n = 12) and females (median 148.6 km, mean 217.6 km, n = 6) in the 1st CY (Mann-Whitney U test: W = 31, *P* > 0.05, LX532 excluded; Table S3) or for the whole study period (W = 37, *P* > 0.05; median: males 288.5 km, females 439.6 km; mean: males 561.4 km, females 410.1 km).

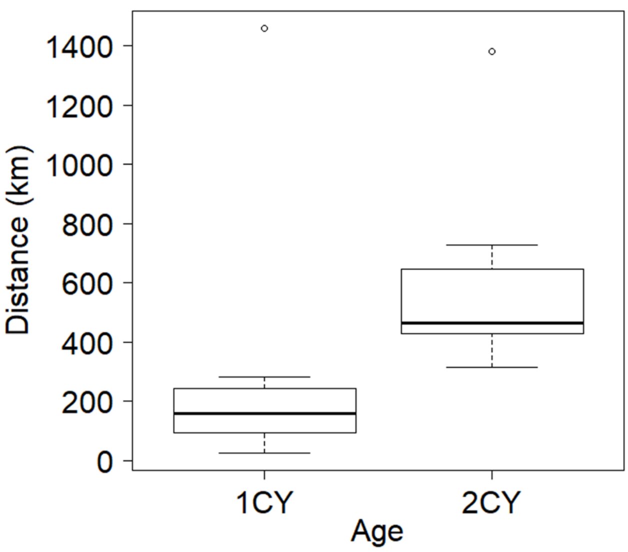

Fig. 5. Differences in maximal recorded distance between night roosting site and natal nest in the first and second calendar year for seven tracked eastern imperial eagles, with complete data for both years.

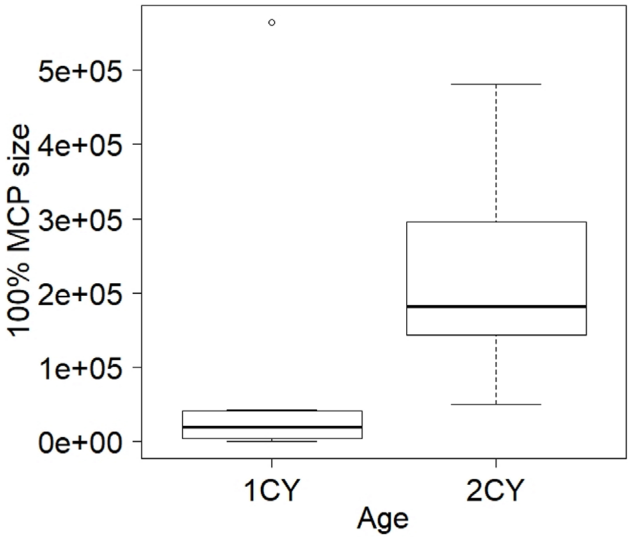

Fig. 6. Differences in 100% minimum convex polygons (MCP; km²) for eastern imperial eagles in their first and second calendar year (n_1 = 7 ind., n_2 = 7 ind.).

MCP size (total occupied area) in the 1st CY did not differ between males and females (logarithmic transformation, two sample t-test, equal variance: t = –0.961, df = 14, *P* = 0.353); however, there was a significant difference in 100% MCP between the 1st CY and 2nd CY (logarithmic transformation, paired t-test: t = –3.992, df = 6, *P* < 0.01; Table S4, Fig. 6). The 100% MCP based on night roosting sites was 432-564,089 km² in the 1st CY (median 27,647 km², mean 86,665 km², n = 16), 49,755-480,991 km² in the 2nd CY (median 182,207 km², mean 227,446 km², n = 7), and 364-179,911 km² in the 3rd CY (median 86,700 km², mean 86,844 km², n = 5; Table S4). Note, however, that a malfunction in the GPS/GSM device on male LX522 resulted in a lower number of locations, which (along with nesting) may have affected minimal MCP size (364 km²) in the 3rd CY (Table S4).

Wintering in the Pannonian Basin and the Mediterranean

Though all tracked individuals surviving until the end of December in the 1st CY (n = 16) moved at least slightly to the south from the natal area during the first winter (Fig. 7), only two individuals (12.5%) spent their first winter in the Mediterranean region (Fig. 8). These two individuals did not repeat the

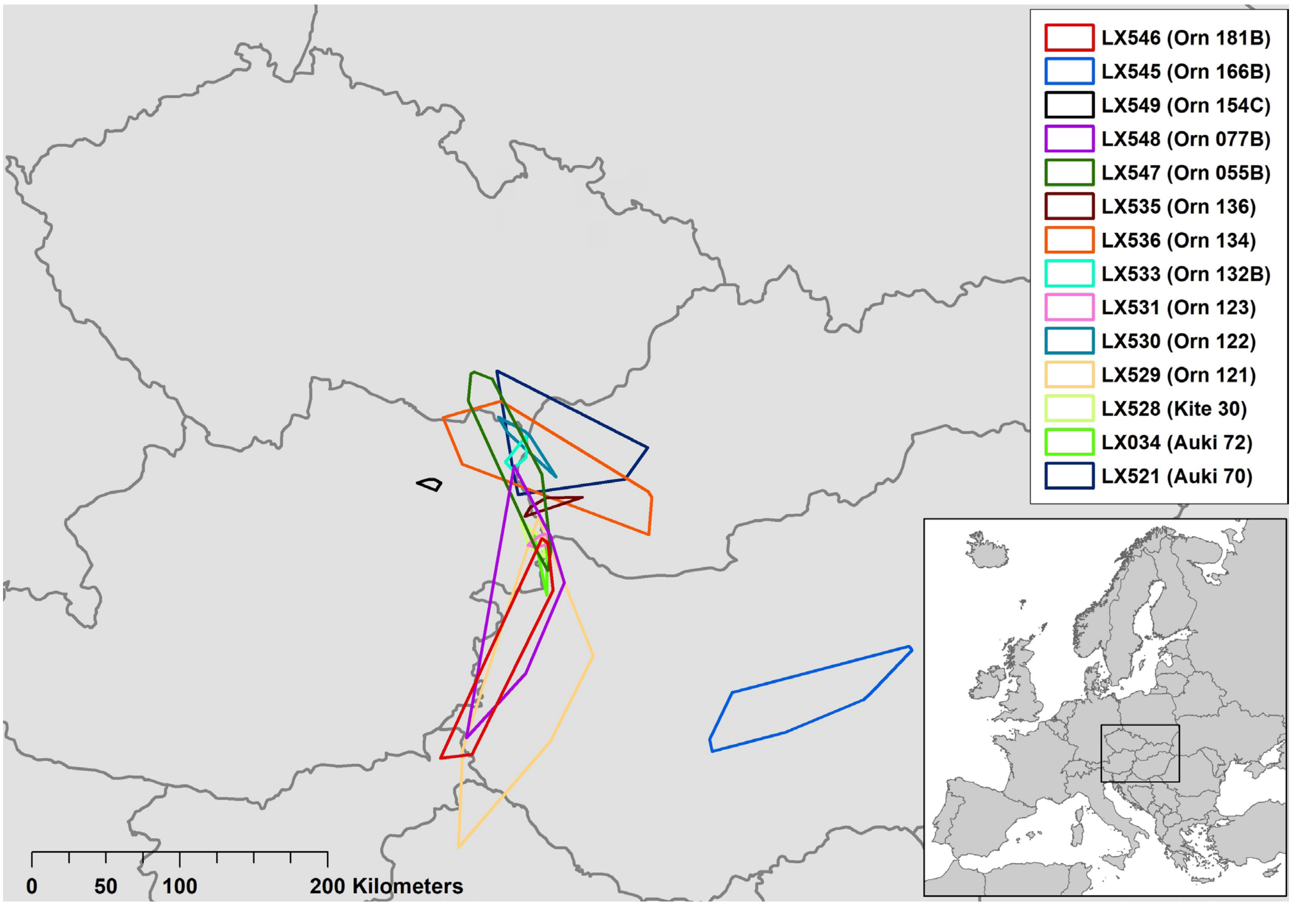

Fig. 7. Areas of December occurrence for 14 eastern imperial eagles based on night locations in the first calendar year (1st CY; 100% minimal convex polygon (MCP)). Explanatory notes: due to a lack of locations for December, locations from January (2nd CY) were used for birds LX535 and LX536. The legend shows individual ring numbers and individual codes used for telemetry. MCPs for individuals with premature signal loss (LX035, LX532, LX523) were not delineated.

same migration pattern to the Mediterranean over subsequent years (Figs. 9, 10).

Natal philopatry

In some birds, a settlement trend prior to the first nesting attempt was already apparent in the 3rd (male LX522) or the 4th CY (male LX034; Table S3), distances between natal nest and first nesting attempt (natal dispersal) being 46 km for LX522 (north-west) and 92 km for LX034 (south, to Austria). Concerning exploratory trips, the furthest locations from the natal nest were oriented north-east (Belarus) and north-west (Germany) for two individuals (Fig. 11). The azimuth for the most distant locations from the natal nest (whole individual dataset) did not differ between sexes (t-test, unequal variance: $t = -0.943$, $df = 15.566$, $P = 0.360$) or age cohort, whether by (a) 1st CY individuals *vs.* older CYs (including 2 CYP according to Table S4; t-test, equal variance: $t = 1.136$, $df = 17$, $P = 0.272$, or (b) 1st CY individuals *vs.* 2nd CY and older CYs (t-test, equal variance: $t = 0.480$, $df = 10$, $P = 0.641$).

Habitat selection at night roosting sites

Compositional analysis indicated that night roosting site locations were not distributed randomly according to the habitat composition in each square ($\lambda = 0.043$, $P < 0.01$). The most preferred night roosting sites were trees in forests (rank seven, especially broadleaf), trees in patches of shrubs and sparsely vegetated areas (six), fields with less trees or other perching sites (five), trees in meadows and pastures (four), trees in gardens and small fields (three), trees near water areas or sea (two), trees in vineyards and orchards (one) and finally urban areas (zero).

Discussion

Dispersal and wintering

This study provides the detailed mapping of the increase in breeding population size and breeding range of eastern imperial eagles in the Czech Republic, and summarises recent data on their occurrence, dispersal and wintering behaviour. Though previous ringing and recovery data for the Czech Republic was

Fig. 8. Areas of December occurrence for two eastern imperial eagles (LX522 and LX527) on Mediterranean islands, based on night locations in the first calendar year (1^{st} CY; 100% minimal convex polygon (MCP)).

unable to document wintering of young individuals in the Mediterranean region, this behaviour is known for imperial eagles ringed in Slovakia and Hungary (Meyburg et al. 1995, Cepák et al. 2008, Horváth 2022). The oldest evidence for movements south by Slovak eastern imperial eagles came from a nestling ringed in June 1957 and shot in Croatia in March 1958 (Danko 1996). Five other individuals of Slovak origin ringed between 1984 and 1996 have also been recorded in Greece (Danko 1996), four during their first autumn or winter (97-180 days after ringing) and one in spring of its second winter (663 days after ringing, 3^{rd} CY). Two males from our study reached points 1,460 km and 1,671 km from the natal nest, somewhat more

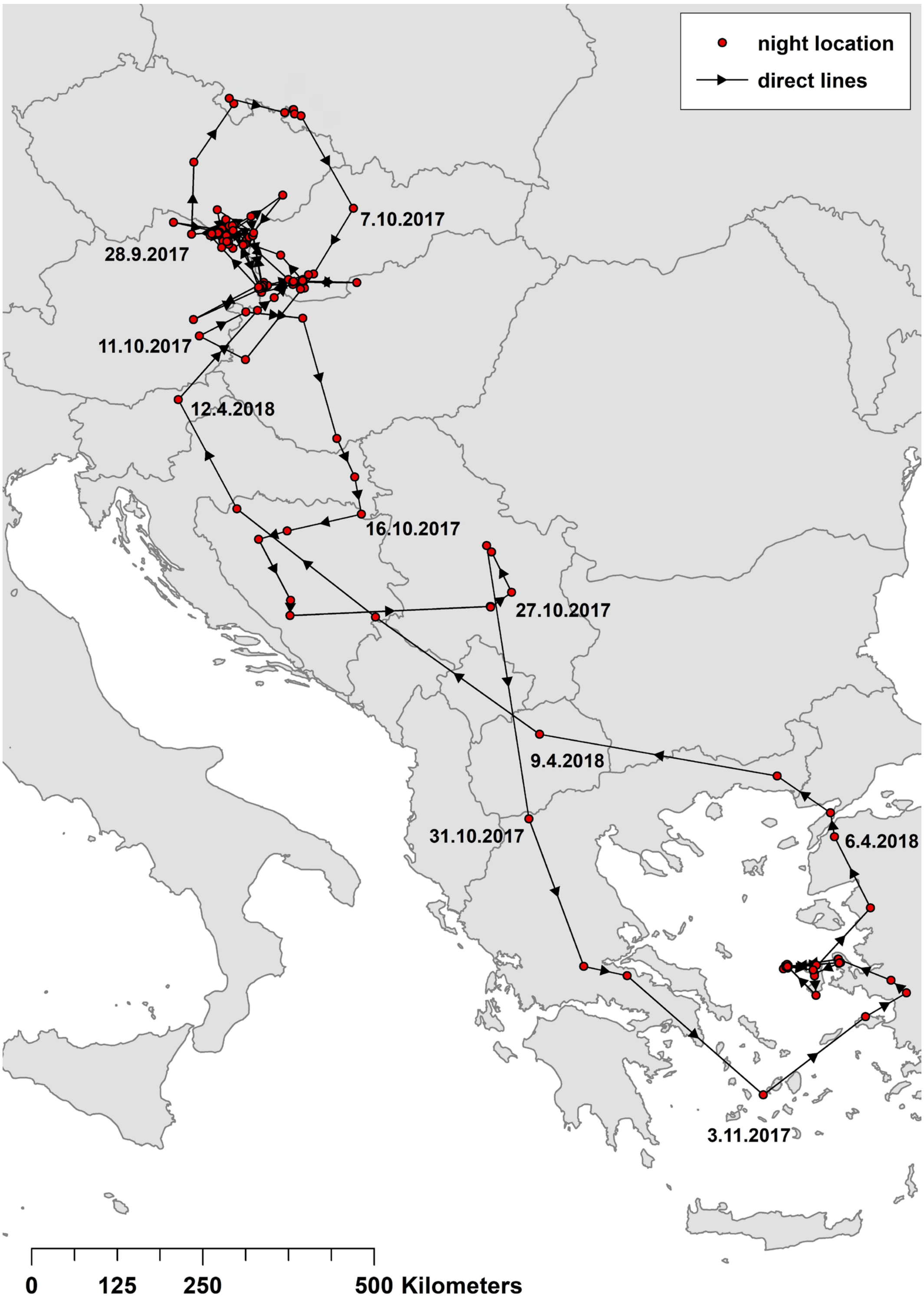

Fig. 9. Journey of eastern imperial eagle LX522 to the Greek islands of Psara and Antipsara during its first winter.

than the Slovak eagles found in Greece (1,151-1,434 km from the natal nest, Czech Bird Ringing Centre database). For imperial eagles of Czech origin, the farthest recovery of a ringed individual came from Slovakia, 397 km from its ringing site (ring no. LX56; Klvaňa & Cepák 2013), while the furthest finding of a Slovak eagle was recorded in Israel in December 1986 at a distance of 2,235 km, 162 days after ringing. One Slovak eagle was also found dead in Albania (788 km) in November 1997, 135 days after ringing. In previous studies, Chavko et al. (2018) described two ringing recoveries of Slovak eagles from Spain and Meyburg et al. (1995) recorded a dead ringing recovery from Hungary, 1,165 km from its ringing site in Greece, while Gradev et al. (2011a) recorded an eagle fitted with a GPS/GSM logger at a Bulgarian

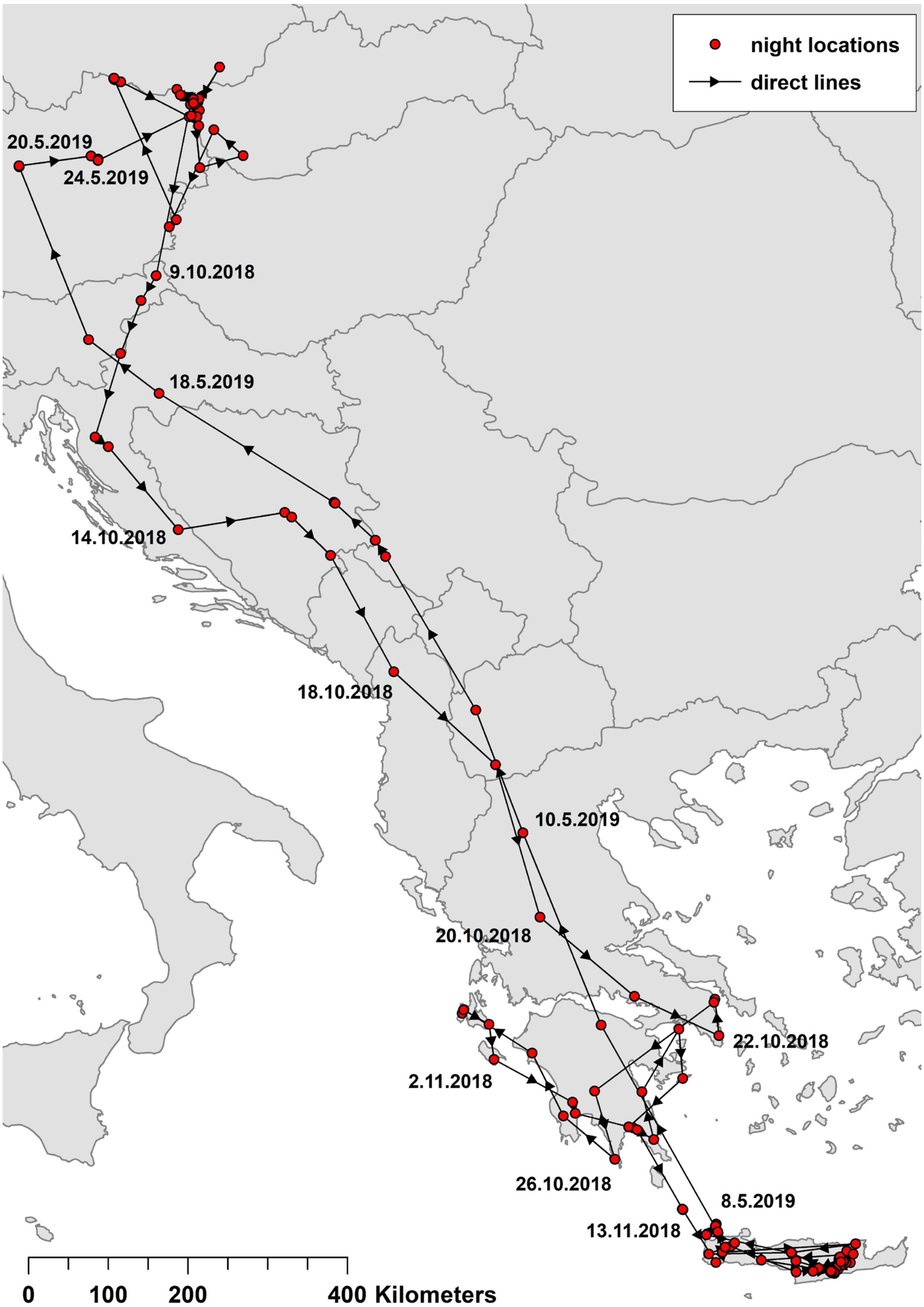

Fig. 10. Journey of eastern imperial eagle LX527 to Crete during its first winter.

rescue station flying to Greece (Rhodos), 720 km from its natal/release site. Note that, Zannetos et al. (2018) were the first to report the journey of Czech eagle LX522 to Greece.

As most of the tagged eagles only migrated short distances or stopped sending data early on, it was only possible to map detailed migration routes for two individuals during this study (LX522 and LX527). In both cases, their long-distance journeys to the Mediterranean in autumn, and their subsequent return to Central Europe the next spring, were not repeated, despite individual LX522 being tracked for four CY. Unfortunately, the final data from individual LX527 was sent in his second autumn, after which no more data were received. Our result

Fig. 11. Farthest points reached by the 18 eastern imperial eagles tracked with telemetry in this study (LX532 not included).

of 12.5% migrating individuals in 1st CY (two of 16) appears to be comparable with published data on tagged nestlings from Hungary and Austria, where just 12.3% of birds (seven of 57; Bragin et al. 2021) performed long-distance movements to Greece (five ind.), Syria (one ind.) and Ghana (one ind.). At least two different migration strategies were recorded by Meyburg et al. (2018) for tagged eagles from Slovakia, with two females from five nestlings fitted with PTT transmitters migrating to Turkey and Greece, and the other nestlings only visiting neighbouring countries. While neither of the two birds wintering in Greece in our study used the same winter site in following years, Meyburg & Meyburg (2018) noted winter site faithfulness across years in satellite-tracked imperial eagles from Saudi Arabia (birds originating from Russian, Kazakhstan and Chinese breeding populations). Thus, while our data suggests that wintering in the Mediterranean region is a minority strategy for Czech eastern imperial eagles in their first winter, the larger dataset from other countries must also be taken into account. Individuals breeding in Central and Southeast Europe and south of the Black Sea are usually year-round residents or partial- or short-distance migrants wintering in the Balkan Peninsula, Northern Africa or western parts of the Middle East, while eagles that spent summer to the east of the Black Sea are usually medium-distance migrants wintering in the Middle East or south Asia (Bragin et al. 2021).

At present, eastern imperial eagle telemetry projects are currently in operation in at least Hungary, Austria, Slovakia, Romania, Bulgaria, Northern Macedonia, Georgia and Russia (https://www.satellitetracking.eu/, retrieved 28th June 2022). However, papers and contributions have previously been published on telemetry-tracked eastern imperial eagles from Bulgaria (Gradev et al. 2011a, b, Stoychev et al. 2014, 2018, Demerdzhiev et al. 2015), Hungary (Meyburg et al. 1995, Kovács et al. 2008), Slovakia (Danko et al. 2011, Nemček et al. 2014, Meyburg et al. 2018), Turkey (Horváth et al. 2018a), Saudi Arabia (Meyburg & Meyburg 2008, 2018), Kazakhstan (Poessel et al. 2018) and Russia (Ueta & Ryabtsev 2001, Karyakin et al. 2018, Korepov & Kovalev 2018). In addition, migration patterns of the species have also been summarised for Asia by Bragin et al. (2021). Horváth et al. (2018b) also summarised data for 171 satellite-tracked individuals from Hungary (Min. No. 74, from 2011-2018), Austria (26, 2011-2018), Bulgaria (25, 2008-2014), Georgia (15, 2016-2018), European Turkey (two, 2009), Asian Turkey (11, 2017-2018), Czech Republic (seven, 2017-2018), Slovakia (six, 2017-2018) and Northern Macedonia (five, 2013).

De Rosa et al. (2017) described the journey of an imperial eagle ringed as a nestling in Slovakia to Italy, where it wintered in Sicily between 15th September 2016 and 19th April 2017, part of the time being spent in a rescue station (19th September 2016 to 22nd December 2016) after a collision with a medium voltage cable. Three of six adult eagles fitted with satellite tags at their wintering grounds in Saudi Arabia migrated back to European Russia, where they later bred (Meyburg & Meyburg 2008). Likewise, four of eight tagged individuals trapped in Saudi Arabia migrated to Russia in the spring, while one flew to Kazakhstan and one to China, the distances between summer home ranges and the wintering areas ranging between 3,900 and 5,000 km (Meyburg & Meyburg 2008). Korepov & Kovalev (2018) recorded migration distances ranging from 4,000 to 7,000 km in five imperial eagles tagged with GPS/GSM devices as nestlings in Russia (4,135, 5,223, 5,692, 5,801 and 6,952 km), with four of the five young eagles spending winter in the Arabian Peninsula and one in the Ethiopian Highlands. Ueta & Ryabtsev (2001) tracked four juvenile eastern imperial eagles from Russia (Lake Baikal) to their wintering grounds with satellite telemetry (PTT transmitters, 65 g) during 1998 (two siblings) and 1999 (two siblings from a different brood), recording migration distances of 4,215 to 4,765 km, the maximum migration distance per a day being 175-483 km. On their way, the eagles passed through eastern Mongolia and central Inner Mongolia (China), and wintered from over a region spreading from south China to Thailand. Karyakin et al. (2018) tagged 13 young eastern imperial eagles from Russia and tracked their migration routes, while Poessel et al. (2018) tracked one adult and four nestlings by telemetry (three PTT transmitters and two GPS-GSM devices) in Kazakhstan between 2004 and 2015, these birds wintering on the Arabian Peninsula, in Iran and in India (Bekmansurov et al. 2018, Poessel et al. 2018).

The higher action radius noted in the 2nd CY compared with the 1st CY is unsurprising as the eagles will have a shorter period of independence during the 1st CY, when their flying abilities may not be fully developed. Stoychev et al. (2018) summarised dispersal of 23 tracked juveniles from Bulgaria and found that their dispersal distances varied, with some birds reaching Israel, Syria, Saudi Arabia and Sudan while others stayed on the Balkan Peninsula and in Turkey. The three maximal distances travelled by 20 juveniles from natal nests were 1,132 km (ending in Turkey), 2,790 km (last location in Saudi Arabia) and 3,029 km (ending in Sudan) (Stoychev et al. 2014). Gradev et al. (2011b) demonstrated that young floaters (three nestlings with radio transmitters) were able to move freely through active territories of other breeding pairs, at least outside the breeding season.

While data on eastern imperial eagle MCP sizes are scarce, Meyburg & Meyburg (2018) recorded the wintering home range size of a four-year-old female migrating between Saudi Arabia and China as 1,360 km^2, and an adult male also tagged while wintering in Saudi Arabia as 5,900 km^2. Korepov & Kovalev (2018) reported the area covered by winter movements as 162,600 and 15,055 km^2 for two juveniles tagged in Russia and wintering in Arabian Peninsula and Ethiopian Highlands, respectively. The main weak point of some previous studies has been the relatively short research period, usually caused by the technical limitations of telemetry equipment available at that time, e.g. 4-9 months for five individuals (battery-powered satellite tags, 90 g; Danko et al. 2011), 2-6 months for two radio-tracked individuals (Danko et al. 2011), 3.5 months for one individual (PTT transmitter; Meyburg et al. 1995) or 2-10 months for five individuals (leg-mount radio transmitters, 25 g; Nemček et al. 2014). Though Nemček et al. (2014) provided MCP sizes for their tracked eagles, the sizes were obtained from a subset of all points for post-fledging areas (PFA; 89-941 km^2, n = 3) and temporary settlement areas (TSA; 68 km^2, n = 1), and were obtained using a different method than we used, meaning the results may not be fully comparable. While nobody doubts the existence of PFAs and TSAs, selection of points for delineation of these areas on the basis of a given distance is rather subjective and often results in areas containing discontinuous time data and differing numbers of individual points, making it difficult to compare polygon area sizes. However, while methodological reasons mean they are not comparable between individuals, they can serve to visualise hotspots of occurrence. Considering the variety of methods used by different authors to obtain the activity area of birds of prey, we believe that the MCP 100% method used in this study represents the best overall option, despite its known limitations (i.e. overestimation of home range and inclusion of areas with no confirmed locations; Walter et al. 2011), not least as it is minimally, it is the oldest basic measure of total space used and the only method comparable with the results of older studies.

Habitat selection in night roosting sites

We chose to analyse preferences for night-roosting sites by examining percentage use in 10 × 10 km squares with the highest number of locations. Normally, habitat preference is assessed based on all locations obtained at the individual level; however, owing to the variable number of locations obtained with regard to primary setting, different individual survival and transmission failure in our study, only the first location after midnight was used for analysis. Danko et al. (2011) described the preferred roosting sites of eastern imperial eagles, in order, as treelines and patches (81%), broadleaf forest (14%), ploughed fields (4%) and grassland (1%), which compares reasonably well with our own findings for a preference for forests (especially broadleaf), trees in patches of shrubs and sparsely vegetated areas and trees in fields or meadows and pastures.

Other studies assessing habitat selection include those of Horváth (2009); Danko et al. (2011), who looked at preferences for hunting areas; Horváth et al. (2014), who tested for the effect of age (adult/non-adult pair) and habitat (mountain or lowland agricultural landscape) on breeding success; Nemček et al. (2014), who examined general habitat composition in TSAs and PFAs; Kovács et al. (2008), who assessed available habitats in nesting territories (delimited without telemetry) and Juhász et al. (2018), who compared habitats in 14 nestling territories with telemetry (five Argos transmitters in 2011-2012 and nine GPS/GSM tags in 2013-2015), deducing that that higher diversity areas could sustain smaller territories. Finally, Poessel et al. (2018) performed a highly detailed analysis of habitats, counting with unequal availability of different habitat types in the landscape.

Population trends and threat factors for eastern imperial eagles

Between 2000 and 2010, there was a sevenfold increase in the number of known eastern imperial eagle breeding pairs in Europe (Demerdzhiev et al. 2011). The concurrent increase in the Czech breeding population is likely to have been, at least partly, part of the same positive population trend seen in Slovakia (Danko et al. 2011, Chavko et al. 2014) and Hungary (Bagyura et al. 2002, Horváth et al. 2011), the Hungarian population in particular increasing from six to 329 breeding pairs between 1980 and 2020 (Horváth 2022). Nevertheless, Bragin et al. (2021) listed a series of factors still threatening the species, including electrocution, persecution and capture for sale, while Stoychev et al. (2014, 2018), alongside electrocution, also specified factors such as shooting, poisoning and collisions. Danko et al. (2011), summarising cause of mortality in 25 eastern imperial eagles from 2003 to 2007, listed electrocution (32%), poisoning (20%), shooting (4%), collisions with power lines (8%), exhaustion (4%) and traffic (4%) as the most common factors (unknown factors 28%), while Horváth et al. (2011) rated poisoning slightly higher than electrocution as the main mortality factors in Hungarian eagles from 1980 to 2009. Finally, Schmidt & Horal (2018) and Demerdzhiev et al. (2014) both highlighted human disturbance (mainly by forest works) as key anthropogenic threatening factors causing brood loss. Importantly, no study to date has reported the use of tagging-devices to play an important role in causing traumatic injuries (Lazarova et al. 2020).

Based on the climate models described by Huntley et al. (2007), it is likely that the population will continue to expand to the north (Baltic states, Belarus and western Russia), though the publication did not then include primary breeding data for the Czech Republic. While Czech telemetry data show some random exploratory trips to the north, final data on natal dispersal for the two oldest males studied indicates that they returned to their natal area to nest for the first time (ca. 50-100 km from the natal nest). While these distances appear far from a human perspective, they most likely represent homing behaviour taken in the context of the long-distance floaters´ movements of eastern imperial eagles (Penteriani et al. 2011). A similar northerly and westerly spreading trend was also apparent from locations for newly confirmed breeding attempts in new regions (i.e. Central Moravia, Southern Bohemia) and the furthest locations for Czech floaters during the non-breeding period. Consequently, we fully expect the Czech eastern imperial eagle breeding population to expand to both Poland and Germany (Karyakin 2020) in the near future.

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Author Contributions

All authors participated in fieldwork and data collection. The first tagging in 2017 was organised by I. Literák, and that between 2018 and 2021 by D. Rymešová. D. Horal and H. Matušík supervised the field monitoring, R. Raab obtained financial support for the study, P. Spakovszky mounted the devices, D. Rymešová analysed the GIS data and wrote the first draft of the paper on the basis of I. Literák's suggestions, after consultation with D. Horal. All co-authors then improved the manuscript with their comments.

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Supplementary online material

Table S1. Eastern imperial eagle nestlings tracked with GPS/GSM devices in the Czech Republic between 2017 and 2021.

Table S2. Eastern imperial eagle breeding population size and number of nestlings ringed in the Czech Republic between 1997 and 2022.

Table S3. Longest recorded distances (km) from the native nest in different calendar years for 19 tracked eastern imperial eagles.

Table S4. Sizes of 100% minimum convex polygons (MCP; km^2) based on night roosting sites in different calendar years (CY 1-5), number of points used to create the polygon (no.) and azimuth to north of the most distant night location from the natal nest (for the whole dataset, in degrees).

(https://www.ivb.cz/wp-content/uploads/JVB-vol.-72-2023-Rymesova-et-al.-Tables-S1-S4.pdf)