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Research article

Using juvenile movements as a proxy for adult habitat and space use in long-lived territorial species: a case study on the golden eagle

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Effective conservation management of wildlife species depends on understanding their space and habitat use. Telemetry has become the primary source of data for information on how species use space and habitats. However, animals can be difficult to capture, leading to limited sample sizes and thus low quality inferences. As some individuals may be easier to capture than others, it may be tempting to use them to make inferences about the studied population as a whole. Juvenile birds, in contrast to adults, are easy to capture while they are still in the nest. However, there are few studies on when and how they might serve to obtain a representative characterization of the habitat or space use of adults. This study investigated this by using GPS-tracking data of 35 adult/juvenile dyads of golden eagles *Aquila chrysaetos*, with the juvenile and adult in a dyad sharing the same home-range. We assessed juvenile-to-adult home-range overlap and also compared their relative use of habitats within that space. We also analysed how these metrics evolved throughout the post-fledging dependence period (PFDP). During this period, juvenile-to-adult similarity was more than 80% for the entire home-range, whereas it was lower for the core area (approximately 60%). Habitat-use similarity was high, at approximately 90% for both the home-range and core area, both in land-cover and topography. The similarity increased following the improvement of juvenile flight skills over a period of two months, to the extent that two months after fledging and until the end of the PFDP, habitat and space use of juveniles can be used to infer the home-range and habitat requirements of adults. It would be valuable to study this 'adult-by-juvenile replacement' approach in other species to determine whether it could be generalized, notably for species with a shorter dependence period or more complex social interactions.

Keywords: *Aquila chrysaetos*, GPS telemetry, home-range, land-cover, topography

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Introduction

Habitat use is a central process in ecology, and information on habitat use is necessary for planning wildlife management (Morris 1992, Begon et al. 2006, Hunter and Gibbs 2007, Krausman and Cain 2022). Understanding the relationships between species and their environment (i.e. habitat or space use) is crucial for identifying species-specific habitat features of importance, a prerequisite for effective, evidence-based wildlife management, conservation and fundamental ecology (Garshelis 2000, Krausman and Cain 2022).

Since the early 2000s, GPS-tracking has allowed a significant increase in the quality and quantity of data available to study animals' habitat use (Allen and Singh 2016, Katzner and Arlettaz 2020). Yet animals can be difficult to capture, leading to limited sample sizes and to low-quality inferences regarding habitat and space use at the population level (Camacho et al. 2017, Brehm and Mortelliti 2018). Several studies have focused on the trappability of species and the difficulty of capturing certain individuals. These have highlighted differences between 'trap-shy' and 'trap-happy' personalities (Carter et al. 2012, Brehm and Mortelliti 2018) or between sexes or ages (Domènech and Senar 1997, Byrne et al. 2012, Camacho et al. 2017). When individuals are too difficult or risky to catch, studies may opt for the alternative of using individuals that are easier to catch to obtain the required telemetry data. In birds, for example, chicks in the nest are generally easier and safer to catch than adults, and in this respect would be good alternative candidates to study habitat or space use. However, this use may differ depending on an individual's sex or age class (Bolnick et al. 2003) or on its personality (Schirmer et al. 2019). These possible differences could limit making general inferences. Before using easily captured individuals as a proxy for the studied population, it is thus essential to ensure that they are representative of the space and habitat use at the population scale.

In various bird species, including seabirds and raptors, once flight skills are acquired, movement patterns are generally similar between juveniles and adults (Thorup et al. 2003, Gutowsky et al. 2014, Weimerskirch et al. 2016). For instance, in seven out of nine species of seabirds, the direction of flight path and other movement metrics were found to be very similar between adults and juveniles (De Grissac et al. 2016). Juvenile white storks *Ciconia ciconia* show similar movement metrics to adults during postnuptial migration (Rotics et al. 2016). However, in some species such as Scopoli's shearwater *Calonectris diomedea*, juveniles (1st year), immature birds (2nd–6th year) and adults (7th year and older) display differences in flight path, timing, behaviour and habitat preferences during migration (Péron and Grémillet 2013). These contrasting examples suggest that only in certain species can juveniles be used as a proxy for adults to study the space and habitat use of adults. One way to determine this is to track both adult and juveniles in the same home-range to compare and quantify their use of the same space and habitats.

Golden eagles *Aquila chrysaetos* in sedentary populations are a good model to assess such similarity between juveniles and adults. They are territorial birds whose juveniles can remain in their natal home-ranges for several months before becoming independent (Soutullo et al. 2006, Weston et al. 2018). This learning stage with their parents, the post-fledging dependence period (PFDP), lasts on average six months, including the first two months after departure from the nest when flight skills are progressively acquired (Walker 1987, Hemery et al. 2023).

Using GPS-tracking data of 35 dyads of adult/juvenile eagles, with the juvenile and adult in a dyad sharing the same home-range, we studied whether tracking a juvenile during its PFDP allows a reliable inference of space and habitat use of adults. We also assessed when this good adequacy could be achieved. Specifically, we estimated home-range overlap to compare space use, and compared habitat use within home-ranges of juveniles and adults. Since the juvenile is learning flight and hunting skills with its parents during its PFDP (Walker 1987, Watson 2010), we hypothesized that the juvenile would explore the entire home-range of its parents, and would use the same habitats (Watson 2010). However, because of this learning stage, we assumed that this would be less true in larger home-ranges, as juveniles would have more difficulty than adults in covering long distances and accessing the entire home-range (Soutullo et al. 2006). Because the flight skills of juvenile golden eagles improve in the first two months of their PFDP (Hemery et al. 2023), we also predicted that their exploration pattern would be very different over the first two months, gradually coming closer to the space and habitat uses of their parents over the following months.

Material and methods

Study species and area

The golden eagle is a large raptor of the Holarctic that occupies a wide range of habitats, from arctic tundra to subtropical deserts (Katzner et al. 2020). This species mainly hunts medium-sized mammals and birds in open areas or scrub (Watson 2010). Pairs are monogamous and build their nests on cliffs or in tree canopies (Watson 2010). Adult golden eagles actively defend a territory that constitutes their home-range (between 20 and 200 km^2), including several hunting areas (Watson 2010, Katzner et al. 2020).

In France, the species is sedentary and breeds in mountain ranges of the Alps, Massif Central, Pyrenees and Corsica (Issa and Muller 2015). We focused on two study areas: the 'Alps' (a central part of the French Alps, altitude range 205–4102 m) and the 'Massif Central' (the southern part of the Massif Central, altitude range 65–1753 m) (Supporting information). The Alps have a typical alpine climate, with extended snow cover during six months in winter and cool summer temperatures (Joly et al. 2010). The Massif Central has a more temperate climate, with little snow during winter (Joly et al. 2010), and the southernmost areas can be subject to heatwaves in summer. In the Massif Central, golden eagle pairs have much larger home-ranges (between 90 and 170 km^2) than in the Alps (between 30 and 50 km^2), due to the difference in topography and limited food resources (Ricau and Decorde 2009, Issa and Muller 2015).

In France, pairs usually raise one, or rarely two, fledglings per year (mean productivity is approximately 0.5 fledglings per year and is density dependent (Chambert et al. 2020)). Egg-laying occurs around 20 March (range: 27 February–30 April); eggs hatch around 1 May (range: 11 April–27 May); and nestlings fledge around 20 July (range: 21 June–22 August) (Hemery et al. 2023). Juveniles have a long but highly variable PFDP, averaging 177.9 days (range 44–395) after departure from the nest (Hemery et al. 2023).

Bird tagging and GPS data filtering

Between 2014 and 2022, 160 golden eagles (32 territorial adults and 128 juveniles) were equipped with GPS/GSM transmitters in the two study areas. Adults were captured with a clap-net at baited sites, whereas juveniles were captured in the nest at 48–58 days old. Age and sex were determined according to bird size and plumage (Mathieu 1985). The sex was genetically confirmed from feather samples, using the pair of primers 2550F–2718R (Fridolfsson and Ellegren 1999). Transmitters were fitted using a 14 mm Teflon Bally Ribbon harness and the X-strap thoracic backpack technique (Anderson et al. 2020). Six models from four manufacturers (Ornitela, Ecotone, E-obs and Microwave Telemetry) were used; the whole device, rings and harness weighed between 74 and 105 g: i.e. between 1.8% and 3% of an adult's body weight, as recommended by Kenward (2001).

The GPS transmitters were set to record 3D positions at intervals of 5–15 minutes. In sunny weather, with a fully charged battery, the devices could record positions at 1-minute intervals. As the interval between two locations varied between individuals, we resampled the whole dataset to 15-minute intervals. The GPS data were stored on the www.movebank.org online platform (see Data availability statement), then extracted and edited using R ver. 4.2.2 (www.r-project.org) in R-studio 2022.07.2 (www.r-project.org, RStudio Team 2022). We cleaned up the datasets to remove outliers, especially inaccurate locations, following the recommendations from Gupte et al. (2022). We applied a spatio-temporal filter by deleting obvious errors in dates and locations that were > 5000 km from the study areas and kept only data with a horizontal dilution of precision (Hdop) < 10 or a satellite number > 3 (D'Eon and Delparte 2005, Silva et al. 2017).

We tracked birds in 35 dyads composed of one adult and one juvenile in 20 home-ranges (Supporting information). In the Massif Central, we studied 26 dyads from 12 home-ranges (including five home-ranges with one specific dyad each, and seven home-ranges where the adult was tracked with two to four juveniles simultaneously or in successive years). In the Alps, we studied nine dyads in eight home-ranges (including seven home-ranges with one specific dyad each, and one home-range where the adult was tracked with two juveniles in successive years). Because adults were difficult to capture, and breeding was not successful every year, we had access to simultaneous monitoring (adult and juvenile in the same year) only for 19 of these 35 dyads; while, for the other 16 dyads, the adult was tracked in different years than its juveniles. For those 16 dyads, there was sometimes a gap of several years (from four months to six years, but usually one or two years) between the monitoring of the adult and the juvenile in the same home-range (Supporting information).

Home-range calculation

We estimated home-range by calculating kernel density estimators (KDEs) with the R-package 'amt' (Signer et al. 2019). We resampled the dataset to a 15-minute interval, which allowed us to use KDE instead of autocorrelated-KDE, and saved computational time (Fieberg 2007, Silva et al. 2022). Moreover, an animal that moves by flying, such as a bird, can easily cover its entire home-range in 15 minutes. This 15-minute interval is then often used in studies based on GPS data from birds of prey (Braham et al. 2015, Martens et al. 2018, Murgatroyd et al. 2021). We selected the 50% KDE as an estimator of the core area of each home-range as is conventionally done (Kie et al. 2010). To estimate the entire home-range, we preferred using the 99% KDE instead of the more conventional 95% KDE (Kie et al. 2010). This is because when using the 95% KDE, we noticed 'holes' inside each home-range, where many tracks were nevertheless recorded. These tracks were not 'occasional sallies outside the area' (Burt 1943), but commuting flights inside the home-range between different areas of activity, which were still included in the home-range when using the 99% KDE.

During their PFDP, juvenile golden eagles sometimes perform long-range excursions out of their natal home-range (Weston et al. 2013). The characteristics of these excursions vary between individuals in terms of length, duration or frequency (Hemery and Itty unpubl.). As the aim of our approach was to find a method to approximate adult home-range by tracking only juveniles during the PFDP, we had to discard these long-range excursions from the dataset. As we knew the adult home-range boundaries for all dyads (the 99% KDE), we visually inspected all dyads on maps and found that long-range excursions were always at distances > 1 km beyond the boundaries of the adult home-range. Therefore, we kept only the locations of the juveniles within a 1 km buffer around the corresponding adult home-range. However, in future applications of our approach, the adult home-range will be unknown. Thus, we defined another method to infer long-range excursions of juveniles. We relied on the distribution of the size of KDEs estimated using juvenile data only: the more numerous and longer the excursions, the larger the size of the KDE, with an exponential increase (Supporting information). Using a piecewise regression per juvenile, we estimated the breakpoint in the KDEs levels that best separated moderated size KDEs, assumed to characterize local movements within the natal home-range, from exponentially increasing KDEs, a priori resulting from the increasing inclusion of long-range excursions (see Supporting information for more details on this second method). We then discarded all data beyond these individual breakpoints from the juvenile datasets. As this method (hereafter referred to as the 'unknown adult home-range' method) is completely naive about the actual adult home-range, it should yield lower values of juvenile-to-adult similarities than the first method (hereafter referred to as the 'known adult home-range' method). These similarity values are those to be expected in studies that have no adult tracking data, and completely substitute adult tracking by juvenile tracking.

One year of tracking data is a minimum to have a good approximation of a golden eagle adult home-range, because of possible seasonal variations (Watson et al. 2014). For that reason, the duration of adult tracking kept for this study ranged between at least one year to seven years, depending on the date of tagging, the model of transmitter used, the survival of the individual and transmitter failures. Adult golden eagles are very faithful to their home-range, but they can use different nests inside their home-range from one breeding event to another (Watson 2010). We therefore retained all the tracking years to estimate the adult's home-range, due to our overall objective to examine the potential use of juvenile data to infer habitat use by territorial adults, encompassing variations between years and seasons. No individual was included both as a juvenile in a dyad and as an adult in another dyad. All adults were already in adult plumage at the time of the GPS-equipment (6-year old or more). Only two of them were of known age, having been ringed in the nest a few years earlier as chicks (Supporting information).

For each juvenile, we first calculated both KDEs with the individual's whole dataset during the PFDP (hereafter the 'complete period'). To analyse the temporality of home-range expansion in juveniles, we also adopted a cumulative procedure by calculating KDEs for the first 30 days after fledging, then adding 30 days at each step (60 days, 90 days, etc.) until the end of the PFDP (hereafter called the 'gradual expansion'). The last step, including the whole dataset for each juvenile, was thus the same as the complete period. Because the duration of PFDP varied between juveniles (from two to nine months), the gradual expansion combined a set of two to nine 'monthly' steps depending on the juvenile.

Similarity indices and environmental data

We compared adult and juvenile home-ranges for each dyad in terms of home-range size and shape and of habitat use within the respective home-range. For each dyad and both KDEs, we quantified the percentage of spatial similarity by using the Bhattacharyya index (hereafter 'SI' for spatial index) (Fieberg and Kochanny 2005). We transformed this index into percentages; these ranged from 0% (completely different) to 100% (completely overlapping).

As golden eagles usually require open areas for hunting and cliffs for breeding, we compared habitat using two indices: one comparing habitat use in terms of land-cover and a second in terms of topography. For land-cover, we used the Occupation du Sol (OSO) classification (www.theia-land.fr/carte-doccupation-des-sols-millesime-2018) built from remote-sensing data from the Sentinel-2 satellite with a 10 × 10 m resolution (Inglada et al. 2017). We reclassified the original OSO data from 23 classes into six classes of land-cover (Supporting information). We calculated the proportion of each land-cover class with a circular moving window of 564 m radius (i.e. 1 km^2), resulting in six different raster maps. For topography, we used the Base de Données ALTImétrique (BDALTI) digital elevation model (DEM) from France's National Geographic Institute (IGN https://geoservices.ign.fr) with a 25 × 25 m resolution. From this DEM, we calculated the vector ruggedness measure (VRM) (Sappington et al. 2007), which combined the variability of a surface in slope and aspect into a single measure. As land-cover and topography data did not have the same resolution, we rescaled them into a 50 × 50 m resolution using the averaging method of the R function *aggregate()*. From this resampled raster, we classified the ruggedness into three classes: flat terrain (VRM < 0.01), hilly terrain (VRM between 0.01 and 0.05) and rugged terrain (VRM > 0.05) (Hobson 1972) (Supporting information).

We annotated each individual location with the corresponding land-cover and VRM classes and calculated the percentage of use of each class in both KDEs. We used the Manly distance (Manly et al. 2002, Manly and Navarro 2016) in two separate indices (land-cover index, LCI; and topography index, TI) to quantify the overall habitat similarity between dyads for both KDEs. We transformed the Manly distance into percentages, and these ranged from 0% (complete difference in habitat use) to 100% (complete similarity in habitat use). For each index, to better detect differences in habitat use between adults and juveniles, we calculated, for each land-cover or topography class, the difference between a juvenile and the corresponding adult in the ratio of an individual's locations per class to the individual's total locations.

Statistical analyses

We analysed the effect of the region (Massif Central versus Alps), the size of the adult's home-range, the sex of the juvenile and the PFDP duration (two classes: early departure (departure from the natal home-range ≤ 189 days, the median of the studied population) versus late departure (departure from the natal home-range > 189 days)) (Hemery et al. 2023) on all three similarity indices (SI, LCI, TI) for both KDEs, and for both the complete period and throughout the gradual expansion. As several studies about golden eagles have shown no substantial difference between male and female territorial adults in the use of their home-range (Marzluff et al. 1997, Moss et al. 2014, Watson et al. 2014), we did not include the sex of the adult in our analyses. For the complete period, we fitted linear models (normal error distribution and identity link function) with region, sex, size and PFDP included as fixed factors. The number of repetitions of dyads in home-ranges was too low and unbalanced to add a nested dyad/home-range random effect. For the gradual expansion, we fitted linear mixed-effects models (using the 'lme4' R-package (www.r-project.org, Bates et al. 2015) with normal error distribution and identity link function), with the same fixed factors, and with dyad ID as a random term to take into account the non-independence of indices from the same dyad over time. We converted the 30-day additive steps into a numerical variable from 1 to 9 ('time' variable) used as a fixed term with a log transformation. We did not add a nested dyad/home-range random effect for the same reason as in the complete period. We performed a backward stepwise procedure and looked at p-values for each variable to determine which model was most relevant using a threshold of $p = 0.05$ (Zuur et al. 2009). We explored the residuals using the 'DHARMa' R-package (www.r-project.org, Hartig 2022). All analyses were carried out using R studio software ver. 4.2.2 (www.r-project.org). All estimates are reported as their mean [± SE] and statistical significance was set at $\alpha < 0.05$.

Results

Complete period

Spatial and habitat uses were highly similar between juveniles and adults within their home-ranges (Fig. 1; Supporting information). For 99% KDE, similarity indices averaged 83.8% [± 3.9 SE] for SI, 90.8% [± 2.0] for LCI and 94.0% [± 1.7] for TI with the 'known adult home-range' method. With the 'unknown adult home-range' method, the similarity indices were slightly lower (Table 1). For 50% KDE, both habitat use indices were high with both methods, and SI was lower (much lower with the 'unknown adult home-range' method than with the 'known adult home-range' method) (Table 1). For all six indices and the 'known adult home-range' method, the best model was the null one, meaning that the similarity between juveniles and adults was not affected by region, adult home-range size, juvenile sex or PFDP duration (Table 2; Supporting information). Estimates and 95% confidence intervals were always above 0.5, meaning that, for all six indices, the similarity between juveniles and adults significantly differed from random.

As similarity in habitat use did not reach 100% in the complete period, we explored the potential differences. Land-cover use tended to differ between juveniles and adults mainly for two classes: adults seemed to use open areas more than juveniles, whereas juveniles seemed to use forested areas more than adults, although confidence intervals were overlapping (Fig. 2). Results were similar for both KDEs. Regarding topography, for 50% KDE, juveniles seemed to use flat terrain slightly more often than adults, whereas adults used more hilly terrain (but this pattern was not observed for 99% KDE).

Gradual expansion

The three similarity indices increased during the first two months after departure from the nest (for both KDEs), reaching a plateau of high similarity at three months (mean at plateau for 50% KDE: SI = 60%; LCI = 87%; TI = 90%; mean at plateau for 99% KDE: SI = 85%, LCI = 90%; TI = 95%) (Fig. 3; Supporting information). For the SI of both KDEs, similarity was low during the first month with both methods (Table 3) showing a strong dissimilarity between juveniles and adults, whereas the values of habitat use similarity indices were already high in the first month (Table 3). For all six indices and the 'known adult home-range' method, the best model included only the 'time' variable, meaning that the similarity values between juveniles and adults did not statistically differ between region, juvenile sex, adult home-range size or PFDP duration (Table 4; Supporting information).

As similarity in habitat use did not reach 100% in the gradual expansion period, we explored potential differences. The relative underexploitation of open areas by juveniles observed for the complete period was also noticeable throughout the gradual expansion period (Supporting information).

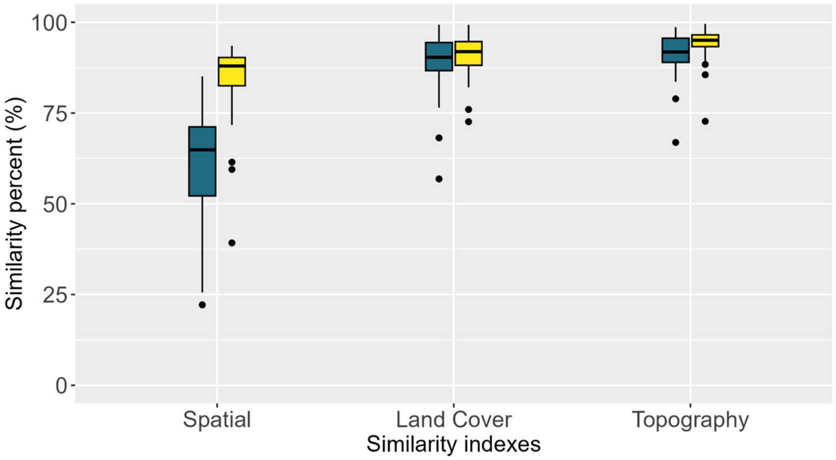

Figure 1. Distribution of the three similarity indices (spatial index, land-cover index, topography index) in home ranges of adult and juvenile golden eagles for the complete period and both 50% (blue) and 99% (yellow) kernel density estimators (KDEs).

Table 1. Mean and standard error of the three similarity indices (spatial index (SI), land-cover index (LCI), topography index (TI)) in home ranges of adult and juvenile golden eagles for the complete period and both 50% and 99% kernel density estimators (KDEs), calculated with both the 'Known adult home-range' and 'Unknown adult home-range' methods.

Method	KDE	SI [± SE]	LCI [± SE]	TI [± SE]
'Known adult home-range' method	99%	83.8% [± 3.9]	90.8% [± 2.0]	94.0% [± 1.7]
	50%	61.0% [± 5.4]	88.9% [± 2.9]	91.2% [± 2.2]
'Unknown adult home-range' method	99%	78.1% [± 5.1]	90.4% [± 2.0]	94.3% [± 1.6]
	50%	53.4% [± 6.2]	90.1% [± 2.8]	91.2% [± 1.8]

The main changes in differential habitat use throughout the PFDP was that juveniles used rocky areas more than adults at the beginning (first month), but ended up using less rocky areas than adults at the end of the PFDP (for both KDEs: Supporting information). Concerning topography, in the first month juveniles used hilly terrain more often than adults, but this difference diminished through time (for both KDEs: Supporting information).

Discussion

The spatial and habitat uses of dependent juvenile golden eagles, whether in terms of land-cover or topography, were highly similar to those of adults in the entire home-range. During their PFDP, juvenile eagles were already prospecting their natal home-range as the adults did. We expected a larger difference in behaviour between juveniles and adults for larger home-ranges because we predicted that juveniles might have more difficulty than adults in covering long distances and thus accessing the entire home-range (Soutullo et al. 2006, Guido et al. 2023). However, we did not detect any significant effect of the size of adult home-ranges or of regions, even though home-ranges were smaller in the Alps than in the Massif Central. Moreover, the lack of variation in the similarity indices despite the total PFDP duration suggests that juveniles explored their natal home-range entirely regardless of when they left it, contrary to the behaviour of Spanish imperial eagles *Aquila adalberti* (Ramos et al. 2019).

The only component of space use that differed between juveniles and adults, even at the end of the gradual expansion period, was the core area of the home-range: juveniles spent most of their time in a smaller core area than adults. However, habitat use was similar within this core area. The fact that we used the data for each adult over their whole tracking period, in order to integrate breeding and non-breeding years, could explain this weaker spatial similarity. This allowed us to obtain a good estimate of the long-term use of the home-range by adults with a reduced effect of the central-place foraging behaviour. Moreover, in breeding years, the adult pair can use a different nest site each year within the core area of their home-range (Orians and Pearson 1979, Watson 2010). The observed difference in spatial pattern for the core area may thus be because the data for the juveniles were associated to the nest where they hatched (Soutullo et al. 2006, Hemery et al. 2023), while the data for the corresponding adult may have included several years, and thus several nests. We chose to include all available years per adult because we wanted to assess juvenile-to-adult habitat use similarity in general, at the home-range scale. We did not want to restrict our approach to synchronous parent–offspring similarity (i.e. half-shared genomes in the same year) because of our ultimate goal was to investigate when juvenile data could be used to infer habitat use by a territorial adult, including differences between years and between seasons. Nonetheless, even though the core area of the adults was delimited less precisely than the entire home-range, it was still representative of their core area (index above 50%), and the similarity in habitat use was strong for these core areas. High similarity in habitat use has also been demonstrated between territorial and non-territorial golden eagles in Scotland: intruders/newcomers use habitat in a very similar way as the home-range owners (Fielding et al. 2023). This suggests that habitat use is primarily determined by the local conditions, rather than individual familiarity with the site.

The results showed some differences in space and habitat use between juveniles and adults, since none of our indices reached 100% similarity. Land-cover use tended to differ between juvenile and adult golden eagles mainly in two land-cover classes: adults seemed to use open areas more than juveniles, whereas juveniles seemed to use forested areas more than adults. During the first weeks after fledging, juveniles stayed more in forested areas, which may conceal them from predators and thus be safer (Watson 2010). Moreover, perching on steep cliffs could also be challenging for juveniles

Table 2. Estimates from the best linear models for each similarity index and for the two home-range metrics (50% and 99% kernel density estimators (KDEs)) over the complete period.

Response variable	KDE	Model	Parameters	Estimates	SE	95% Confidence Interval
Spatial index	99%	Null	Intercept	0.84	0.02	[0.80; 0.88]
	50%	Null	Intercept	0.61	0.03	[0.55; 0.67]
Land-cover index	99%	Null	Intercept	0.91	0.01	[0.89; 0.93]
	50%	Null	Intercept	0.89	0.01	[0.87; 0.91]
Topography index	99%	Null	Intercept	0.94	0.01	[0.92; 0.96]
	50%	Null	Intercept	0.91	0.01	[0.89; 0.93]

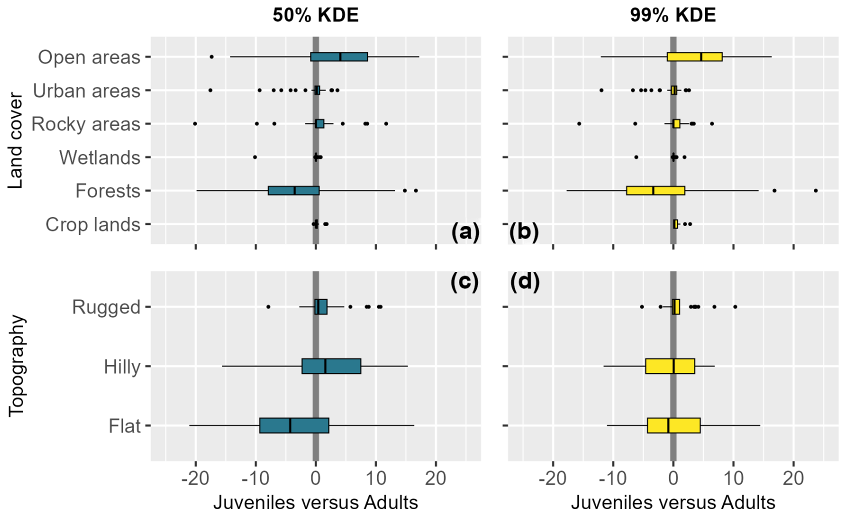

Figure 2. Differences in habitat use between juveniles and adult golden eagles in terms of land cover (a) and (b) and topography (c) and (d) for the complete period. Results of the 50% kernel density estimators (KDE) are in the left panel (blue), and those of the 99% KDE are in the right panel (yellow). On each graph, the x-axis represents the differences in habitat use between adults and juveniles, which were calculated for each habitat class as the difference between a juvenile and the corresponding adult in the ratio of an individual's locations per habitat component to the individual's total locations. The grey line shows a lack of difference in habitat use between juveniles and adults. Positive values indicate a habitat used more by adults than juveniles, and negative values indicate the reverse.

at first, due to the more turbulent airflow close to rugged terrain (Reddy et al. 2016). Juveniles may thus spend more time in refuge areas and less time hunting than their parents. Indeed, during their PFDP, only 26% of the daily locations of juvenile golden eagles involved flying; the remaining 74% locations involved perching. Whereas for adult golden eagles, 39% of the daily locations involved flying and 61% involved perching over the whole period they were tracked (Hemery and Itty unpubl.). As long as the juveniles are fed by adults, they are likely to hunt less and use open areas less, spending more time in resting areas (Watson 2010, Katzner et al. 2020). It would be of interest to investigate whether parents and offspring move together and how often, depending on the habitats and the different areas of the home-range. Studying simultaneous trajectories of juvenile–parent pairs would make it possible to evaluate if these differences in habitat use are related to moments when adult and juvenile trajectories diverge.

Spatial and habitat similarity indices increased during the first two months after juveniles left the nest, before reaching a plateau in the third month. The pattern was similar for all indices for the entire home-range and the core area. Furthermore, the spatial index of the core area and the entire home-range showed a strong dissimilarity during the first month, meaning that the monitoring of juvenile golden eagles during this first month provided a biased assessment of the space use of the adults. With an extra month of monitoring, the spatial index of the entire home-range rose from rather dissimilar to rather similar and became more representative of the adult home-range. For the core area, only in the third month did this index rise above this threshold. This lower similarity in the first two months was not related to a sampling effect due to a smaller number of locations during the first month, because a 15-minute interval over 30 days provided datasets large enough to estimate home-ranges (Silva et al. 2022). These patterns most likely resulted from limited juvenile flight skills during the few weeks following fledging, as has been described in golden eagles (Soutullo et al. 2006, Hemery et al. 2023) and in other raptor species such as vultures and condors (Harel et al. 2016, Martens et al. 2018, Guido et al. 2023). During the first few weeks, juveniles remain in the immediate vicinity of the nest, move little and are not yet able to follow their parents and explore their natal home-range. Juvenile bearded vultures gradually increase the distance from the nest and their home-range size during the PFDP (López-López et al. 2014, Krüger and Amar 2017). The home-range of juvenile Spanish imperial eagles also extends continuously during their PFDP, as their soaring and gliding skills improve (Ramos et al. 2019). The increase in similarity we observed is likely synchronized with the acquisition of better flight skills, which occurs in the first two months after fledging in juvenile golden eagles (Weston et al. 2018, Hemery et al. 2023).

Knowledge about a species' space and habitat uses is fundamental for many wildlife management programmes, but it often takes a long time to acquire. Yet, in some cases, a quick and easy assessment of individuals' home-range is required: for example, in environmental impact assessments for planned anthropogenic infrastructures. For instance, in micro-siting to determine the position of turbines in windfarms, it can be a long, complex and risky process to obtain representative telemetry data for locally breeding adults of at-risk large birds. In cases such as this, inference of potential habitat loss and collision risk would be more readily and rapidly obtained by equipping some locally born juveniles with tags before fledging. In the populations we studied, tracking juveniles does

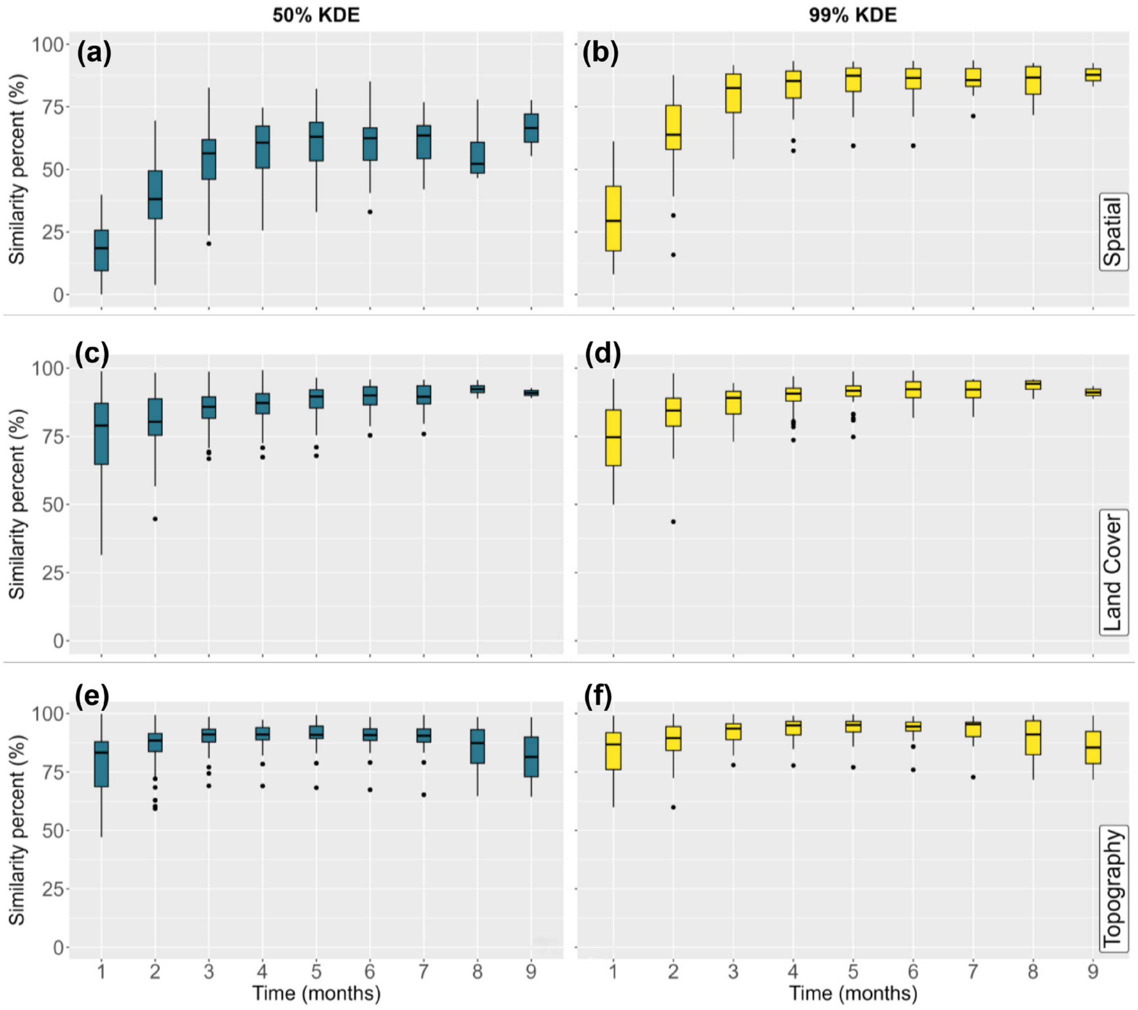

Figure 3. Distribution of the three indices for the gradual expansion analysis: spatial index (a) and (b), land-cover index (c) and (d), and topography index (e) and (f), for the 50% KDE (left panel, blue), and the 99% KDE (right panel, yellow).

not introduce much of a bias or financial risk, as the mortality of juveniles before they leave their natal home-range is very low (among juveniles, which were equipped with GPS since 2016, only 3% died before fledging – of natural causes – and only 11% died between fledging and the end of their PFDP – of natural and anthropogenic causes). However, for species with higher juvenile mortality rate, wildlife biologists and practitioners must balance the benefits of easily tracked juveniles with the financial costs of losing tags prematurely due to death. Furthermore, our results show that, in the case of golden eagle, it is essential to collect data beyond the first two months after fledging, when juveniles are still learning to fly (Hemery et al. 2023). In the case of other species or other populations of golden eagles, a wise precaution would be to check how long after fledging the juvenile tracking data differ from those of their parents.

As expected, the space use of juveniles differs significantly from that of adults during the first two months after departure from the nest. It is only from the third month onwards that juveniles' space use becomes comparable to that of adults. In the case of sedentary populations of golden eagles with a low juvenile mortality rate, the results of our study

Table 3. Mean and standard error of the three similarity indices (spatial index (SI), land-cover index (LCI), topography index (TI)) in home-ranges of adult and juvenile golden eagles for the first month of the gradual expansion and both 50% and 99% kernel density estimators (KDEs), calculated with both methods 'Known adult home-range' and 'Unknown adult home-range'.

Method	KDE	SI [± SE]	LCI [± SE]	TI [± SE]
'Known adult home-range' method	99%	31.4% [± 5.2]	74.3% [± 4.3]	83.1% [± 4.0]
	50%	18.2% [± 3.8]	75.4% [± 6.1]	78.2% [± 5.1]
'Unknown adult home-range' method	99%	33.4% [± 4.9]	74.8% [± 4.2]	81.9% [± 4.3]
	50%	18.8% [± 3.6]	73.6% [± 5.4]	85.0% [± 4.3]

Table 4. Estimates from the best linear mixed-effects models for each similarity index and for the two home-range metrics (50% and 99% kernel density estimators (KDEs)) over the gradual expansion, with a log effect on the 'time' variable and the dyad ID as a random term (IDdyad).

Response variable	KDE	Model	Parameters	Estimates	SE	t-value	p-value	Pseudo-R^2 (total)
Spatial index	99%	log(Time) + (1|IDdyad)	Intercept	0.39	0.02	19.18	< 0.001	78%
			log(Time)	0.29	0.01	23.99	< 0.001	
	50%	log(Time) + (1|IDdyad)	Intercept	0.22	0.02	9.34	< 0.001	85%
			log(Time)	0.24	0.01	25.44	< 0.001	
Land-cover index	99%	log(Time) + (1|IDdyad)	Intercept	0.76	0.01	59.14	< 0.001	70%
			log(Time)	0.09	0.01	14.27	< 0.001	
	50%	log(Time) + (1|IDdyad)	Intercept	0.75	0.02	45.28	< 0.001	69%
			log(Time)	0.07	0.01	9.66	< 0.001	
Topography index	99%	log(Time) + (1|IDdyad)	Intercept	0.84	0.01	73.91	< 0.001	56%
			log(Time)	0.06	0.01	9.21	< 0.001	
	50%	log(Time) + (1|IDdyad)	Intercept	0.80	0.01	55.28	< 0.001	62%
			log(Time)	0.07	0.01	9.46	< 0.001	

indicate that juveniles, which are easier and safer to catch than adults, could then be a suitable alternative for identifying key habitats components and home-ranges. However, the longer juveniles are monitored during their PFDP, the better the proxy, for the same reasons as for territorial adults, for whom the longer the monitoring period, the better the home-range estimate (Watson et al. 2014). Nevertheless, the juveniles leave their natal home-range after a few months, averaging six months in our study population (Hemery et al. 2023). Similarity will therefore never reach 100%, as the one-year tracking period cannot be achieved. When looking for a proxy, the challenge is not to obtain maximum precision and representativeness, but rather to achieve optimal representativeness while maximizing the cost/risk/benefit trade-off. Using juvenile tracking data as a proxy of adults could maximize this trade-off and correctly identify the habitats of importance for adults within their core area. These core areas are the parts of the home-range on which the main activities of individuals are concentrated (Burt 1943), including breeding and perching sites, and foraging areas (Sergio et al. 2006, Watson et al. 2014).

Identifying the key habitat components that characterize these core areas is also of major value for wildlife management and conservation (Balbontín 2005, Katzner and Arlettaz 2020). Our findings show that using juvenile tracking data, even just after fledging, allows the rapid identification of the habitats used within the core area. In another study, Miller et al. (2017) studied a migratory population of golden eagles in North America and noticed that in winter and in summer areas, even if juveniles had larger home-ranges than adults, both were composed of the same habitats. In this migratory population, juveniles could then be used as a proxy to highlight the key habitat components for this species throughout the year. We suspect this would also be the case for other territorial species with a relatively long PFDP such as the harpy eagle *Harpia harpyja* or the martial eagle *Polemaetus bellicosus* (Muñiz-López et al. 2012, Kemp et al. 2020). Conversely, other raptor species have a short PFDP, with juveniles leaving their natal home-range as soon as they have acquired flight skills, such as Bonelli's eagles *Aquila fasciata* (Cadahía et al. 2008) and red kites *Milvus milvus* (Bustamante 1993). For these species, the tracking of adults is likely irreplaceable, as juvenile space use is likely to be insufficiently precise and representative of that of adults at the time of their departure from the natal home-range. The length of the PFDP varies between species and may also vary between populations of the same species. Further research could provide additional information on the possible use of juveniles as proxies, depending on the length of the PFDP of the species and/or populations concerned.

In this study, long-range excursions of juveniles out of their natal home-range were discarded using two different methods ('known adult home-range' method and 'unknown adult home-range' method). However, the spatial and habitat inferences were the same with both methods: the similarity was always high for the spatial index of the 99% KDE for the complete period and for all of the habitat indices. With both methods, the pattern was also the same for low similarity, which was found for the spatial index of the 50% KDE for the complete period and for the spatial indices of both KDE for the first two months of the gradual expansion. This overall very high similarity, even with the method that ignores actual adult home-range, supports the hypothesis that adult-by-juvenile replacement is a robust option for assessing local habitat use when capturing an adult for tagging is too risky or costly.

The PFDP is an ontogenetic stage during which juveniles improve their flight skills and their foraging ability while they follow their parents until they become autonomous (Walker 1987, Watson 2010). They are frequently observed using the same perching and roosting sites as their parents, or flying with them above hunting grounds or soaring together in thermals (Watson 2010). This learning stage with adults has been described in many raptor species, e.g. in the eastern imperial eagle *Aquila heliaca* (Alonso et al. 1987) and in the Spanish imperial eagle (Ramos et al. 2019). Juveniles following their parents during their learning stage is also common in many other species and is sometimes used as a proxy to study different processes such as migration or foraging. In migrating birds, mixed flocks of adults and juveniles are common, especially for storks, geese and cranes (Rotics et al. 2016, Kölzsch et al. 2020, Batbayar et al. 2021). Juveniles stay with adults and follow them during the migration, allowing them to learn migration routes and stopovers (Batbayar et al. 2021), as well as how to fly in an efficient way (Rotics et al. 2016, Kölzsch et al. 2020). Apart from birds, in studies on ungulates and other large mammals, for instance, the tracking of the mother is used as a proxy of the juvenile in its natal homerange (Espmark 1971, Larue et al. 2018). In various species, once motion skills are acquired, movement patterns are then similar between juveniles and adults, and using some individuals as a proxy for the studied population is therefore possible.

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Author contributions

Arzhela Hemery: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal). **Olivier Duriez**: Methodology (equal); Supervision (equal); Writing – original draft (equal). **Christian Itty**: Conceptualization (equal); Data curation (equal); Investigation (equal); Resources (equal). **Pierre-Yves Henry**: Methodology (equal); Supervision (equal); Writing – original draft (equal). **Aurelién Besnard**: Conceptualization (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – original draft (equal).

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Supporting information

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

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