# Space use and site fidelity in the endangered Northern Bald Ibis *Geronticus eremita*: Effects of age, season, and sex

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**Summary**

Understanding space use of endangered species is critical for conservation planning and management. The advances in technology and data analysis allow us to collect data with unprecedented quality and inform us about the movements and habitat use of individuals and groups. With only about 700 individuals left in the wild, the Northern Bald Ibis *Geronticus eremita* is currently categorised as 'Endangered'. However, little is known about the movements of this avian species in relation to breeding and individual differences. Using GPS transmitters we studied the movements of 32 Northern Bald Ibis from a semi-wild free-flying colony at the Konrad Lorenz Research Center in Austria during 1–4 years per individual. We investigated how sex, age class, breeding and non-breeding season affect space use and site fidelity. We found that individuals consistently showed high site fidelity, adults more than juveniles, and space use was highly overlapping between individuals and over successive years. When moving between different areas birds used consistent flyways thereby avoiding direct routes over mountainous areas. Adults had more expansive space use during the breeding season as compared to the non-breeding season, while juveniles only showed a slight decrease during the non-breeding season. We found no sex differences regarding space use or site fidelity. Our results lead to a better understanding of how Northern Bald Ibis move through their environment and how they use foraging areas, roosting sites, and space in general that in turn can help to inform conservation management of extant colonies and reintroduction programmes for new colonies.

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## Introduction

Movement patterns and space use of individuals and populations are closely linked with survival and fitness and are therefore a key topic in conservation (Berger-Tal *et al.* 2011). Technologies, such as GPS transmitters, have greatly improved wildlife monitoring and generate valuable information for management decisions that involve patterns of habitat use (Berger-Tal and Lahoz-Monfort 2018). Distribution patterns, abundance and biodiversity are affected by land-scape characteristics (Saïd and Servanty 2005) and fragmentation (Fritz *et al.* 2003). Human pressures on the environment (i.e. land cover change, infrastructure, access into natural areas), including actions that inhibit road-crossing movements (Laurance *et al.* 2004, Ascensao *et al.* 2017) or human sea traffic that affects marine mammals' movement patterns (Timmel *et al.* 2008, Rutz *et al.* 2020), highlight the need to implement conservation measures (Venter *et al.* 2016, Rutz *et al.* 2020). About 40% of the world's bird populations are already in decline, mostly because of agriculture, logging, hunting, invasive species, and climate change (BirdLife International 2018, Rosenberg *et al.* 2019), emphasizing the need to generate new or improve existing conservation management strategies. Thus, knowledge about individuals' home ranges and individual variation in habitat use, as well as information about where foraging activities, mating and offspring rearing occur are relevant to better manage threatened populations and species.

Individual space use is affected by abiotic factors, such as habitat quality (Betts *et al.* 2008, Bjørneraas *et al.* 2012) or season (King *et al.* 2016, Ofstad *et al.* 2019), and individual factors, such as age (Šklíba *et al.* 2016), sex (Aronsson *et al.* 2016, Ofstad *et al.* 2019), or reproductive status (Aronsson *et al.* 2016, Wikenros *et al.* 2016). In Black-Throated Blue Warblers *Dendroica caerulescens*, older individuals tend to occupy high quality habitats and leave lower quality

habitats to younger individuals (Holmes *et al.* 1996). Such studies underscore the significance of age in space use patterns. In moose *Alces alces*, males showed greater space use than females during summer (calve rearing period) but not during winter (Ofstad *et al.* 2019). Similarly, Eurasian lynx *Lynx lynx* had sex-specific and seasonal space use: males reduced their space use during mating season and were near females, while females reduced their space use during post-partum when constrained by the impeded movement of offspring (Aronsson *et al.* 2016).

Individuals often return to specific areas within their home range, such as profitable foraging areas or water holes. In red deer *Cervus elaphus*, for example, individuals regularly return to high value foraging patches (Seidel and Boyce 2015), while in forest elephants *Elephas maximus borneensis*, individuals return frequently to foraging areas where they had spent more time in the past (English *et al.* 2014). Site fidelity has been found to be dependent on various factors, such as habitat variability and quality (Switzer 1993, 1997), but also age (Switzer 1997, Pyle *et al.* 2001), sex (Beheler *et al.* 2003) or breeding success (Shields 1984). Site fidelity is expected to be favoured in predictable habitats, while increasing unpredictability is expected to lead to an increase in movement to more 'attractive' habitats when habitat quality is unequal among available habitats (Switzer 1993). In particular, species showing a high degree of site fidelity are more likely to face population decline due to habitat degradation and loss (Warkentin and Hernández 1996). In forest passerines, site fidelity increased with age in declining species that use shrubland during migration (Schlossberg 2009). Different levels of site fidelity would require different conservation strategies (Theobald *et al.* 2000, Schlossberg and King 2007), demanding in some cases tailored conservation approaches at the species or even population level.

The colonial Northern Bald Ibis *Geronticus eremita* is an 'Endangered' avian species (BirdLife International 2020), with only about 700 individuals left in the wild in the Souss Massa National Park in Morocco (Oubrou and Bekkay 2018) and additionally about 230 individuals in semi-captivity in the Birecik Breeding Centre in Turkey with the last wild birds in Syria thought now to be locally extinct (Böhm *et al.* 2020). The main factors leading to the disappearance from its former range are habitat destruction, persecution, and agricultural pesticides (Hirsch 1976, 1979, Collar *et al.* 1985). Due to reintroduction projects across Europe, the Northern Bald Ibis is also present in Spain, Austria, and Germany (Quevedo *et al.* 2004, Unsöld and Fritz 2014); but these populations are not self-sustaining yet and rely on management. Despite occupying different environments to that of the remaining wild birds in Morocco and elsewhere, valuable lessons can be learned from tracking a semi-wild but free-flying colony, as all birds are individually marked and long-term data collection is possible allowing conclusions at individual and group level. The birds are seasonally monogamous, and both older individuals (Sorato and Kotrschal 2006) and males (Böhm and Pegoraro 2011) have higher social dominance rank compared to younger individuals and/or females. Northern Bald Ibis perform movements on different scales, i.e. migration (Syrian population; Lindsell *et al.* 2009, Serra *et al.* 2015) and dispersal (Serra *et al.* 2015, Böhm *et al.* 2020) on a large scale, and diurnal movement patterns when they forage in different sized subgroups during the day and roost together at night on a smaller scale (Smith *et al.* 2008, Böhm and Pegoraro 2011). Younger birds are more likely to disperse than older birds (Böhm *et al.* 2020) and younger individuals in the extinct migratory eastern population in Syria (Böhm and Bowden 2016) seemed to have a different overwintering area than adults (Lindsell *et al.* 2009). Only

a few data on movement and habitat use exist from extant or recently extinct populations and these data indicate that Northern Bald Ibis are rather consistent in habitat use (Serra *et al.* 2008). However, to protect the remaining colonies and aid the reintroduction of further populations, a better knowledge about their movement behaviour is needed.

In this study, we investigate space use of individually marked and free-flying Northern Bald Ibis. Specifically, we measure (1) the area used, (2) the consistency of space use over time, (3) the consistency of flyways between areas, (4) site fidelity to locations of interest, and (5) factors (sex, age class, biological relevant season) that may influence space use and site fidelity. We tested the prediction that Northern Bald Ibis will differ in space use between age classes (juveniles and adults) and seasons (breeding and non-breeding season), but still show large overlap between individuals and years. We expect a consistent use of particular sites over time and consequently a consistent use of flyways between areas. Specifically, we predict (1) no sex differences in space use and site fidelity due to relatively similar behavioural patterns in both females and males (Sorato and Kotrschal 2006), (2) restricted space use by adults compared to juveniles during the breeding season compared to the non-breeding season due to parental care in breeding individuals (Zurell *et al.* 2018) and juvenile dispersal during autumn (Böhm *et al.* 2020), and (3) consistent high site fidelity to locations of interest (e.g. foraging habitats) due to rather predictable habitats, and higher site fidelity in adults than juveniles as site fidelity increases with age (Switzer 1993).

## Methods

### Field site and study animals

This study was conducted at the Konrad Lorenz Research Center in Grünau im Almtal (Upper Austria, 47°48'E, 13°56'N; Figure 1). The colony at the research center was the first semi-wild free-living colony north of the Alps in 400 years (Kotrschal 1999). The year-round free-flying Northern Bald Ibis colony has access to an open aviary at the local Herzog-von-Cumberland game park (approximately 20 x 15 x 7 m [L x W x H]). The only exception to this free-flight access was in 2013, when all birds were locked inside the aviary from 2 to 12 July 2013 as part of an experiment (Puehringer-Sturmayr *et al.* 2020). During the post-fledging period, birds forage in the Almtal valley and return to the aviary for roosting and breeding. During summer and early autumn (approximately from July to September), the birds usually fly to the vicinity of Molln (a village 25 km linear distance from the research centre) and return late autumn to Grünau im Almtal when decreasing temperature constrains food availability (Frigerio and Gegendorfer 2013). All birds are individually marked with combinations of coloured leg rings and a metal leg ring with a unique alphanumeric code from the German or Austrian ornithological station. During the winter and breeding season, birds are food supplemented (hash made from 1-day-old chicks and beef heart, mixed with soaked dry dog food and insects) at the meadow in front of the research center or in the aviary. During winter (November to February), food is available *ad libitum* and all individuals are able to feed to saturation; during the breeding season (March to June), the supplemental feeding is made available twice per day (08h00, 15h00) and birds regularly forage on the nearby foraging grounds. The birds are not supplemented with food during summer and autumn. At the time of data collection, the colony had the following group sizes: $N_{2013} = 70$, $N_{2014} = 53$, $N_{2015} = 41$, $N_{2016} = 51$ birds. On average, $17 \pm 8$ (mean $\pm$ SD) chicks fledge each year. In 2013, a population
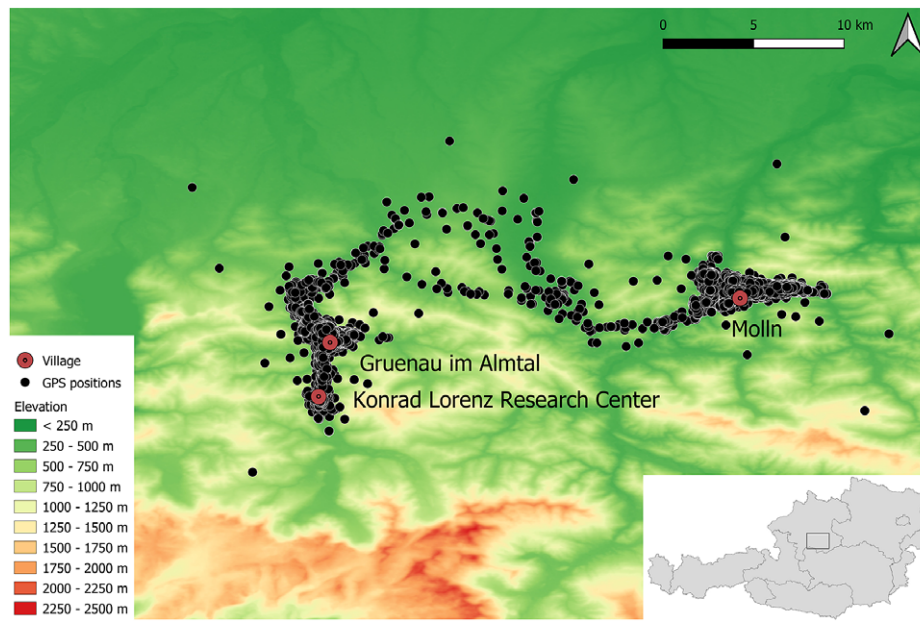
**Figure 1.** Study area in the northern Austrian Alps. The GPS positions of 32 Northern Bald Ibis are shown (black dots). On the bottom right a map of Austria is shown with a rectangle indicating the main map. Background digital elevation model (DEM) was derived from oe3d in spatial resolution 1 arc second (approximately 20–30 m, http://www.oe3d.at/).

increase was recorded because of the exceptionally large number of fledged chicks (27 individuals). The population decreased between 2013 and 2014 due to juvenile dispersal (Böhm et al. 2020) and higher predation by birds of prey.

### Study design

From 2013 to 2016 during the breeding and non-breeding season a total of 32 focal individuals (17 males and 15 females; sex of the individuals was determined genetically, from blood samples after polymerase chain reaction done at Laboklin GmbH and Co.KG; for details on individuals see Table 1) were equipped with backpack-mounted GPS transmitters using a harness (as described in Lindsell et al. 2009; GPS transmitters were removed during winter from November to March). Out of those, 12 birds were GPS-tagged over several successive years (i.e. between 2 and 4 years; Table 1). Focal individuals were classified into two age classes according to Böhm and Pegoraro (2011): (1) juveniles, i.e. immature and subadult birds (first to third year after hatching; $N_{2013} = 5$ [two males and three females], $N_{2014} = 0$, $N_{2015} = 7$ [three males and four females], $N_{2016} = 2$ [two females]), and (2) adults (from fourth year on; $N_{2013} = 6$ [four males and two females], $N_{2014} = 4$ [one male and three females], $N_{2015} = 10$ [five males and five females], $N_{2016} = 14$ [nine males and five females]). The potential lifespan for the Northern Bald Ibis in captivity is 30–40 years (Böhm and Pegoraro 2011). The start and end of the breeding season were determined separately for each breeding individual depending on the individual variation in the start of egg-laying. Breeding season started with the first laid egg (laid between 6 February and 27 March) and ended with the last fledged chick (fledged between 8 June and 9 July) in a single clutch for breeding individuals (average number of days breeding = 74 days). To be able to compare the spatial use of breeders and non-breeders during the breeding season, we defined this period for the non-breeders as the time from the first laid egg till the last fledged chick of the colony. Non-breeding season

comprised summer and autumn (i.e. period in which no supplemental food was provided), but not the wintering season.

### Measuring space use patterns with GPS transmitters

GPS data were collected from April 2013 to October 2016 during the breeding and non-breeding season. Focal individuals (with body mass ranging from 1,020 g to 1,500 g at the start of the study) were equipped with GPS transmitters (Ecotone® Telemetry, Sopot, Poland; http://ecotone-telemetry.com/en) that were all solar powered and data were downloaded via a UHF link (model: HARIER, weight: 20 g) or using the GSM network (model: DUCK-4 Solar, weight: 28 g; model: SAKER M, weight: 19 g). Fitting the loggers on the birds lasted on average 18.6 ± 4.7 minutes (mean ± SD) per bird. The loggers constituted less than 3% of the body mass of the smallest bird (Phillips et al. 2003). Although GPS transmitters are suspected to cause unilateral corneal opacity in two other Northern Bald Ibis populations (Fritz et al. 2020), we did not observe such a physiological effect or any physical damage, such as abrasion or feather loss, in our study population. We also could not find effects of the GPS transmitters on behaviour or body weight in Northern Bald Ibis, but we found an increase in the excretion of corticosterone metabolites about a month after deployment (Puehringer-Sturmayr et al. 2020).

We monitored complete daily movements between 04h00 and 19h00. The average tracking interval between GPS fixes was 62.46 ± 22.71 minutes (mean ± SD). In case of low battery status during bad weather conditions, we increased the time between two fixes to enable a quicker recharging of the batteries.

### Data analysis

Calculations of space use and site fidelity to locations of interest were treated separately over successive years since GPS transmitters were removed during winter. As the sampling rate differed between individuals, we reduced the GPS data points to an hourly sampling

**Table 1.** Focal individuals. Name, sex (m = male, f = female), year of hatching, age class, year/s with GPS data (2013–2016), number of GPS positions (*n* fixes), space use size of the 95% utilisation distribution (95% UD) and number of days the individuals were tagged are indicated.

| Individual | Sex | Year of hatching | Age class | Year of deployment | *n* fixes | 95% UD [km²] | Days tagged |
|---|---|---|---|---|---|---|---|
| Agatha | f | 2011 | juvenile | 2013 | 1234 | 0.36 | 86 |
| Aleppo | f | 2006 | adult | 2014 | 2289 | 1.28 | 201 |
| | | | | 2015 | 2792 | 0.21 | 173 |
| | | | | 2016 | 3955 | 0.72 | 217 |
| Azzurro | m | 2015 | juvenile | 2015 | 2772 | 0.18 | 171 |
| Balu | m | 2010 | adult | 2015 | 2472 | 1.54 | 175 |
| Cian | m | 2008 | adult | 2013 | 1502 | 0.17 | 84 |
| | | | | 2016 | 2868 | 2.30 | 190 |
| Diabolo | f | 2014 | juvenile | 2016 | 2684 | 0.79 | 150 |
| Ferdinand | m | 2013 | juvenile | 2013 | 1378 | 0.45 | 86 |
| Gina | f | 2013 | juvenile | 2013 | 749 | - | 64 |
| Goran | f | 2005 | adult | 2013 | 1193 | 0.07 | 66 |
| Hermine | f | 2012 | adult | 2015 | 3136 | 2.23 | 211 |
| | | | | 2016 | 1021 | 0.39 | 48 |
| Hilda | m | 2009 | adult | 2013 | 1098 | 0.22 | 86 |
| | | | | 2016 | 159 | 0.81 | 25 |
| Hombre | m | 2002 | adult | 2015 | 3202 | 1.59 | 205 |
| Jarmusch | m | 2005 | adult | 2013 | 1853 | 0.12 | 110 |
| Khan | m | 2013 | adult | 2016 | 3102 | 1.81 | 207 |
| Kleopatra | f | 2013 | juvenile | 2015 | 2998 | 1.03 | 201 |
| | | | adult | 2016 | 3812 | 0.66 | 210 |
| Loki | f | 2006 | adult | 2014 | 2684 | 1.02 | 238 |
| | | | | 2015 | 3363 | 1.01 | 214 |
| Lukas | m | 2012 | juvenile | 2013 | 1403 | 0.45 | 86 |
| | | | adult | 2016 | 2940 | 1.54 | 196 |
| Othello | m | 1999 | adult | 2015 | 3229 | 0.91 | 191 |
| | | | | 2016 | 3096 | 0.79 | 215 |
| Ozzy | m | 2010 | adult | 2016 | 3439 | 1.96 | 208 |
| Rob | m | 2010 | adult | 2013 | 1533 | 0.16 | 86 |
| Rosa | f | 2013 | juvenile | 2013 | 1448 | 0.29 | 85 |
| Sandro | f | 2015 | juvenile | 2015 | 2869 | 0.24 | 171 |
| Saphira | f | 2015 | juvenile | 2015 | 2804 | 0.19 | 171 |
| Schreckse | f | 2008 | adult | 2015 | 2502 | 2.07 | 180 |
| | | | | 2016 | 3657 | 0.75 | 202 |
| Sequoia | f | 2009 | adult | 2013 | 1523 | 0.14 | 88 |
| | | | | 2014 | 2270 | 1.24 | 189 |
| | | | | 2015 | 3780 | 1.91 | 216 |
| | | | | 2016 | 3611 | 1.05 | 191 |
| Shannara | m | 2007 | adult | 2014 | 2201 | 1.21 | 148 |
| | | | | 2015 | 3826 | 1.12 | 215 |
| | | | | 2016 | 322 | 0.78 | 44 |
| Simba | m | 2015 | juvenile | 2015 | 2623 | 0.30 | 213 |
| Simon | m | 2006 | adult | 2015 | 3803 | 1.75 | 215 |
| | | | | 2016 | 3023 | 1.33 | 217 |

(*Continued*)

**Table 1.** (Continued)

| Individual | Sex | Year of hatching | Age class | Year of deployment | n fixes | 95% UD [km²] | Days tagged |
|---|---|---|---|---|---|---|---|
| Sino | f | 2014 | juvenile | 2015 | 3054 | 0.22 | 171 |
| Smirne | m | 2015 | juvenile | 2015 | 2082 | 0.22 | 156 |
| Taska | f | 2014 | juvenile | 2016 | 3451 | 1.03 | 201 |
| Tiffi | m | 2011 | adult | 2016 | 2956 | 2.09 | 196 |

rate for further analyses (i.e. only the first data point of each hour was included in the final data set). All analyses were conducted with the program R version 4.0.2 (R Core Team 2020).

### Estimation of space use

We used the home range bootstrap method to calculate the number of locations required to provide robust estimates of space use. This method allowed us to assess from which focal individuals we had collected sufficient GPS data points to include in the analyses to calculate accurate estimations of space use. To estimate the space use for each individual in each year and season, we calculated the utilisation distribution (UD). A UD is a probability density representing an animal's relative frequency of occurrence in space and time. Thus, strictly speaking we did not estimate the entire home range (see definition of Burt 1943), instead we were interested in the birds' occurrence distribution during the tracking period. Subsequently, area size was calculated in km² for the 95% space use per individual, season, and study year.

The home range bootstrap function (Kranstauber et al. 2020) was used to calculate and plot the area size of the minimum convex polygon (MCP, a traditional home range estimation method compared to the dBBMM used to calculate the UD; the MCP is meanwhile rarely used to estimate home ranges, but rather to describe the distribution of locations required for home range estimation; Nilsen et al. 2008) of the trajectories per season using an increasing number of coordinates that first leads to an increase in area size until it reaches a plateau. This plateau indicates whether an individual's home range is stable, which marks the minimum number of GPS points required to realistically represent the animal's space use that we identified through visual inspection of the plot. Thus, individuals with fewer than 90 GPS positions during the breeding season (Figure S1 in the online supplementary material pertains the data collected during the breeding season of one individual) and individuals with fewer than 800 GPS positions during the non-breeding season (Figure S2, pertains the data collected during the non-breeding season of three individuals) were not included in the analyses. Consequently, the final data set included 31 focal individuals (in total 17 males and 14 females; 13 juveniles – five males and eight females; 20 adults – 13 males and seven females; the number of GPS-tagged juveniles and adults does not add up to 31 individuals because two individuals were allocated to different age classes, depending on their age in the respective year), which was used for all further analyses regarding space use and site fidelity.

We calculated the utilisation distribution (UD) with dynamic Brownian bridge movement models (dBBMM; Kranstauber et al. 2012) using the 'move' package (Kranstauber et al. 2020). Space use was defined as the area within the 95% contour of the estimated UD. The dBBMM is a method incorporating the detection of change in movement patterns (e.g. movement versus resting, foraging versus moving between sites) along an animal's trajectory by using behavioural change point analysis (Kranstauber et al. 2012). To account for changes in behaviour, the dBBMM allows the Brownian motion variance (detection of changes in turning angles, speed, step length) to vary along an animal's trajectory for a pre-specified subset of n locations (windows sliding along an animal's trajectory). Following the recommendations of Kranstauber et al. (2012) to select a margin size of 9–11 locations and a window size of around 30 locations, we selected the following parameters for the dBBMM to account for potential variations in movement patterns between days, as Northern Bald Ibis are rather consistent in habitat use: (1) window size (i.e. size of the sliding window along an animal's trajectory) was chosen based on the temporal resolution of each trajectory and was set to 31 GPS positions (i.e. with a maximum number of 15 GPS positions received per day for an individual this would translate into a window length of 2 days) and (2) margin size for the behavioural change point analysis (i.e. margins at the start and end within each window in which no changes of behavioural state can occur) was set to 11 GPS positions (11 hours). Average telemetry error associated with each location was determined by the transmitter manufacturer as ± 20 m. Focal individuals had varying numbers of GPS positions, due to different tagging dates and sampling rates, variation in battery recharging and/or possible GPS transmitter failures. Consequently, segments with time gaps larger than 960 minutes were removed (i.e. when two consecutive GPS positions had a large time gap, those two GPS positions were not included in the calculation of the dBBMM) to avoid uncertainties of where the animal may have been during the missing data. For visualisation, we exported UDs as shapefiles and overlaid them with a digital elevation model (derived from oe3d, spatial resolution approximately 20–30 m, http://www.oe3d.at/) of the study area in QGIS (QGIS Development Team 2019).

### Step-selection function

We used a step-selection function (SSF; Fortin et al. 2005) using the 'amt' package (Signer et al. 2019) to investigate whether Northern Bald Ibis use consistent flyways along valleys between areas or direct routes over mountainous areas. The environmental covariate (elevation) was derived from the ASTER Global Digital Elevation Model (spatial resolution 1 arc second, 30 m) using the environmental-data automated track annotation (Env-DATA) System of Movebank (Figure S3; Dodge et al. 2013).

GPS points within a trajectory were converted to steps including step lengths and relative turning angles. For each observed step (movement between two consecutive locations), we created 10 random steps (as it was suggested that a low number of random steps is sufficient to calculate availability of locations; Thurfjell et al. 2014). Each observed step with its corresponding random step was assigned to a unique step ID. From this step representation, used locations can then be compared to available locations (Thurfjell et al. 2014). We implemented a two-step approach provided by the

'TwoStepCLogit' package (Ts.estim function; Craiu *et al.* 2016) to obtain population level selection patterns and relate individual β coefficients to animal-specific characteristics (sex, age class). We used a mixed-effects conditional logistic regression with the binary response of used and available locations as response variable. Subject identity was set as the cluster and the unique step ID as the strata. The model was fit with additive fixed- and random-effects of the environmental covariate elevation across clusters. The mixed-effects conditional logistic regression was fitted to each animal (subject ID as cluster). Afterwards, (1) coefficients and standard errors were summarized across all individuals to infer population level selection patterns, and (2) to infer sex- and age class-specific effects, β coefficients of each individual were extracted and the estimates treated as data to relate coefficients to animal-specific characteristics (see 'Statistical modelling' section for details on the animal-specific characteristics model).

### Site fidelity to locations of interest

To identify areas that were frequently visited (e.g. nesting, roosting and foraging sites) by the 31 focal individuals, we used the package 'recurse' (Bracis *et al.* 2018). Highly visited sites were identified and we extracted the top 5% (calculated from the number of revisitations) of the most revisited locations per individual. Because the focal individuals frequented a high number of different locations in the study areas (up to 192 highly visited locations during the breeding season and 179 highly visited locations during the non-breeding season), only the top 5% were extracted to analyse locations with the highest frequency of revisitations, which reflects site fidelity (i.e. few highly visited sites would imply relatively high site fidelity compared to many highly visited sites). For further analysis the number of top 5% locations was counted per individual.

The recurse method creates a radius moving along an animal's trajectory. Each time the trajectory enters and exits the radius, it is counted as a revisitation. Areas of high usage are identified by the number of revisitations. Each individual was separately analysed for each study year (2013–2016) and season (i.e. breeding and non-breeding season). Constraints such as the accuracy of the GPS transmitters used in this study (± 20 m) and an hourly sampling rate were taken into consideration when selecting the radius size of 100 m.

### Statistical modelling

We assessed which factors influence the following response variables: (1) area size (95% space use), (2) individual β coefficients of the SSF models, and (3) site fidelity (number of top 5% highly visited locations). To avoid collinear factors in the model, reproductive status was not included as a fixed factor in the analyses, as most adult focal individuals were breeders and juveniles do not breed. Prior to fitting the models, the predictor 'number of GPS positions' was z-transformed to get a more easily interpretable model (Schielzeth 2010) and ease model convergence.

To assess the influence of sex, season (breeding and non-breeding season), and age class (juveniles and adults; all three variables included as fixed effects) on area size, we used a Generalized Linear Mixed Model (Baayen 2008) with a gamma error distribution, log link function and the optimizer 'bobyqa'. We also included the interaction between season and age class (as we anticipated seasonal differences between juveniles and adults) as well as number of GPS positions (to control for potential effects of number of GPS positions) as further fixed effects. As random effects, we included subject identities and study year. The reason for including these random effects was that some individuals were observed more

than once between study years and to control for different conditions (e.g. environment-related) between years. To relate SSF β coefficient estimates (calculated for the environmental covariate elevation) from each individual to animal-specific characteristics, we performed a Multiple Regression including sex and age class as predictors.

To analyse the influence of sex, season (i.e. breeding and non-breeding season), and age class (juveniles and adults) on site fidelity (number of top 5% highly visited locations), we used a Generalized Linear Mixed Model (Baayen 2008) with a negative binomial error distribution (due to overdispersion of the poisson model: over-dispersion parameter$_{poisson}$ = 24.27, overdispersion parameter$_{negative\ binomial}$ = 1.20) with these three variables and the interaction between season and age class included as fixed effects into the model. As random effects, we included subject identities and study year.

An information theoretic approach (Burnham and Anderson 2002) was used to calculate all possible candidate models and select the best models. The top models were ranked according to their AICc values (second order form of Akaike's information criterion to account for small sample sizes; Hurvich and Tsai 1989) and we selected the models with a ΔAICc ≤6 (Harrison *et al.* 2018). The relative importance of each predictor is calculated from the Akaike weight by summing the weights of the top-ranked models in which the predictor occurs. Thus, relative importance informs about the degree of importance of the predictor. The top-ranked models were averaged in order to create model-averaged coefficients following Burnham and Anderson (2002). Statistical modelling was conducted using the functions 'lm' and 'glmer' of the package 'lme4' (Bates *et al.* 2015) and the information theoretic approach was done with the package 'MuMIn' (Barton 2020).

## Results

### Space use

In total, we recorded 113,643 GPS positions between April 2013 and October 2016 (minimum and maximum numbers of GPS positions per bird and season: breeding season – min = 92, max = 1,134; non-breeding season – min = 1,098, max = 3,075) from the final sample size of 31 individuals. The space use utilisation distribution (UD) for each individual comprised on average 0.56 ± 0.44 km² (95 % UD, mean ± SD, range = 0.005 to 1.92 km²). Space use was on average greater during the breeding season (mean ± SD = 0.91 ± 0.48 km²) than during the non-breeding season (mean ± SD = 0.31 ± 0.14 km²). The UD overlap between individuals and years was extremely high (Figure 2).

### Step selection

At the population level, birds consistently used flyways along valleys rather than direct routes over mountainous areas when moving between areas (β = -0.023, SE = 0.001, relative selection strength for low elevations [RSS, exp(β)] = 0.98; Avgar *et al.* 2017; Figure S4). Sex and age class did not improve model fit over the null model (assessed by AICc) indicating that these factors had no impact on locations used related to elevation (Table 2).

### Site fidelity to locations of interest

Across different years, Northern Bald Ibis showed a consistent use of particular locations with some specific foraging grounds having a
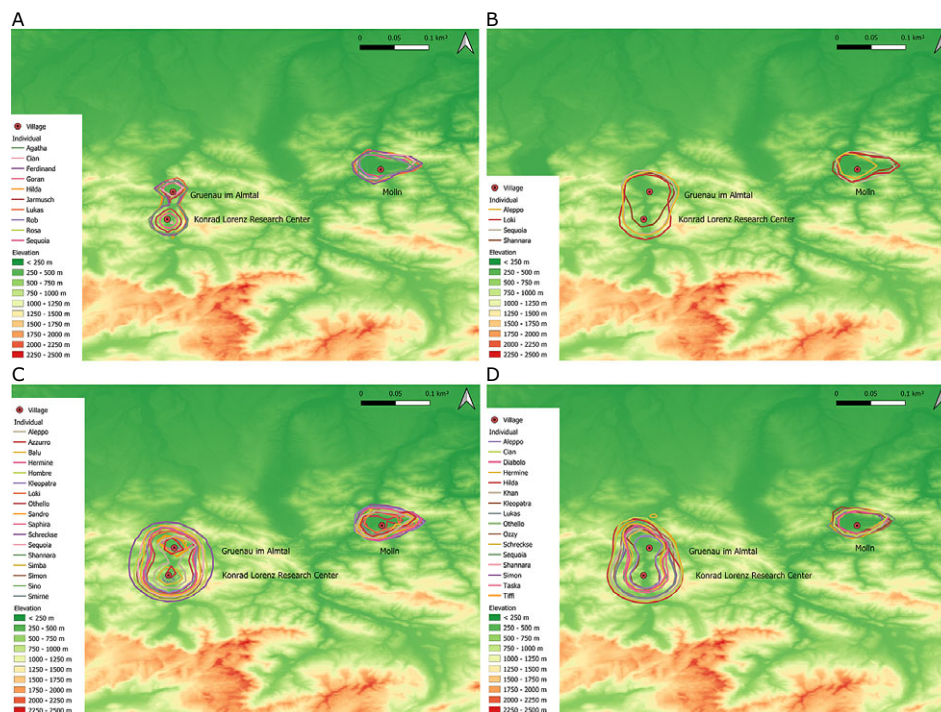
**Figure 2.** Space use polygons for the 95 % utilisation distribution are shown with different colours for different individuals. Data collected in (A) 2013 (n = 10), (B) 2014 (n = 4), (C) 2015 (n = 17) and (D) 2016 (n = 16). Background digital elevation model (DEM) was derived from oe3d in spatial resolution 1 arc second (approximately 20–30 m, http://www.oe3d.at/).

**Table 2.** Top-ranked models with a $\Delta$AICc $\leq$6 for SSF $\beta$ coefficient estimates in relation to animal-specific characteristics. Given are the predictors influencing the $\beta$ coefficient estimates as well as degrees of freedom (df), log-likelihood (logLik), delta AICc (differences of the second order Akaike information criterion between the best model and the other top-ranked models) and Akaike weight.

| Predictors | df | logLik | $\Delta$AICc | weight |
|---|---|---|---|---|
| age class | 3 | 162.482 | 0.00 | 0.717 |
| age class, sex | 4 | 162.532 | 2.28 | 0.229 |
| intercept only | 2 | 158.752 | 5.18 | 0.054 |

higher re-use between years than others. The more frequently visited sites were located on meadows along valleys in both study areas Grünau im Almtal and Molln (Figure 3). Furthermore, the highly visited sites appear to be clumped in some areas. One of those sites in Grünau im Almtal is used as a nest site (aviary in the game park). The other locations are foraging and roost sites. The nest site and nearby foraging areas around the Almtal valley (i.e. Grünau im Almtal) were especially frequented during the breeding season and late non-breeding season (autumn, season shortly before wintering season). In contrast, foraging areas around Molln were frequented during the non-breeding season.

### Factors influencing space use and site fidelity

Splitting up the data per individual, season and study year resulted in 76 space use estimations (95% UD) from 31 individuals. The interaction between age class and season best explained the size of the 95% UD of Northern Bald Ibis (Table 4 and 5). Adult and juvenile space use was more expansive during the breeding season as compared to the non-breeding season, but this effect was less

pronounced for juveniles (Tables 3 and 5, Figure S5). Furthermore, juveniles had more restrictive space use than adults during the breeding and non-breeding season (Table 3 and 5). Compared to the interaction term age class x season, the relative importance of sex and number of GPS positions was very low (Table 5); thus, these factors had a less important influence on the size of the 95% UD.

The main effects season and age class best explained site fidelity (Table 4 and 5). Individuals had a higher site fidelity during the non-breeding season than the breeding season (Figure S6) and adults showed a higher site fidelity as compared to juveniles (Tables 3 and 5, Figure S7). Compared to season and age class, the relative importance of sex and the interaction between age class and season was very low (Table 5).

### Discussion

We found a range of factors that affected space use patterns in Northern Bald Ibis. (1) In this study Northern Bald Ibis had a high degree of spatial overlap between different individuals and across successive years, and (2) they used consistent flyways along valleys but avoided direct routes over mountainous areas. (3) Individuals showed a consistent use of particular sites across years. There was an interaction effect between age class and season with (4) adults and juveniles showing more expansive space use during the breeding season than the non-breeding season, but this effect was less pronounced in juveniles. (5) Site fidelity was overall higher during the non-breeding season compared with the breeding season irrespective of individual age, and adults generally had higher site fidelity than juveniles irrespective of the season.

Our food-supplemented colony of Northern Bald Ibis had comparable space use (on average 89.01 km² from April to October calculated with a minimum convex polygon) to the resident
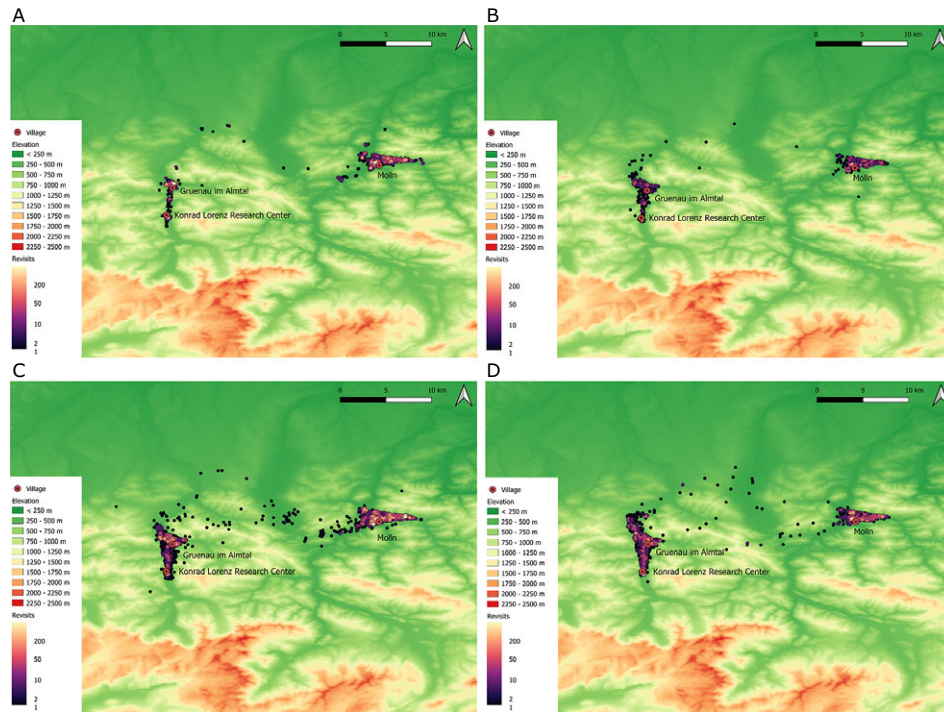
**Figure 3.** Movement data in the breeding and foraging habitats Grünau im Almtal and Molln, Upper Austria, Austria. The number of revisitations to a location is shown on a logarithmic scale from black (low) to yellow (high), with several areas of concentrated visits apparent. Data collected in (A) 2013 (*n* =11), (B) 2014 (*n* = 4), (C) 2015 (*n* = 17) and (D) 2016 (*n* = 16). Background digital elevation model (DEM) was derived from oe3d in spatial resolution 1 arc second (approximately 20–30 m, http://www.oe3d.at/).

**Table 3.** Response variables with corresponding predictor variables including their levels, mean and standard deviation of the raw data are shown.

| Response variable | Predictors | Levels | Mean | SD |
|---|---|---|---|---|
| 95% Space use [km²] | sex | females | 0.51 | 0.39 |
| | | males | 0.61 | 0.49 |
| | age class | adults | 0.64 | 0.47 |
| | | juveniles | 0.32 | 0.20 |
| | season | breeding season | 0.91 | 0.48 |
| | | non-breeding season | 0.31 | 0.14 |
| | age class x season | adults x breeding season | 1.01 | 0.44 |
| | | adults x non-breeding season | 0.32 | 0.16 |
| | | juveniles x breeding season | 0.38 | 0.35 |
| | | juveniles x non-breeding season | 0.29 | 0.11 |
| Site fidelity (i.e. number of the top 5 % of highly visited locations) | sex | females | 33.11 | 65.42 |
| | | males | 20.13 | 27.06 |
| | age class | adults | 21.91 | 43.43 |
| | | juveniles | 41.06 | 65.34 |
| | season | breeding season | 38.50 | 70.99 |
| | | non-breeding season | 17.68 | 22.02 |
| | age class x season | adults x breeding season | 30.04 | 60.04 |
| | | adults x non-breeding season | 14.84 | 18.67 |
| | | juveniles x breeding season | 84.20 | 111.95 |
| | | juveniles x non-breeding season | 24.46 | 28.22 |

**Table 4.** Top–ranked models with a ∆AICc ≤6 for 95% space use and site fidelity. Given are the predictors influencing the response variables 95% space use and site fidelity as well as degrees of freedom (df), log–likelihood (logLik), delta AICc (differences of the second order Akaike information criterion between the best model and the other top–ranked models) and Akaike weight.

| Predictors | df | logLik | ∆AICc | weight |
|---|---|---|---|---|
| **95% Space use** | | | | |
| age class, season, age class x season | 7 | −352.140 | 0.00 | 0.426 |
| age class, season, number GPS positions, age class x season | 8 | −351.236 | 0.69 | 0.301 |
| age class, season, sex, age class x season | 8 | −352.138 | 2.50 | 0.122 |
| age class, season, sex, number GPS positions, age class x season | 9 | −351.185 | 3.17 | 0.087 |
| season | 5 | −357.039 | 5.01 | 0.035 |
| age class, season | 6 | −356.041 | 5.37 | 0.029 |
| **Site fidelity (i.e. number of the top 5% of highly visited locations)** | | | | |
| age class, season | 6 | −312.894 | 0.00 | 0.359 |
| age class, season, age class x season | 7 | −312.490 | 1.62 | 0.160 |
| age class, season, sex | 7 | −312.890 | 2.42 | 0.107 |
| season | 5 | −315.374 | 2.60 | 0.098 |
| age class | 5 | −315.389 | 2.63 | 0.097 |
| intercept only | 4 | −317.217 | 3.99 | 0.049 |
| age class, season, sex, age class x season | 8 | −312.482 | 4.11 | 0.046 |
| season, sex | 6 | −315.291 | 4.79 | 0.033 |
| age class, sex | 6 | −315.303 | 4.82 | 0.032 |
| sex | 5 | −316.982 | 5.82 | 0.020 |

**Table 5.** Model–averaged coefficients for 95% space use and site fidelity. Given are the coefficients with adjusted standard errors, lower and upper confidence intervals, and relative importance of the top–ranked models.

| Predictors [levels] | Estimate | Adjusted SE | CI lower limit (2.5%) | CI upper limit (97.5%) | Relative importance |
|---|---|---|---|---|---|
| **95% Space use** | | | | | |
| intercept | 4.573 | 0.200 | 4.181 | 4.966 | |
| age class [juvenile] | −1.070 | 0.426 | −1.854 | −0.362 | 0.97 |
| season [non–breeding season] | −1.274 | 0.297 | −1.856 | −0.692 | 1.00 |
| age class [juvenile] x season [non–breeding season] | 1.075 | 0.471 | 0.383 | 1.913 | 0.94 |
| number GPS positions | 0.078 | 0.135 | −0.095 | 0.495 | 0.39 |
| sex [male] | 0.006 | 0.083 | −0.323 | 0.383 | 0.21 |
| **Site fidelity (i.e. number of the top 5% of highly visited locations)** | | | | | |
| intercept | 3.106 | 0.331 | 2.369 | 3.733 | |
| age class [juvenile] | 0.725 | 0.577 | 0.036 | 2.685 | 0.80 |
| season [non–breeding season] | −0.514 | 0.381 | −1.206 | 0.085 | 0.80 |
| age class [juvenile] x season [non–breeding season] | −0.136 | 0.435 | −2.255 | 0.784 | 0.21 |
| sex [male] | −0.015 | 0.179 | −0.640 | 0.741 | 0.24 |

western population in Morocco (74.54 km² on cultivations/recent fallows; Bowden *et al.* 2008), but more restricted space use compared to the migratory eastern relict population (c. 150 km² at the breeding site calculated with a minimum convex polygon and c. 80.8 km² at the wintering site calculated with a fixed-kernel range estimator; Serra *et al.* 2011, 2013). However, habitat use of the Moroccan population was only estimated for foraging areas by observing and following individuals from colonies and roosts to their foraging grounds and marking the exact position on aerial photos (Bowden *et al.* 2008). Thus, space use for this population may be larger than estimated. The more restricted space use compared to the eastern relict population is probably a consequence of food supplementation. In addition, the surrounding meadows of the Alm Valley and Molln area are rich in food (Markut 2005) with

high prey densities during spring and summer and provide abundant freshwater sources as compared to Near East or North African environments. In contrast to the conditions in Austria, the desert habitats also pose stringent costs on reproductive success (Smith *et al.* 2008) and possible restraints on space use and time budgets in the Moroccan population due to water shortages.

Despite excellent flight capacity in Northern Bald Ibis (Portugal *et al.* 2014), our study birds consistently used flyways between study areas along valleys rather than direct routes over mountainous areas. Updrafts are often associated with mountains and are used by large raptors (e.g. Goshawk *Accipiter gentilis*, Golden eagle *Aquila chrysaetos*; Duerr *et al.* 2012), which might increase predation risk along mountainous routes. In addition to consistency of travel routes, we also found a high degree of overlap between space use of single individuals and consistent space use across successive years, indicating high space use stability and site fidelity. Similar patterns of consistent space use by individuals were found in Northern Bald Ibis at an Ethiopian wintering site (Serra *et al.* 2013), Crested Ibis *Nipponia nippon* (Dongping *et al.* 2003), and in non-breeding ravens *Corvus corax* (Loretto *et al.* 2016).

Individual space use patterns may differ across age (Mlyashimbi *et al.* 2020), sex (Lidgard *et al.* 2020, Mlyashimbi *et al.* 2020), and reproductive status (Robinson *et al.* 2017) or may vary with external factors, such as season (Ofstad *et al.* 2019). Similar to observations in King Rails *Rallus elegans* (Kolts and McRae 2017), we found that adults had more expansive space use during the breeding season than during the non-breeding season. Adults increased their foraging radius during breeding, likely to acquire resources to provision offspring. A similar pattern was found in Bearded Vultures *Gypaetus barbatus,* though not in White Storks *Ciconia ciconia* (Krüger *et al.* 2014, Zurell *et al.* 2018). Up to 50% of the juveniles in our study population disperse at the end of summer/beginning of autumn and fly north/north-east (e.g. to Germany, Poland, Czech Republic, Latvia, the Netherlands), even though some individuals return during late autumn (Böhm *et al.* 2020), which may explain the minor seasonal differences in juvenile space use. Our data did not reveal sex differences in space use as shown for many other bird species (e.g. Aronsson *et al.* 2016, Johansson *et al.* 2018, Tisell *et al.* 2019). For instance, male King Rails used more space during the non-breeding season than females (Kolts and McRae 2017). Females may adapt their space use according to food availability (Aronsson *et al.* 2016) and spend more time foraging than males (Lidgard *et al.* 2020) to increase survival and fitness. Those differences seemingly scale with sexual dimorphism (Ruckstuhl and Neuhaus 2007). Northern Bald Ibis, however, are hardly sexually dimorphic (Böhm and Pegoraro 2011), not even in their behaviour (Sorato and Kotrschal 2006). Northern Bald Ibis exhibit bi-parental care, are colonial and spend most of their time in a group (Böhm and Pegoraro 2011), explaining the similar space use patterns we observed in males and females. From a conservation perspective, it is useful to know that males and females in this population tend to occupy the same areas at the same times of year.

Animals regularly return to specific sites, such as foraging grounds, nest sites, roosting sites, and watering holes (Bracis *et al.* 2018). Site fidelity reflects stability in patterns of space use (Harris and Leitner 2004). In this study, we found evidence for site fidelity with consistent patterns of use of particular sites, such as foraging sites, across successive years at the population level. This could perhaps be attributed to rather predictable and stable habitats during the times when monitoring occurred. Previous studies showed that site fidelity increases with age (Switzer 1993), which could explain the higher site fidelity in adults as compared to

juveniles. Adult breeders may have to trade-off exploiting known resources and exploring new ones, which could result in lower site fidelity during the breeding season because of the need to search for high quality resources. Site fidelity can also entail certain risks, including anthropogenic effects. For instance, predator species of Africa and Eurasia (mammals: e.g. Caracals *Caracal caracal*, Honey Badger *Mellivora capensis*; raptors: e.g. Cape Eagle Owl *Bubo capensis*, Palm Nut Vulture *Gypohierax angolensis*) are highly exposed to poison used to control rodent populations mostly associated with proximity to human habitats (Santangeli *et al.* 2019, Serieys *et al.* 2019). Such site-specific risks of the current population are not known for Northern Bald Ibis, but should be kept in mind for future research, specifically because site fidelity appeared to be strongly associated with the size of the relevant area, and site fidelity increased when the utilised space was smaller. As above with regard to the size of space use, there was no effect of sex on site fidelity, which matches well the lack of anatomical or behavioural sexual dimorphism in Northern Bald Ibis (Sorato and Kotrschal 2006, Böhm and Pegoraro 2011).

## Conservation implications

Northern Bald Ibis populations decreased over the last century and many colonies disappeared from most of their former range (Bowden *et al.* 2003). This species seems rather consistent in habitat use and foraging sites (Kirnbauer 2004, Serra *et al.* 2008), indicating that site fidelity may play a major role in selecting foraging habitats. Such lack of adaptive flexibility has also been suggested as a reason for the decline of the species throughout its original distribution range. Our work provides insights into the movement ecology of the Northern Bald Ibis, which broadens our understanding of factors that shape space use and site fidelity patterns in an endangered species. As the extent of space use by the study population was comparable to that of the Moroccan population (last persisting viable wild population), our findings can be relevant for any population in the wild and for the adaption of conservation strategies accordingly.

Here, we show that Northern Bald Ibis are extremely consistent in their patterns of space use for resources such as foraging and roosting, despite the availability of similar areas elsewhere. The seasonal- and age-specific differences in movement and space use patterns point to benefits of implementing age-specific approaches to manage movement and space use. In particular, conservation interventions should be encouraged along migration and dispersal routes, as up to 17% and 31% of annual losses in reintroduced colonies are still accounted for by illegal hunting and electrocution, respectively (Fritz *et al.* 2017, Böhm *et al.* 2020), mainly occurring during long distance movements. Thus, designation of protected areas should also be seasonally based. Furthermore, we show that mountainous routes are avoided, which informs reintroduction projects to rather select migration routes along valleys and, by extension, which habitat characteristics (i.e. migration and dispersal corridors through the mountains should be present) to consider when establishing new colonies. This information can be used to improve the protection of existing habitats, but also to identify new habitats for potential re-introduction. These insights can aid the assessment of different reintroduction strategies, the viability and vulnerability of the population in a particular habitat, and be used to estimate the potential distribution range of this species (e.g. Macdonald *et al.* 2000, Macdonald and Rushton 2003).

Site fidelity could constrain the viability of a population in case of habitat degradation and loss, especially when populations inhabit restricted habitats (Warkentin and Hernández 1996). To counteract population decline associated with high site fidelity, threatened and declining species displaying site fidelity need to be monitored and conservation actions need to be adapted. Particularly their habitats need to be monitored and protected against degradation. Small populations are more vulnerable to extinction compared to large stable populations because of loss of gene flow and variability in environment and population size (Caughley and Gunn 1996). Thus, populations with high site fidelity could face higher mortality rates when current habitat quality of highly revisited sites is not optimal or even declining. Insectivorous birds are rapidly declining (Bowler *et al.* 2019), emphasizing the need to prevent unsustainable farming practices and to control climate change to maintain insect biodiversity (Raven and Wagner 2021), which is also the main food source for Northern Bald Ibis, and which would also be essential for the survival of numerous other species and may be directly beneficial to agriculture itself. Thus, identification of seasonally revisited habitats, such as foraging areas, is essential in order to foster long-term monitoring and protection of relevant areas.

In sum, our results from the semi-wild Northern Bald Ibis colony observed in this study have quite some potential for informing conservation and re-introduction programs because they show the influence of individual traits on spatio-temporal patterns and the importance to conserve existing foraging and roosting areas that are frequently used by this threatened species.

**Supplementary Materials.** To view supplementary material for this article, please visit http://doi.org/10.1017/S0959270922000053.

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