


Identifying the environmental drivers of corridors and predicting connectivity between seasonal ranges in multiple populations of Alpine ibex (*Capra ibex*) as tools for conserving migration

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Abstract

Aim: Seasonal migrations, such as those of ungulates, are particularly threatened by habitat transformations and fragmentation, climate and other environmental changes caused by anthropogenic activities. Mountain ungulate migrations are neglected because they are relatively short, although traversing heterogeneous altitudinal gradients particularly exposed to anthropogenic threats. Detecting migration routes of these species and understanding their drivers are therefore of primary importance to predict connectivity and preserve ecosystem functions and services. The populations of Alpine ibex *Capra ibex* have all been reintroduced from the last remnant source population. Despite a general increase in abundance and overall distribution range, ibex populations are mostly disconnected but display intra-population migrations. Therefore, its conservation is strictly linked to the interplay between external threats and related behavioural responses, including space use and migration.

Location: Austria, France, Italy and Switzerland.

Methods: By using 337 migratory tracks from 425 GPS-collared individuals from 15 Alpine ibex populations distributed across their entire range, we (i) identified the environmental drivers of movement corridors in both spring and autumn and (ii) compared the ability of a connectivity modelling algorithm to predict migratory movements between seasonal ranges of the 15 populations, using either population-specific or multipopulation datasets, and three validation procedures.

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Results: Steep, south-facing, snow-free slopes were selected while high elevation changes were avoided. This revealed the importance of favourable resources and an attempt to limit energy expenditures and perceived predation risk. The abilities of the modelling methods we compared to predict migratory connectivity from the results of those movement analyses were similar.

Main Conclusions: The trade-off between energy expenditure, food and cover was the major driver of migration routes and was overall consistent among populations. Based on these findings, we provided useful connectivity models to inform conservation of Alpine ibex and its habitats, and a framework for future research investigating connectivity in migratory species.

KEYWORDS

corridor mapping, cross validation, habitat selection, integrated step selection analysis, migration conservation, mountain ungulate, movement ecology, randomized shortest paths

1 | INTRODUCTION

Global human-induced environmental changes are causing severe biodiversity loss, and habitat destruction and fragmentation are among the main causes of this decline (Díaz et al., 2019; Newbold et al., 2016). The development of linear infrastructures associated with human activities also contributes to impede species mobility (Torres et al., 2016). For instance, the extent of terrestrial mammalian movements was reduced by 50% in areas with a high human footprint compared with areas undisturbed by human activities (Tucker et al., 2018). By limiting animal movements between favourable habitats, human activities and infrastructures also reshape landscape connectivity (Taylor et al., 1993). Yet, connectivity is essential for individual and gene flows, for the local persistence of populations (Hanski, 1998) and for ecosystem functioning (Bauer & Hoyer, 2014).

In the context of degraded connectivity, seasonal migrations, that is movements to track the spatiotemporal fluctuations in environmental conditions on seasonal ranges (Dingle & Drake, 2007), are of particular concern (Bolger et al., 2008). Most large herbivores, as primary consumers, migrate or may show migration propensity in heterogeneous and predictable habitats (Mueller et al., 2011; Teitelbaum et al., 2015). They are often restricted to well-defined corridors used by most migrants with low tendency to change migration routes when corridors are altered (see e.g. Xu et al., 2021). Migration can increase survival and reproduction through better access to high quality resources and reduced intra- and inter-specific competition or predation risk (Avgar et al., 2014; Eggeman et al., 2016; van Moorter et al., 2021). However, migratory movements also implies energetic costs and can be risky, or perceived as such, as animals may move through unfamiliar areas (Blagdon & Johnson, 2021; Klaassen et al., 2014). Hence, migration is a behavioural tactic whose fitness returns can vary through space and time, depending on individual traits, and spatial heterogeneity in occurrence and intensity of predation, harvesting, or competition in a population's range. Accordingly, migration can be partial, with some

individuals choosing to migrate while others are residents, and with individual behaviour that can change from year to year (Cagnacci et al., 2011). Given that migration can affect population dynamics and species persistence by shaping their spatio-temporal distribution, there is a crucial need to increase our understanding of the link between habitat use and drivers of movement during seasonal migration at a fine spatial scale, the resulting ecological connectivity of a landscape and how human activities affect this connectivity level (Panzacchi et al., 2016; Sawyer et al., 2011).

Migration corridors and their environmental characteristics are well-documented in spectacular collective and long-distance migrations in North American, Scandinavian or African ungulates (Boone et al., 2006; Joly et al., 2019; Merkle et al., 2016; Panzacchi et al., 2016) but remain poorly known in other parts of the world and for many species (Kauffman et al., 2021). Recently, the focus has been put on spring migration revealing how migratory species can surf the green wave by tracking the green-up, which moves like a wave across the landscape (Bischof et al., 2012; Merkle et al., 2016). Although less spectacular, migrations also occur in mountain ungulate populations occupying highly heterogeneous and fragmented landscapes (Herfindal et al., 2019), which are under threats from rapid climate changes and increasing anthropogenic pressure (Parmesan & Yohe, 2003; Schmeller et al., 2022). In mountain areas, green waves occur along altitudinal gradients and therefore green wave surfing seems to not always fully explain the choice of routes travelled between seasonal home ranges (Gaudry et al., 2015; Herfindal et al., 2019; but see Semenzato et al., 2021 for seasonal tracking of the altitudinal green and senescence waves). Several other factors can affect migration routes, particularly in complex topographic landscapes. Indeed, in addition to the diversity of migratory portfolios, migration is most often partial and takes place among multiple winter and summer ranges (Crampe et al., 2007; Denryter et al., 2021; Lowrey et al., 2020) and, up to now, little is known about migration patterns and migration routes for these mountain populations. Yet,

this information is essential to improve the conservation of migratory species (e.g. through the establishment of protected areas, or to inform landscape planning; McCollister & Manen, 2010) and preserve the ecological functions and ecosystem services migratory species support (Semmens et al., 2011). In this context, the importance of reliable connectivity maps for the identification of realistic corridors has been stressed (Sawyer et al., 2011; Zeller et al., 2012). A deeper understanding of the link between fine-grain habitat use and movements has been particularly invoked, and up-to-date algorithms have been developed and used to model connectivity while accounting from iterative decisions of animals trading off exploration and optimal use of their environment (Goicolea et al., 2021; Panzacchi et al., 2016). However, population-specific movement analyses and connectivity predictions may be difficult to generalise over species and contexts when relying on samples from a single population not always representative of the species/habitat. Multi-population analyses may be crucial to extend population-specific knowledge to species conservation, but such comparative analyses remain particularly scarce (Urbano et al., 2021).

Here, we investigated migration routes in several populations of Alpine ibex *Capra ibex* across the Alps in order to model and predict connectivity between summer and winter ranges. This emblematic mountain species almost went extinct during the XIXth century and recovered a large distribution thanks to intensive reintroduction programmes (>55,000 individuals distributed across 178 populations still poorly connected; Brambilla et al., 2020), after drastic bottlenecks and founder effects that resulted in a very low level of genetic diversity (Biebach & Keller, 2009). Seasonal migrations seem to occur in most populations but are threatened by the increasing anthropogenic pressure on mountain habitats (Schmeller et al., 2022). Thus, effective conservation of this species and its migratory movements would highly benefit from better knowledge of the landscape characteristics used by ibex during migration, and from an assessment of the connectivity offered by available habitats. Owing to a unique GPS telemetry dataset from 425 ibex and 15 populations across the entire distribution range of the species, we first aimed at determining the environmental drivers of migratory tracks accounting for several factors hypothesised to influence how ibex choose their migration routes. We specifically tested whether individuals (i) minimised energy expenditures and difficulties to travel by avoiding elevation changes, rugged terrain and snowy areas as travelling costs are paramount in all optimality models aiming at understanding the costs and benefits of migration tactics (Holt & Fryxell, 2011), (ii) selected habitats offering food resources and refuge from perceived predation risk, (iii) used visual landmarks (linear features such as ridges, tree lines and valley bottoms) as 'compasses' (Alerstam & Bäckman, 2018), and (iv) avoided proximity to anthropogenic infrastructures (roads and ski resorts; Table 1) during migration. We then compared the ability of a connectivity modelling algorithm to predict migratory movements between seasonal ranges of the 15 populations, using either population-specific or multi-population datasets, and three validation procedures. One of the procedures consisted

in an external validation of the capacity of our model to accurately predict ibex migratory movements despite having no data on ibex locations, a crucial step to provide reliable information for species migration conservation across its native range.

2 | MATERIALS AND METHODS

2.1 | Study areas and GPS data

We relied on a GPS dataset collected between 2003 and 2020 (Appendix S1 for details) on 425 individual Alpine ibex (*Capra ibex*; 41% females and 59% males; 77% being adults >4 years old) from 15 reintroduced populations. These populations were distributed across the whole Alps (10 in France, 2 in Italy, 1 in Switzerland, and 2 in Austria; Figure 1; latitudinal gradient: 44–47°N, longitudinal gradient: 6°–13°E and altitudinal gradient: 1700–2700m). Alpine ibex can share habitats with northern chamois (*Rupicapra rupicapra*), less frequently with red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), and with livestock during summer (sheep, goats and cows). The grey wolf (*Canis lupus*) is present throughout most of ibex distribution range, but rarely predaes ibex.

Sample sizes varied between populations (minimum: 7 individuals in Hohe Tauern National Park; maximum: 117 in the Bargy population). Several types of collars were used (Vectronic: GPS Plus, Vertex Plus, or Vertex Lite models; Lotek: 3300S or Litetrack models; Followit: Tellus model). All models weighed <3% of individual body weight. They were programmed to record ibex locations at variable frequencies and during variable periods (from 1 location per hour during one year to 1 location per 6 hours during 2–3 years, Appendix S1), resulting in 1068 seasonal tracks (an individual monitored during 1 year resulted in 2 potential migratory tracks).

2.2 | Determining migratory status and migration tracks

The migratory status of each ibex (migrant or resident) and migration tracks (for migrants) were visually determined using the application Migration Mapper™ (version 2.3, Merkle et al., 2022; see Appendix S2 for the parameters used). This application provides tools to visually identify migrants, migration periods and tracks using the Net Squared Displacement (NSD; squared Euclidean distance between the first location of the GPS trajectory and the following ones; Börger & Fryxell, 2012; Appendix S3). Spring and fall migration periods and migratory tracks started at the last location preceding the increase/decrease in the NSD and ended at the first location when the NSD stabilised. Migratory movements were identified irrespective of distance separating seasonal ranges as ibex exhibited several forms of migratory movements within populations (short-altitudinal movements or long-distance movements). However, only distinct migrations (i.e. two movements between distinct seasonal ranges) were selected to reduce uncertainty in the displayed behaviour (see

TABLE 1 Hypotheses tested in the integrated Step Selection Analyses and their corresponding predictions.

Hypotheses	Covariables	Predictions	References
Ibex minimise energy expenditures and travelling difficulties	Total elevation change	Ibex should perform steps with relatively low total elevation change.	Passoni et al. (2021)
	Ruggedness	Ibex should avoid rugged terrain, which tends to increase movement costs and reduce visibility.	Halsey and White (2017), Wall et al. (2006)
	Snow cover index	Ibex should avoid snowy areas which impede ibex movements.	Richard et al. (2014), Sheppard et al. (2021)
Ibex select areas that can provide forage, security and thermal shelters.	Northness	Ibex should prefer south exposed terrain as they present snow-free areas with access to early growing vegetation in spring or thermal shelters in autumn.	
	Proximity to refuges (steep slopes)	Ibex should stay close to steep slopes to reduce perceived predation risk.	Grignolio et al. (2007), Iribarren and Kotler (2012)
	Forest	Ibex should avoid forests as they prefer open habitats, being primarily grass roughage eaters.	Parrini et al. (2009)
Ibex use landmarks for orientation.	Proximity to ridges	Ibex should select for proximity to ridges and follow ridges during their migration.	Marchand et al. (2017)
	Proximity to valley bottoms	Ibex should avoid going down to valley bottoms in spring only.	Marchand et al. (2017)
	Proximity to tree lines	Ibex should follow tree lines as a landmark in sites where the population range includes forest.	Marchand et al. (2017)
Ibex avoid human-linear infrastructures	Proximity to roads	Ibex should avoid roads constituting physical barriers or because associated with humans.	Seigle-Ferrand et al. (2022)
	Proximity to ski resorts	Ibex should avoid ski resorts because associated with humans.	Dickie et al. (2020)

Appendix S4 for details on distance and altitudinal interval between seasonal ranges of migrant and resident individuals).

2.3 | Assessing environmental drivers of ibex migratory movements

2.3.1 | Environmental variables

We investigated the influence of 11 environmental variables (see Appendix S5) that could affect movement choices during migration (Table 1). We considered the total elevation change (sum of changes in elevation values along a step, using a DEM with a 25m×25m resolution), the ruggedness (Vector Ruggedness Measure; Sappington et al., 2007) and a snow cover index for the year of tracking (calculated as the total annual number of days a pixel was covered by snow) as metrics reflecting the energetic costs and difficulties to travel during migration. We used this snow cover index because the inadequacy between coarse temporal resolution of the snow data (8 days) and fine scale movement of the ibex (1–6h intervals) prevented us from measuring the snowpack on the dates of migration accurately. Furthermore,

given that the migration often occurs over a matter of days, the snow cover index was used to test the hypothesis that ibex might avoid areas that have extended periods of snowpack (i.e. early snow in the autumn or late snow in the spring). We used the northness (cosine of aspect derived from the same DEM) and the snow cover index to reflect the accessibility and quality of vegetation resources and the presence of snow cover, as well as the availability of thermal shelters. Contrary to what is commonly done in studies on migratory ungulates, we did not use vegetation variables or derived metrics (NDVI, Instantaneous Rate of Green-Up; e.g. Bischof et al., 2012) as we judged the information given by the northness and snow cover more relevant considering the short duration and distance of ibex migrations (see Section 3). As ibex mostly use open areas (Parrini et al., 2009) and often steep slopes as refuge from perceived predation risk and human disturbance, we expected forests to be avoided and proximity to slopes >40° to be selected during migration (Grignolio et al., 2007; Iribarren & Kotler, 2012). We considered ridges, valleys and tree lines as potential visual landmarks used for navigation (Alerstam & Bäckman, 2018). Finally, we hypothesised that the proximity to roads and ski resorts (i.e. human infrastructure that occasionally occurred in the surrounding of ibex population ranges) would be avoided as both can constitute barriers

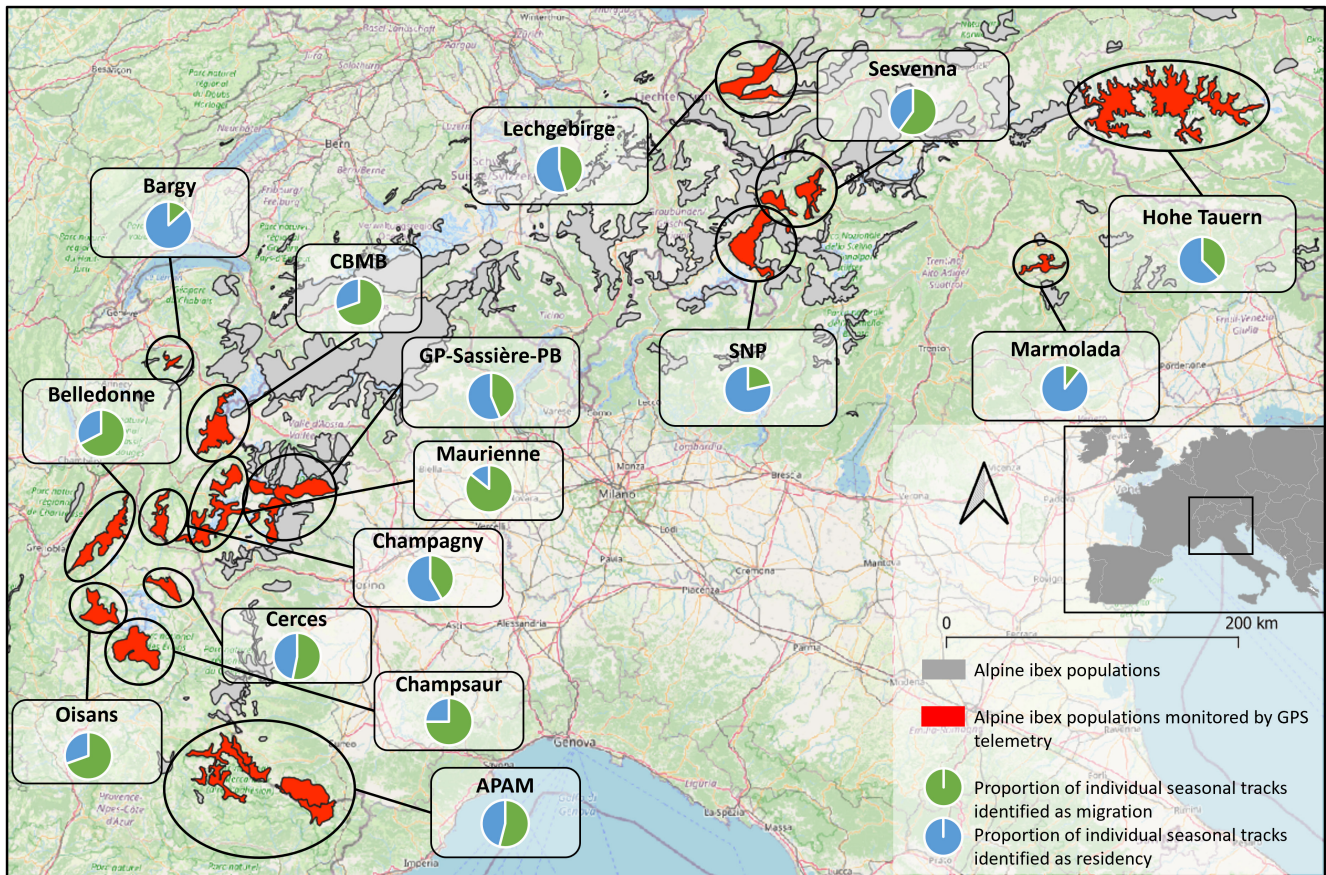


FIGURE 1 Location of the 15 Alpine ibex *Capra ibex* populations monitored by GPS telemetry (red) over the distributional range of the species in the Alps (grey; *Source*: Brambilla et al., 2020); see Appendix S1 for more details. The pie charts display the proportion of individual seasonal tracks identified as migration (green) or residency (blue) within each population (see below and Appendix S3 for details on individual status identification).

– physical barriers such as roads – or perceived as such because they are associated with human presence for both roads and ski resorts.

2.3.2 | Habitat selection analyses during migration

We used integrated Step Selection Analyses (iSSA; Avgar et al., 2016) to assess the environmental drivers of ibex habitat selection during migratory movements. An iSSA compares the environmental characteristics along or at the end of each observed step of an animal (i.e. movement between two consecutive locations) with those along or at the end of random steps (i.e. representing available steps that the animal could have taken) using conditional logistic regression. It also allows accounting for the link between movement and habitat selection, particularly expected during migration due to the frequent alternance between actual movements and stopovers. To do so, and depending on the assumed distribution of step length (i.e. exponential, half-normal, gamma or log-normal), information on movement characteristics (i.e. step length, $\log(\text{step length})$ and cosine of turning angles) is included as a covariable, together with environmental attributes of each step. The movement components of iSSA are yet inherently ‘correlation-prone’ and are hence vulnerable to estimability issues (Avgar et al., 2016; but

see below and Appendix S6). The habitat variables along (total elevation change) or at the end (all other habitat variables) of each used movement step (considered as the straight lines between recorded ibex locations) travelled by one individual ibex during migration were compared with the habitat characteristics along/at the end of 15 available steps it could have travelled, using conditional logistic regressions (Fortin et al., 2005; Thurfjell et al., 2014). We generated those available steps by sampling step lengths (corrected to get three-dimensional lengths using a DEM at a resolution of 25m, which are particularly relevant in mountainous landscapes) and turning angles in parametric distributions (gamma distribution for the step length and Von Mises distribution for the turning angles; Duchesne et al., 2015) derived from the observed step length and turning angle distributions of the used steps. We accounted for the variable step duration in our dataset by deriving specific distributions for each step duration and checked if habitat selection regarding environmental covariates was similar for the different timesteps by using the method of Used Calibration Plots (see Appendix S6).

We scaled habitat variables across all populations (i.e. variables were centred and divided by their standard deviation) to make their effect size comparable in iSSA outputs. We also checked for potential correlations between our variables using Pearson correlation

coefficients. The correlation coefficients were notably >0.3 for some variables such as forest and proximity to forest ($\rho=0.5$), as well as for movement characteristics, including step length, $\log(\text{step length})$ and total elevation change ($\rho=0.6$ step length/ $\log(\text{step length})$, $\rho=0.6$ total elevation change/ $\log(\text{step length})$, $\rho=0.9$ step length/total elevation change), which is a common observation. Despite these correlations, we retained all those covariates in our models to enable testing hypotheses based on movement attributes, such as avoidance of total elevation change (see above), while remaining in the iSSA design (Avgar et al., 2016; Forester et al., 2009). However, we assessed for the absence of estimability issues associated with this choice (see Appendix S6). For all other covariates, correlation coefficients were <0.3 .

The logistic regressions included the 11 environmental variables (Table 1), and the movement variables step length, \log of step length and cosine of turning angles (Avgar et al., 2016). We included both step length and \log of step length in our regressions since step lengths were sampled from gamma distributions (Fieberg et al., 2021). We only included an interaction between step length and elevation change covariates and between forest and proximity to forest covariates to simplify our models. We fitted one model for each season (i.e. spring or autumn migration) and each of the 15 populations. For 6 populations in spring and 5 in autumn, the variables 'forest' and 'proximity to ski areas' were excluded from models as forest or ski areas were rare or absent in the distributional range of those populations. We chose to fit models at population scale because we were more interested in modelling migratory movements within each population. Accounting for sex-specific differences can be important for a species like Alpine ibex knowing to exhibit different patterns of movements between sexes (Herfindal et al., 2019). However, numbers of migrant females (or even migrant animals) were too small in several populations to test sex-specific differences (see Appendix S7). We investigated if habitat selection results differed between sexes in Appendix S8. We fitted models using the *clogit* function from the package *survival* in R V. 4.2.2 (R Core Team, 2022; Therneau, 2022). We conducted a model selection based on AICc with the *dredge* function in package *MuMIn* (Bartoń, 2022). The coefficients from the best models, that is models with a $\Delta\text{AICc} < 2$, were averaged using the *model.avg* function in the package *MuMIn*. We included 'individual' as a random effect in each model. We finally produced Used Habitat Calibration plots (UHC plots; Fieberg et al., 2018) to check for the agreement between model predictions and observed values of our covariates at or along used steps (Appendix S6). This analysis also enabled us to evaluate the consequences of cross-correlations among movement covariates on estimability issues (Avgar et al., 2016).

2.4 | Building and validating models of migratory connectivity in ibex

We proceeded in five steps (see below and step II of Figure 2) to build and validate connectivity models based on the 15 populations to perform three different validation procedures (i.e. using three

different pairs of training/validation datasets; Figure 2) designed to understand how our models could inform different management measures. With the first procedure ('leave 10% of whole data out'), we seek to understand if, based on all information we have on ibex habitat selection, we can predict migratory movements of non-marked individuals in monitored populations. We used the second procedure ('leave 10% of population data out') to assess if, based on data from a limited number of animals in a population, we can predict the migration paths of other animals. Finally, with the third procedure ('leave one population out'), we aimed to evaluate if, based on all information we have, we can predict migratory movements in populations without monitoring.

2.4.1 | Sampling training and validation datasets

We created three sets of training/validation datasets for two purposes: developing habitat selection models and building resistance maps (training datasets) and assessing connectivity predictions (validation datasets). For the 'leave 10% of whole data out' procedure, we built the training dataset by randomly sampling 90% of individuals from the 15 populations, setting aside 10% for validation. Similarly, for the 'leave 10% of population data out' procedure, we randomly sampled 90% of individuals from each population for training, using the remaining 10% for validation. We repeated both sampling 100 times. In the 'leave one population out' procedure, data from 14 populations constituted the training dataset, while data from the remaining population served as validation.

2.4.2 | Fitting of habitat selection models

After constituting our training datasets, we fitted iSSA models on each dataset. For spring and autumn seasons, we built initial models containing all environmental and movement covariates. We then performed a model selection procedure using the *dredge* function in package *MuMIn* (Bartoń, 2022) and averaged model coefficients over the best models ($\Delta\text{AICc} < 2$, using the function *model.avg*). We included individual identity and population as random effects, except for the population-specific models ('leave 10% of population data out') in which we only included individual as a random effect. Thus, for the 'leave 10% of whole data out' and 'leave 10% of population data out', we fitted 100 models per season and population because we had 100 different training datasets. For both approaches, we could then make 100 resistance maps for each population, and we obtained 100 connectivity maps per population. Although this procedure is computationally challenging, having multiple connectivity maps per population allowed us to assess uncertainty measures in our predictions. For the 'leave one population out', we fitted one model per season and population.

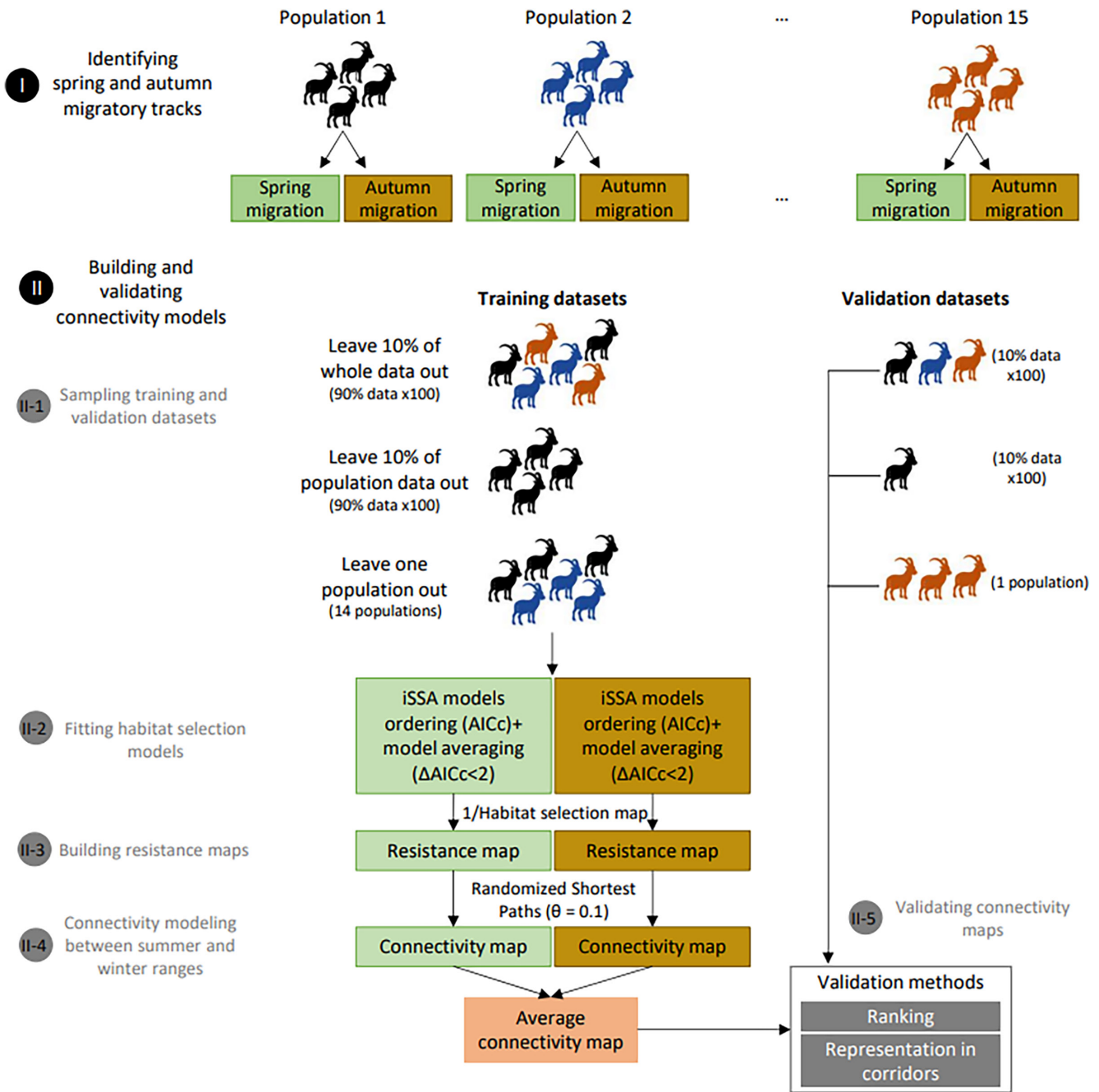


FIGURE 2 Methodological workflow scheme. First, we identified seasonal migratory tracks. Second, we sampled three different types of training and validation datasets: leave 10% of whole data out, leave 10% of population data out and leave one population out. The three types of training datasets were used in iSSAs and we selected the best habitat selection models for these different datasets. We built three (one per training dataset) different resistance maps (100 times for ‘leave 10% of whole data out’ and ‘leave 10% of population data out’) for each population and season and modelled connectivity based on these resistance maps using the Randomized Shortest Path algorithm ($\theta=0.1$; Appendix S10). Finally, for each training dataset, we averaged the two seasonal connectivity maps and combined this average connectivity map with the corresponding validation datasets to perform the ‘ranking’ and ‘representation in corridors’ validation methods.

2.4.3 | Building resistance maps

We then used the different iSSA models to compute seasonal resistance maps that display the relative avoidance of each pixel by an ibex migrating through the landscape. To do so, we multiplied each raster of environmental variables by the corresponding coefficient provided by the iSSA model fitted with a given data source. Then,

we summed those rasters and applied the inverse logit function to get habitat selection maps representing the relative probability that an ibex selected a pixel during migration. The RSP algorithm uses a resistance map to model connectivity. To obtain resistance maps, we applied the inverse function to the habitat selection maps, considering that the cost of movement is higher in avoided habitats (Keeley et al., 2016; Zeller et al., 2018).

2.4.4 | Modelling connectivity between summer and winter ranges

We defined seasonal ranges as 95% kernel areas derived from the corresponding seasonal locations (Worton, 1989), using *kernelUD* function from *adehabitatHR* package (h parameter was set to 400; Calenge, 2022). We restricted our analyses to seasonal ranges connected by migratory tracks to limit our connectivity predictions to the areas actually used by GPS-collared migrant ibex. We used the Randomized Shortest Path approach to model connectivity (RSP; Panzacchi et al., 2016; Saerens et al., 2009; implemented in the *passage* function from R package *gdistance*; van Etten, 2022) between 10 points randomly sampled within each pair of summer and winter ranges. This algorithm estimates the number of times an ibex would cross each pixel of the resistance map during migration. As in other algorithms relying on the graph theory (e.g. least-cost path and circuit theory), the resistance map is represented as a graph with individuals moving from nodes to nodes (i.e. the centre of the pixels) along links/edges with variable costs depending on the values of the resistance map. The RSP computes the least-cost path, the path that minimises the distance and costs accumulated along a trajectory joining a source and a destination. The RSP algorithm also integrates a stochasticity parameter θ , which allows measuring the degree of departure from two extreme strategies, i.e. random walk (full exploration of neighbouring nodes) when $\theta=0$, or least-cost path (i.e. optimal exploitation of the landscape by minimising total costs) for the highest value of θ (see Appendix S10). This allows accounting for intermediate strategies between the two most commonly used methods to model movements in connectivity analyses. We obtained two connectivity maps (one per season) for each training dataset using an optimised stochasticity parameter θ (Appendix S10). We finally obtained unique connectivity maps (one per training dataset) by averaging the two seasonal connectivity maps for each training dataset. Thus, each population had 100 connectivity maps for the 'leave 10% of whole data out' procedure, 100 connectivity maps corresponding to the 'leave 10% of population data out' procedure and 1 connectivity map associated to the 'leave one population out' procedure.

2.4.5 | Validating connectivity maps

We used two different methods to evaluate the accuracy of our connectivity predictions. First, we ranked each used step travelled by ibex during migration versus the 15 associated available steps they could have travelled (previously sampled for iSSAs; see Section 2.3.2) based on connectivity values at the end of each step and assigned them a value between 1 (lowest connectivity) and 16 (highest connectivity; ranking method; Goicolea et al., 2021; McClure et al., 2016). If accurately predicted, the average rank of used steps should be higher than those of available steps. Second, we converted connectivity values to percentile connectivity values (e.g. the 95th percentile corresponds to the 5% highest values of the connectivity map) and delineated five connectivity corridors as the 80th, 85th, 90th, 95th and 99th connectivity percentiles. We then calculated the percentage of ibex locations collected during migration included in each connectivity corridor as a

metric of predictive performance of our connectivity models (representation in corridors; Goicolea et al., 2021; Poor et al., 2012; Zeller et al., 2018). As the percentage of ibex locations during migration that fall within a given corridor is strongly dependent on the area of this corridor, we also computed the proportion of locations in the corridor divided by the corridor surface to get an index of accuracy of connectivity predictions (Appendix S11). We applied both validation methods (ranking and representation in corridors) on the different validation datasets we set aside previously to validate our three procedures to compute connectivity maps.

3 | RESULTS

3.1 | Identification of migrant ibex

Among the 1068 seasonal tracks available in our GPS dataset, we identified 337 migratory tracks (169 in spring, 168 in autumn), distributed between multiple winter and summer ranges within each population. On average, the proportion of seasonal tracks identified as migration was 45% (SD 22.5) over the 15 populations, confirming partial migration. However, it varied greatly between populations, from 13% to 75% in the Bargy and Champsaur populations, respectively (considering populations with enough animals to estimate this proportion). On average, migrant ibex travelled 12 km (SD 8) of topographic distance, with population means that varied from 6 to 22 km and an individual maximum of 62 km. In spring, those migratory tracks lasted 3.5 days (SD 3.6) on average and occurred around May 27 (SD 27 days), while in autumn, they lasted 6.3 days (SD 6.3) on average and occurred around October 30 (SD 29 days).

3.2 | Habitat selection during migration

In both spring and autumn, ibex travelled in areas with less total elevation change (192.4 m on average for 6 h) than if they had moved randomly (207.1 m, 7% less; significant in 12/15 populations in spring and 13/15 in autumn; Figure 3). They also selected for proximity to refuges from perceived predation risk (slopes $>40^\circ$; 11/15 populations in spring and 10/15 in autumn) and avoided north-oriented areas (11/15 and 10/15 populations in spring and autumn, respectively). During autumn migration only, they also avoided areas expected to be the first covered by snow and where snow may accumulate (snow cover index; 7/15). By contrast, neither anthropogenic infrastructures (proximity to ski resorts and roads) nor linear structures considered as potential landmarks (proximity to ridges, valley bottoms and tree lines) influenced ibex migratory tracks during either season.

3.3 | Connectivity modelling

The three modelling procedures performed relatively well and produced similar predictions of ibex migratory corridors. About half of

the migratory tracks were in areas with high connectivity, falling in the 95th connectivity percentile corridor (46.3% (SD 15.2) for 'leave one population out'; 51.7% (SD 14.2) for 'leave 10% of population data out' and 51.8% (SD 14.2) for 'leave 10% of whole data out'; Figure 4). The percentage of tracks included in the predicted connectivity corridor increased rapidly for lower values of the predicted connectivity corridor, as more than 90% of the tracks were included in the 80th connectivity percentile. The best stochasticity value θ in the Randomized Shortest Path algorithm was equal to 0.1 (Appendix S10). This intermediate value largely outperformed the

lower ($\theta=0$; totally random movements) and upper limits ($\theta=3$; deterministic movements) resulting in intermediate connectivity patterns between the diffuse connectivity corridors obtained with the circuit theory approach and the narrow and simple least-cost path that prevented from alternative routes (Figure 5).

According to the ranking validation method, the three connectivity modelling procedures tested (i.e. 'leave 10% of whole data out', 'leave 10% of population data out' and 'leave one population out') provided connectivity maps that predicted ibex migratory movements better than random surfaces (see Figure 5 for examples,

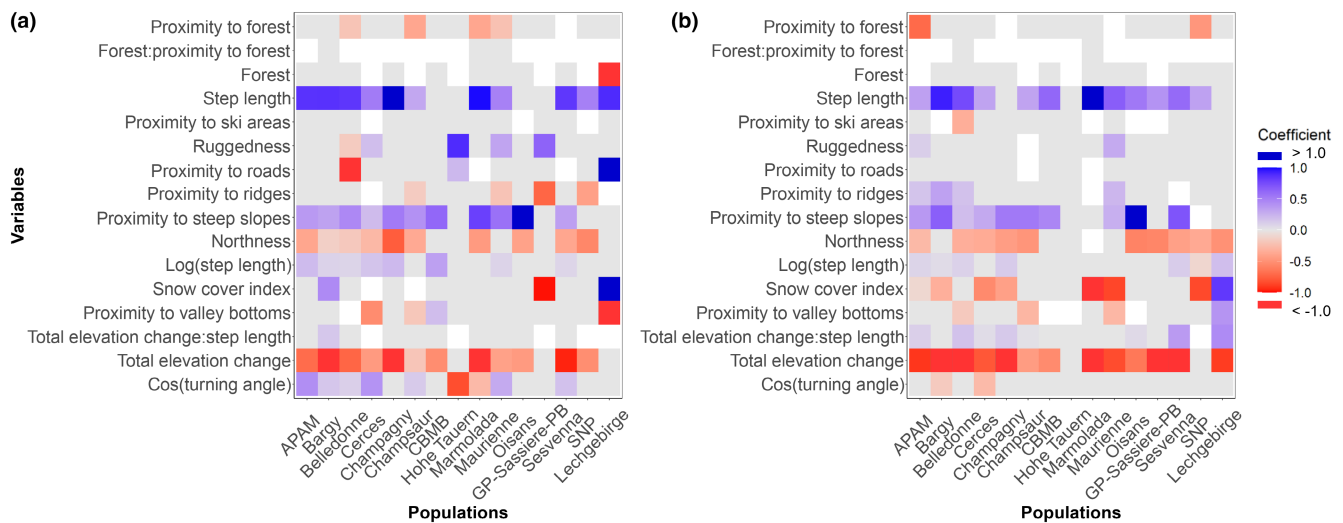
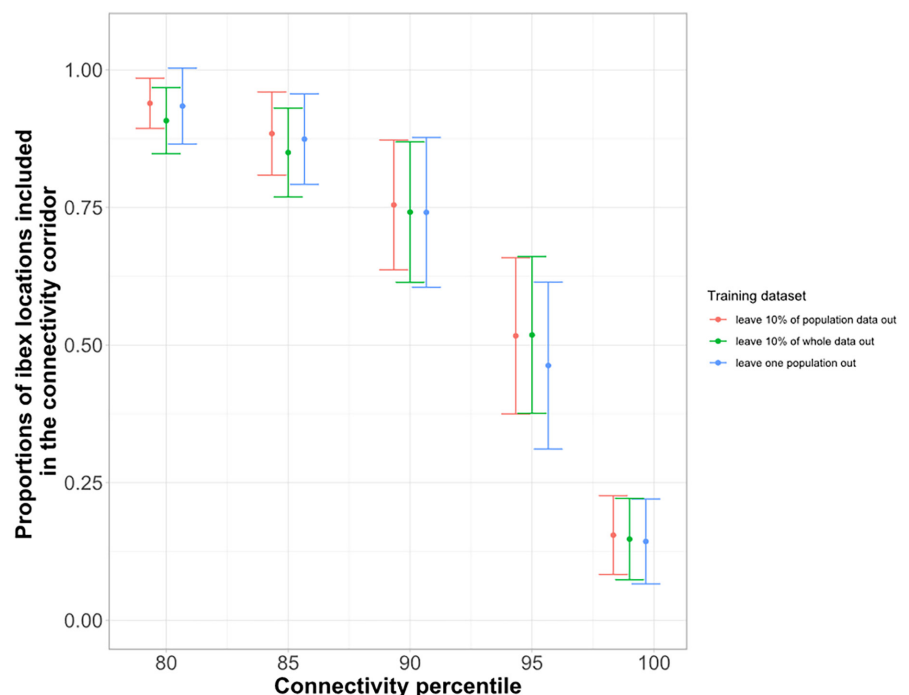


FIGURE 3 Coefficients provided by population-specific model-averaged (models with $\Delta AICc < 2$) integrated Step Selection Analyses investigating the influence of environmental variables on movement steps performed by Alpine ibex from 15 populations during spring (a) or autumn (b) migration. Blue and red cells represent variables that were selected or avoided for migratory movements, respectively. Grey cells represent non-significant coefficients. We calculated the 95% confidence interval (CI) of coefficients resulting from the model averaging. A coefficient was significant if its CI non-overlaps with zero. White cells represent cases for which the influence of a focal habitat variable could not be tested (not retained during model selection).

FIGURE 4 Results of the second validation method, representation in corridors (Goicolea et al., 2021). Proportions of ibex locations from migratory tracks included in the different connectivity corridors defined as the 80th, 85th, 90th, 95th and 99th connectivity percentiles. For the three modelling procedures, the mean proportion calculated over the 15 populations is displayed with its standard deviation.



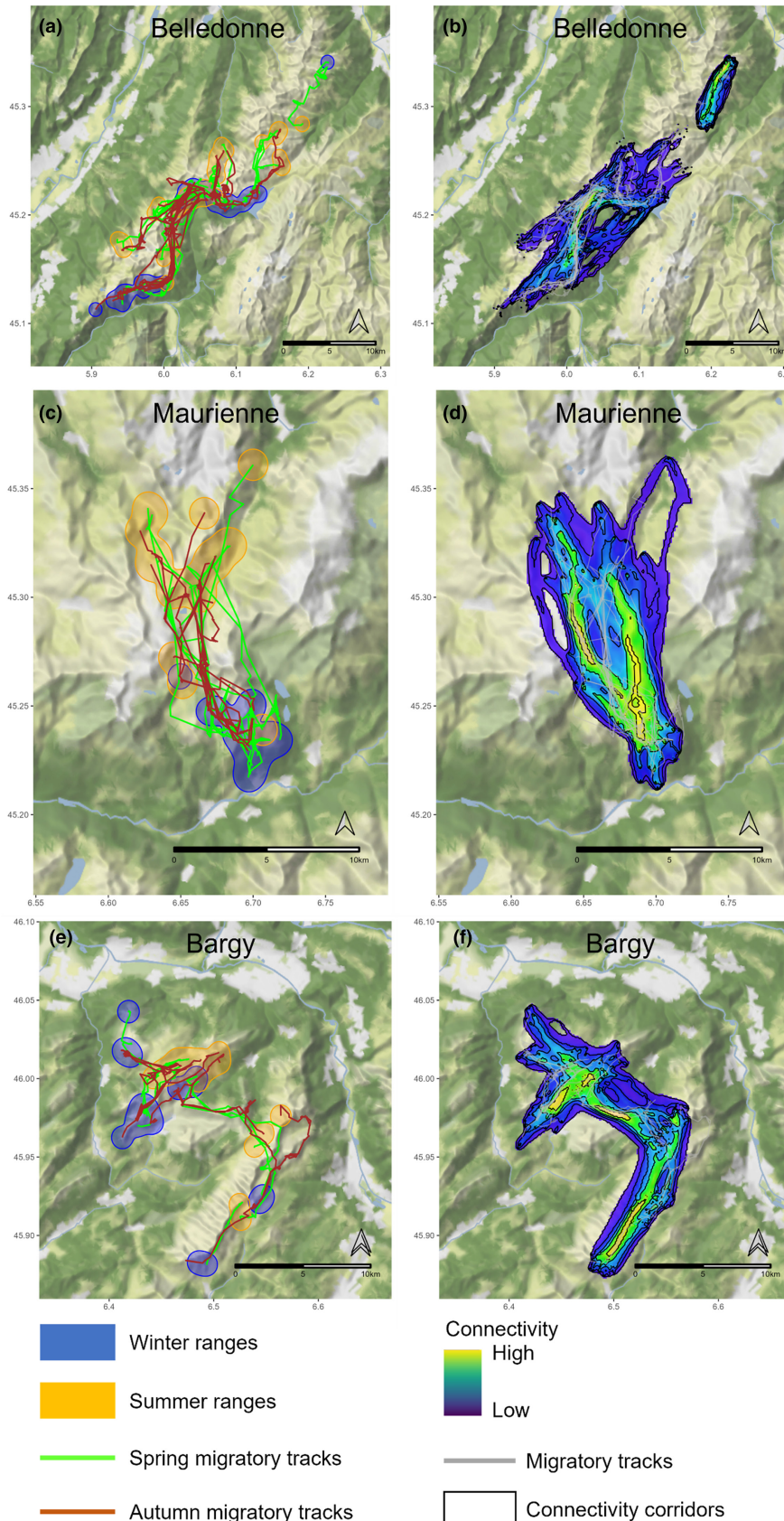


FIGURE 5 Examples of connectivity modelling. Observed migration routes (spring in green and autumn in brown) and summer and winter ranges (orange and blue) of Alpine ibex from Belledonne, Maurienne and Barge populations (a, c, e). Connectivity maps obtained from the 'leave one population out' procedure (b, d, f). The black lines delineate the connectivity corridors as defined in the 'representation in corridors' validation method. We removed very low connectivity values for illustrative purposes. Maps made using *ggmap* package (Kahle & Wickham, 2013) and Stamen terrain background for base data.

and Appendix S12). The mean and median ranks of used steps in the three validation datasets were all >8, with values from 9 to 11 depending on the population, although variability was important (1st

quartile and 3rd quartile ranging from 5 to 15 depending on populations; Appendix S13). However, within populations, results were similar, whatever the training dataset used.

Comparable proportions of locations of migratory tracks were included in connectivity corridors for the three modelling procedures: between 90.8 and 93.9% of locations in the 80th connectivity percentile corridors and between 14.3 and 15.5% in the 99th connectivity percentile corridors (Figure 4, Appendix S14). There was heterogeneity between populations in the accuracy of the predictive models of connectivity, but within the same population, the three connectivity models gave similar results (Appendix S15). The ratio of the proportion of locations included in the corridor over the corridor surface was superior for the 95th and 99th percentile corridors. Therefore, these connectivity corridors captured on average the highest proportion of ibex locations within the smallest surface but the variability in this ratio over the 15 populations was high (Appendix S11).

4 | DISCUSSION

Relying on a dataset assembling 337 migratory tracks collected in 15 Alpine ibex populations distributed across the Alps, we identified the environmental predictors of corridors in this endemic and emblematic short-distance and altitudinal migrant species. While consistently limiting energetically costly elevation change, ibex migrated mostly to south-facing snow-free slopes and close to steep areas, providing refuge from perceived predation risk. By contrast, neither the landmarks (ridges, tree lines, valley bottoms) hypothesised as visual cues for ibex navigation nor human infrastructures (ski areas and roads, when present) affected ibex migratory movements. The randomised shortest path algorithm revealed an intermediate movement strategy in Alpine ibex, trading off optimisation and exploration during migratory movements. The abilities of the three modelling procedures we compared to predict migratory connectivity from the results of those movement analyses, relying on either population-specific or multi-population approaches, were comparable. They provided useful connectivity models to inform conservation of Alpine ibex and its habitats, and a framework for future research investigating connectivity in migratory species from multi-population datasets.

In addition to spring green wave tracking, as evidenced in commonly studied long-distance migrations from North American, Scandinavian and African ungulates, we revealed other predictors, more scarcely investigated, may also drive Alpine ibex during both spring and autumn migration. By focusing on south-facing snow-free slopes, ibex may partly benefit from emerging vegetation during spring migration (although we did not fully investigate the green wave hypothesis, see Section 2; but see Semenzato et al., 2021), while limiting energetically costly movements in snow-covered areas. Limiting energy expenditures seemed particularly important in the Alpine ibex, which also strongly avoided high elevation changes during migration, despite the relatively short distances and durations involved. This behaviour may be adaptive in the steep and rugged terrain in which ibex migration occurs (see Passoni et al., 2021 for another example in roe deer

Capreolus capreolus). Indeed, when travelling through unfamiliar areas for migration, Alpine ibex selected for proximity to steep slopes, habitats commonly used by mountain ungulates to limit perceived predation risk (Grignolio et al., 2007, see also Marchand et al., 2015 for Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp.; Baruzzi et al., 2017 in chamois *Rupicapra rupicapra*). Altogether, these results suggest the persistence of the energy-food-cover trade-off, that is the most important predictor of ungulate habitat selection all year round (Houston et al., 1993; Lima & Dill, 1990; Myrsterud & Østbye, 1999), as a major driver of Alpine ibex migration routes. This trade-off may also explain the intermediate movement strategy of migrant ibex trading off optimization and exploration during migratory movements, as revealed by the randomized shortest path algorithm. By contrast, none of the landmarks tested seemed to be used by migrant ibex as compass for navigation during migration. Yet, recent studies revealed how natural landscape features can be used by mountain ungulates, including Alpine ibex, to delimit their seasonal home ranges and constitute cognitive maps to gather and memorise spatially explicit information for navigation (Seigle-Ferrand et al., 2022). Further research is hence needed to investigate the importance of other navigation cues/mechanisms, and more generally other drivers of migration corridors identified in other contexts/species (e.g. memory; Bracis & Mueller, 2017; Merkle et al., 2019; social learning and cultural transmission; Jesmer et al., 2018) that were not investigated here in the absence of data to do so.

Combined with the randomised shortest path algorithm, the results of three modelling procedures relying either on a population-specific approach or on a multi-population approach provided reliable and similar connectivity maps. Both the 'ranking' and 'representation in corridors' validation approaches indicated relatively high levels of agreement between connectivity corridors and actual migratory tracks, although the dispersion associated with reliability measurements was high. Indeed, in several populations, some predicted high-use areas were not used by ibex, or inversely, ibex used areas that were not predicted as providing high connectivity. Thus, factors such as local idiosyncrasies in landscape features may be involved at the population level.

The occurrence of obvious topographic, climate and anthropogenic differences in the areas used by the 15 studied populations across the whole Alps probably contributed to differences in movement strategies and habitat selection across populations (Figure 3). Accounting for those differences by modelling connectivity based on population-specific habitat selection models rather than population-wide models did not clearly improve the performance of connectivity predictions, except in populations that differed from the general pattern for habitat variables with the greatest importance (e.g. marked avoidance of valley bottoms, ridges, and forest for Champsaur population, contrary to the general pattern, see Appendix S15 for details). The similar performance between our three modelling procedures is likely due to the consistency in the covariates structuring habitat selection patterns in most populations, although these populations were located across the Alps, hence in relatively different

environments. However, when assessed with the same validation method (here 'representation in corridors', easily translatable into management/conservation measures; McClure et al., 2016), the performance of our connectivity models was comparable or better than those reported in other studies (here, 73%–78% locations in the 90th percentile corridor, 68%–72% in Poor et al., 2012 – pronghorn *Antilocapra americana*; 65% in Zeller et al., 2018 – puma *Puma concolor*; 42% in Goicolea et al., 2021 – Iberian lynx *Lynx pardinus*). Moreover, similarly as the above-mentioned studies, our connectivity modelling process implies the transformation of a habitat suitability surface into a resistance surface. Thus, comparing our results to other connectivity modelling methods bypassing this step could be tested (e.g. Nuñez et al., 2022). Testing connectivity predictions is an important step often neglected. By assessing the reliability of our connectivity models, we confirmed their ability to generalise across various populations and environmental contexts within the species' distributional range, even in the absence of spatial data on the population of interest. Our connectivity models thus serve as an invaluable tool for the conservation of this endemic and emblematic species and its habitats.

The migrations of terrestrial species are collapsing worldwide due to the development of human infrastructures that bisect migration corridors (Kauffman et al., 2021; Wilcove & Wikelski, 2008). Even though we did not find any major effects of human infrastructures that could impede ibex migration (i.e. ski resorts and roads, probably due to their scarcity in the vicinity of areas where ibex have been reintroduced) at the scale of individual movements, climate warming and the development of human activities and infrastructures, particularly present in the Alps (Parmesan & Yohe, 2003; Schmeller et al., 2022), could already be at play at broader spatial scales and could reshape movement corridors of alpine animals in the near future (Zeller et al., 2021). In addition, despite the numerical success of the species reintroduction programmes over the Alps, Alpine ibex still face important conservation issues (e.g. dramatically low genetic diversity, lack of functional meta-populations; Biebach & Keller, 2009; Brambilla et al., 2020) and migration corridors remain poorly protected. In this context, preserving and (re-)establishing connectivity within and between ibex populations will probably be a major conservation issue in the next decades, and tools such as our connectivity models could be particularly helpful.

More generally, our study also provided an original methodological framework for future research and conservation efforts dedicated to connectivity analysis and predictions of movements other than migration. Here, the three different procedures (i.e. 'leave 10% of whole data out', 'leave 10% of population dataset out' and 'leave one population out') revealed no major differences in accuracy of corresponding connectivity predictions. Thus, our models could be used to predict migratory movements in monitored populations with either enough data, using population-specific models, or using data from all populations. Moreover, we could predict movements in populations where no GPS data are available but seasonal range locations are known or predicted with habitat selection models. With the advent of animal tracking over the last decades, and the

generalisation of initiatives aiming at gathering those GPS data in common databases (e.g. Movebank, Euromammals, Biologging initiative, Global Initiative for Ungulate Migrations; Kauffman et al., 2021; Urbano et al., 2021), multi-population analyses will develop and testing the reliability of population-specific versus multi-population connectivity predictions is crucial, particularly in a context of demand and need around conserving and restoring connectivity within species distribution ranges.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

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DATA AVAILABILITY STATEMENT

All migratory tracks of Alpine ibex used in this study are available at a Zenodo Digital Repository. <https://doi.org/10.5281/zenodo.7928672>.

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BIOSKETCH

Victor Chauveau is a PhD student at the Laboratoire d'Ecologie Alpine - CNRS in France. He is interested in the behavioural and movement ecology of vertebrate species. Victor's PhD thesis focuses on the migration of Alpine ibex (*Capra ibex*), in particular understanding environmental and individual drivers of migration in this species.

Author Contributions: VC, PM, MG, CT, AC and AL conceived and designed the study. All the co-authors participated in managing animal monitoring and GPS data collection. VC and PM designed statistical analyses. VC analyzed the data. VC wrote the draft of the manuscript with comments from all the other co-authors. VC, PM, MG, CT, AC and AL revised further versions of the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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