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RESEARCH ARTICLE

# It's time to go—Drivers and plasticity of migration phenology in a short-distance migratory ungulate

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## Abstract

1. Recurring events like migrations are an important part of the biological cycles of species. Understanding the factors influencing the timing of such events is crucial for determining how species face the pervasive consequences of climate change in highly seasonal environments.
2. Relying on data from 406 GPS-collared Alpine ibex *Capra ibex* monitored across 17 populations, we investigated the environmental and individual drivers of short-distance migrations in this mountain ungulate.
3. We found that vegetation phenology, including spring growth and autumn senescence, along with snow dynamics—snowmelt in spring, onset of snow cover in autumn—were the main drivers of the timing of migration. In spring, ibex migration timing was synchronized with the peak of vegetation green-up, but more in males than in females. Specifically, a peak of green-up occurring 10 days later delayed migration by 6.4 days for males and 2.7 days for females. This led to increased differences in migration timing between sexes when the peak of green-up occurred early or late in the season. In addition, ibex delayed migration timing when the length of the spring season was longer and when the date of snowmelt on ibex summer ranges occurred later. Similarly, in autumn, prolonged vegetation senescence and delayed onset of snow cover led to later migration.
4. Overall, we observed a high degree of behavioural plasticity, with individuals responding to inter-annual variations in vegetation and snow phenology, even though the extent of these adjustments in migration dates was lower than the

For affiliations refer to page 12.

magnitude of the interannual changes in environmental conditions. Nonetheless, females could be less plastic than males in their timing of spring migration, likely due to the parturition period following migration forcing them to trade off foraging needs with predation risk. As the identified drivers of ibex migration are known to be and will continue to be largely impacted by climate change, the capacity of ibex to respond to such rapid changes could differ between sexes.

**KEYWORDS**
alpine ungulate, Alps, altitudinal migration, behavioural plasticity, migration timing, movement ecology, snow dynamics, vegetation phenology

## 1 | INTRODUCTION

The consequences of climate change on ecological systems and processes are ubiquitous, resulting in changes in the timing of periodic life-history events, behaviours and species distribution (Inouye, 2022; Parmesan & Yohe, 2003). Understanding these effects is crucial to predict future ecological changes and try to mitigate their consequences (Bellard et al., 2012). In seasonal environments, the biological cycles of animal species are often synchronized with the timing of other ecological processes (Both et al., 2009). For instance, the timing of births generally coincides with the burst of food resources, providing favourable conditions for maximizing newborn survival (Durant et al., 2007; Plard et al., 2015). Therefore, changes in temperature and precipitation induced by climate change can have cascading consequences on the timing of biological events related to plant availability and quality, such as animal migration and reproduction by directly affecting plant growth (Post & Forchhammer, 2007; Visser et al., 1998; Walther et al., 2002).

Migration is a critical tactic of organisms to cope with seasonally varying environments. Indeed, movements between distinct seasonal ranges allow animals to cope with seasonal availability of resources, weather conditions, predation risk or competition intensity (Dingle & Drake, 2007). Seasonal migration can provide survival and reproductive benefits (Avgar et al., 2014; Grayson et al., 2011; van Moorter et al., 2021) but also comes with costs (e.g. mortality during migration; Hays, 2014) so that migration may not always be more advantageous than residency (Buchan et al., 2020). The net fitness gain of migration strongly depends on its timing. For instance, in temperate regions, migratory herbivores move across the landscape to maximize energy intake by tracking gradients of plant phenology, that is, “surfing” or “jumping the green wave” (common in birds and ungulates: Bischof et al., 2012; Merkle et al., 2016; Van der Graaf et al., 2006; see also in whales: Abrahms et al., 2019). In alpine mountains, plant phenology strongly varies along short altitudinal gradients. Hence, herbivores can seasonally move along different altitudes to benefit from the gradient of plant phenology (Herfindal et al., 2019), resulting in altitudinal migrations usually shorter than those observed in lowlands along latitudinal gradients (Sawyer et al., 2019). In spring, increasing temperatures and related events such as snowmelt and vegetation green-up have been identified as common drivers of the timing of migrations among birds and ungulate species (Candino et al., 2022; Gurarie et al., 2019; Mallory et al., 2020; van Wijk et al., 2012). In autumn, the return of winter weather conditions, such as snow and cold temperatures, often triggers migrations as individuals need to migrate before snow cover impedes access to forage, reduces mobility and increases predation risk (Monteith et al., 2011; Rickbeil et al., 2019; Weller et al., 2022). In the context of ongoing global warming, the changes in the timing of phenological events, such as shifts in the availability of resources and local weather conditions, stand as a real challenge for migratory species. Indeed, a mismatch between migration timing and environmental conditions could reduce the benefits and increase the costs of migration, with potentially long-term consequences on fitness and population dynamics (Aikens et al., 2020; Middleton et al., 2018).

Migration also occurs around other important biological events often related to internal changes (e.g. physiological/hormonal changes related to parturition or mating season) that may constrain the timing of migration. In sexually dimorphic species, males and females have different energy requirements and may accordingly differ in their migratory behaviour (Peters et al., 2019). Besides, individuals with contrasted reproductive status (i.e. reproductive vs. non-reproductive females) or of variable age (e.g. males in which rut-involvement is age-dependent) may have different needs and constraints, and hence variable costs/benefits to migrate at a given time, resulting in different migration timing in individuals of different sexes or ages (Debeffe et al., 2019; Rodgers et al., 2021). Age is also related to individual knowledge of past conditions and experience in tracking favourable conditions (Abrahms et al., 2021). Hence, understanding migration timing in relation to individuals' needs and constraints, and experience, is crucial to anticipate differing responses to environmental changes between individuals (Balbontín et al., 2009; Verhoeven et al., 2019).

Individuals and populations can respond to changing environmental conditions through phenotypic plasticity and genetic adaptation, whose relative importance depends on species biology (Charmantier et al., 2008; Moyes et al., 2011; Plard et al., 2013). However, adaptive responses are unlikely to keep pace with ongoing rapid climate change, particularly in long-lived species (Alberto et al., 2013; Cotto et al., 2017; Donnelly et al., 2012). Consequently, species rely heavily on phenotypic plasticity to respond to environmental changes, and their level of plasticity can potentially be used as an indirect estimate of their resilience to climate change (Rickbeil et al., 2019; Stepanian & Wainwright, 2018; Xu et al., 2021). At the same time, phenotypic plasticity is sometimes limited (e.g. parturition timing in roe deer *Capreolus capreolus*, Plard et al., 2013) and not much is known about the extent of it in cold-adapted alpine species. On one hand, species living in alpine mountains could be less responsive to climate change due to their unique adaptations to face the strong limiting conditions of their environment (White et al., 2018). On the other hand, phenotypic plasticity, especially behavioural plasticity, may be favoured in such environments as individuals usually need to adjust their behaviour to cope with temperature variability at daily and seasonal scales, along with marked annual fluctuations in resource availability (Enriquez-Urzelai et al., 2020). The ability of alpine species to exhibit behavioural plasticity in tracking the bottom-up processes governing forage and snow conditions still requires further investigation.

In this study, we investigated the factors affecting the phenology and temporal plasticity of short-distance migration in a mountain species, the Alpine ibex *Capra ibex*, using GPS data from 17 populations distributed across the Alps (Figure 1). The Alpine ibex is an emblematic species endemic to the Alps (Rüdisser et al., 2019). Despite a current wide distribution, extending from southern France to Slovenia, almost all ibex populations were reintroduced from the last individuals (estimated fewer than 100) of the only remaining population located in the current Gran Paradiso (Italy) and Vanoise National Parks (France, Brambilla et al., 2020). Therefore, Alpine ibex populations are characterized by a very low genetic diversity, possibly limiting their adaptive potential and behavioural plasticity (Biebach & Keller, 2009; Robin et al., 2022). Migration occurs in most ibex populations, but is partial (i.e. each year, some ibex migrate and others are resident, and this choice can change from year to year) and consists of a short-distance and rapid altitudinal movement (on average 12 km travelled in 3–6 days; Chauveau, Garel, Toïgo, Anderwald, Beurier, et al., 2024). Alpine ibex migration occurs close to important biological events: parturition, from early June to mid-July, and rut, from early December to mid-January, which in turn correspond to times of major variations in environmental conditions. In spring and summer, when spring migration occurs for some of them (from early May to late June, Chauveau, Garel, Toïgo, Anderwald, Beurier, et al., 2024)—ibex reconstitute fat reserves after winter scarcity (Brambilla et al., 2024). This is particularly important for reproductive females whose ability to meet the high energy demand for late gestation and lactation largely contributes to juvenile survival (Post & Forchhammer, 2007; Richard et al., 2017). In autumn, migration, from early October to late November (Chauveau, Garel, Toïgo, Anderwald, Beurier, et al., 2024), allows ibex to reach winter ranges usually lower in elevation and often consisting of steep south-facing rocky cliffs where winter weather conditions are milder (Herfindal et al., 2019) and where males meet females for the rutting season. As a result, plasticity in migration timing may be crucial for fitness and the ability of ibex to cope with ongoing climate change.

Our first objective was to identify the environmental and individual factors influencing the timing of ibex migration in both seasons (Figure 2). Specifically, we tested whether migration timing was driven by environmental conditions such as vegetation phenology, snow conditions, and temperatures experienced by ibex in the days preceding migration (already identified as a key factor for ibex individual behaviour and movements; Aublet et al., 2009; Herfindal et al., 2019; Mason et al., 2017; Semenzato et al., 2021). At a larger temporal scale, we expected seasonal climatic conditions experienced during the whole season preceding migration to also influence its timing because of their effect on ibex body condition and energetic gains throughout the season (Anderson et al., 2019; Brambilla et al., 2024; Cooper et al., 2015; Gurarie et al., 2019). We

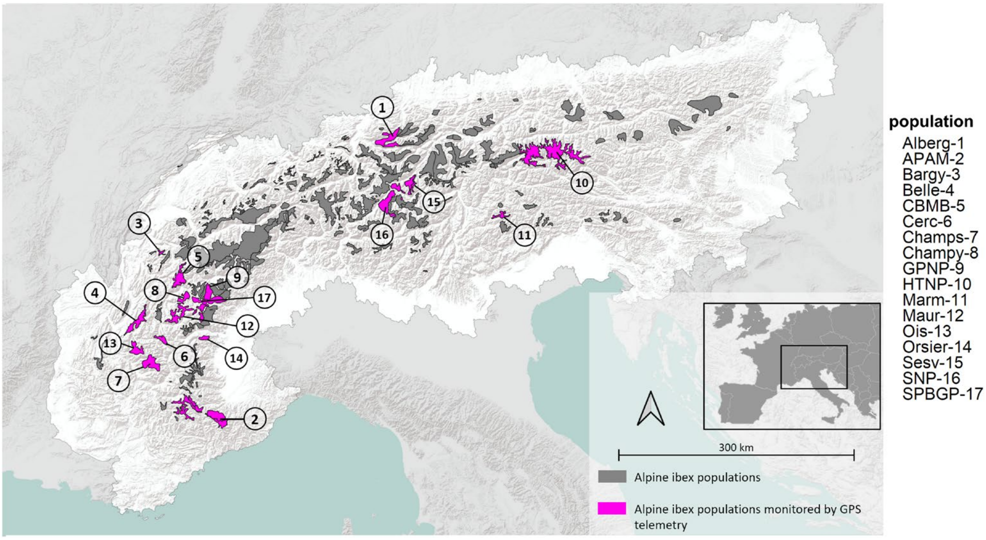

**FIGURE 1** Distribution of Alpine ibex populations across the Alps (grey) and populations monitored with GPS telemetry (pink). Names of populations are abbreviated for clarity, refer to Table S1 for details on population monitoring. Shapefiles of populations from Brambilla et al. (2020). Base layer ESRI terrain.

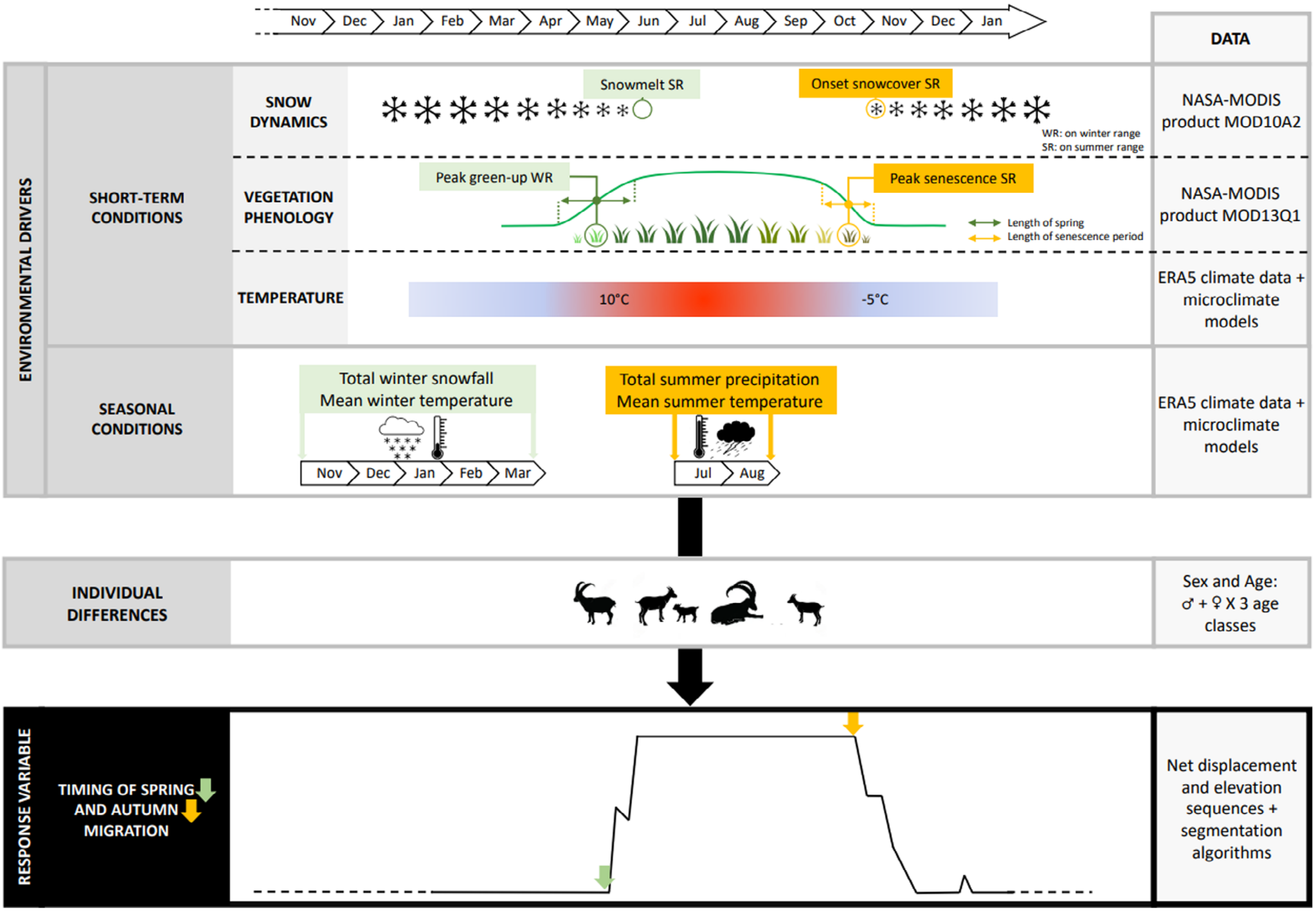

FIGURE 2 Conceptual framework summarizing the environmental (seasonal and short-term) and individual drivers hypothesized to affect the timing of spring and autumn migrations in Alpine ibex *Capra ibex*. The type of data used to test each hypothesis is listed in the column to the right.

also tested for the importance of sex and age-specific biological factors as individual drivers of migration phenology (all our hypotheses and predictions are detailed in Table 1). Our second objective was to investigate the occurrence of behavioural plasticity in migration. We took advantage of repeated measurements on the same individuals to get a direct estimate of the magnitude of change in individual migration timing in response to inter-annual differences in environmental conditions (Charmantier et al., 2008).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area, species and populations

We relied on a GPS dataset collected on 406 Alpine ibex from 17 populations (557 individual-years; 46% females and 54% males; aged from 2 to 18 years old). Alpine ibex is a long-lived partially migratory species with a lifespan of up to 15 years for males and 17 years for females and an average generation length of 8 years (Brambilla, Bassano, et al., 2022; Chauveau, Garel, Toïgo, Anderwald, Beurier, et al., 2024). As a result of the strong sexual dimorphism (with males that can be twice as large as females, Brambilla, Bassano, et al., 2022), this gregarious species with fission–fusion dynamics (Brambilla, Bassano, et al., 2022; Lesmerises et al., 2018) exhibits a strong socio-spatial segregation between the sexes all year round, except during the mating season in December and January, with segregation peaking during spring and summer (Bon et al., 2001; Ruckstuhl & Neuhaus, 2001). However, as migration lasts only a few days, there is little information on social behaviour during this period. The studied populations were distributed across the Alps (France, Italy, Switzerland, and Austria), where ibex may share habitats with other wild (e.g. chamois *Rupicapra rupicapra*, roe deer *Capreolus capreolus* and red deer *Cervus elaphus*, mouflon *Ovis gmelini musimon* × *Ovis* sp., and wild boar *Sus scrofa*) and domestic (sheep, goat and cow) ungulate species. In these regions, predators like the grey wolf (*Canis lupus*) and golden eagle (*Aquila chrysaetos*) are often present but rarely predate on ibex (Palmegiani et al., 2013). Nevertheless, Alpine ibex display antipredatory behaviours (e.g. increasing vigilance or moving towards steep slopes and cliffs) when perceiving risky situations (Grignolio, Rossi, Bassano, et al., 2007). These behaviours are more pronounced in females (Bon et al., 1995; Grignolio, Rossi, Bertolotto, et al., 2007).

GPS data were collected over 20 years, with the first GPS collars deployed in 2003 and the last one that ended activity in 2022

**TABLE 1** Predictions of the effects of environmental factors on the timing of Alpine ibex migration in spring and autumn.

| Season | Environmental drivers | Differences sex and age | Predictions | Sources |
|---|---|---|---|---|
| Spring | Peak of green-up in WR | M > F<br>Old M > Young M | M & F migrate around the peak of green-up, but F are less synchronized because of parturition following migration<br>Older ibex less synchronized with peak of green-up (look for forage quantity over quality) | Debeffe et al. (2017), Grignolio, Rossi, Bassano, and Apollonio (2007), Main and Coblentz (1996) and Rodgers et al. (2021) |
| | Length of spring season in WR | | Ibex migrate later when the spring season is longer because of extended access to high quality forage in WR | Garel et al. (2011), Herfindal et al. (2006) and Pettorelli et al. (2005) |
| | Date of snowmelt in SR | | Ibex delay migration when snowmelt occurs later on their SR | Berger et al. (2022) and Pandraud et al. (2022) |
| | Temperature threshold | | Ibex migrate in response to increasing temperatures. Migrate later when the daily mean of 10°C occurs later in spring | Aublet et al. (2009), Mason et al. (2017) and Semenzato et al. (2021) |
| | Winter severity: winter snowfall and winter temperature | | Winter severity negatively affects ibex body condition leading to delayed migration | Brambilla et al. (2024), Gurarie et al. (2019); Herfindal et al. (2019) and Signer et al. (2011) |
| | Distance | | Ibex migrating longer distances migrate earlier | Gurarie et al. (2019) and Le Corre et al. (2016) |
| Autumn | Peak of senescence in SR | M > F<br>Old M > Young M | Ibex migrate when vegetation quality and quantity decreases. M are more affected by vegetation conditions than F (last forage before rut) | Rivrud et al. (2016) and Cameron et al. (2021) |
| | Length of senescence period in SR | | Ibex migrate later when the vegetation senescence period is extended | |
| | Date of onset of snow cover in SR | | Ibex migrate after installation of snow cover | Jones et al. (2014), Le Corre et al. (2016) and Weller et al. (2022) |
| | Temperature threshold | | Ibex migrate in response to decreasing temperatures. Migrate later when the daily mean of −5°C occurs later in autumn | Ortega et al. (2024), Rivrud et al. (2016) and Weller et al. (2022) |
| | Summer conditions: Summer precipitation and temperature | | Hot and dry summers negatively affect ibex body condition leading to delayed migration | Brambilla et al. (2024) and Gurarie et al. (2019) |
| | Distance | | Ibex migrating longer distances migrate earlier to avoid costly movement in snow | Le Corre et al. (2016) and Rivrud et al. (2016) |

Abbreviations: F, females; M, males; SR, summer range; WR, winter range.

(Table S1; Figure S1 for details). Animals were generally captured during spring or summer using traps, drop nets or chemical immobilization by tele-injection depending on study areas and equipped with several types of GPS collars (Vectronic: GPS Plus, Vertex Plus, or Vertex Lite models; Lotek: 3300S or Litetrack models; Followit: Tellus model). All models weighed <3% of individual body mass. The GPS devices were programmed to record ibex locations at variable frequencies and during variable periods (from 1 location per hour during 1 year to 1 location per 6 h during 2–5 years). After 1–5 years of monitoring, GPS collars were retrieved by using a drop-off system or during a recapture. All capture and marking procedures were done with the approval of the governmental authorities of each concerned country and in accordance with local, national and European animal welfare laws.

## 2.2 | Identification of migration departure dates and migratory status

We divided GPS tracks of each animal into yearly tracks starting on March 1st and ending February 28th or 29th of the following year, thereby including known ibex spring and autumn migration periods, occurring respectively around June and November (Chauveau, Garel, Toïgo, Anderwald, Beurier, et al., 2024). Tracks lasting less than 1 year were kept in the dataset only when the duration was at least 7 months long, centred on spring or autumn migration, and including a few months before and after (i.e. March–September or August–February, respectively) to get enough data and temporal variation for running the segmentation algorithms (see below). For each individual yearly track, we calculated two movement time series: (i) the net displacement (ND), which is the Euclidean distance between the first location of the track and each of the following locations and provides information about changes in the x/y plane (Börger & Fryxell, 2012) and (ii) the net elevation displacement (NED), which is the difference in elevation between the first location of the track and all the following ones, and provides information about changes in elevation (Spitz et al., 2017).

Then, we looked for major changes in terms of distance (using ND) and/or elevation (using NED) using two segmentation and non-parametric algorithms (see examples in Figure S2). Migration departure dates (hereafter called "migration dates") were estimated using two segmentation algorithms able to find significant breakpoints in ND and NED time series (see examples in Figure S2). We relied on the divisive hierarchical estimation algorithm to find a unique and common breakpoint to ND and NED time series at once (*e.divisive* function with $k=1$ in *ecp* package, James et al., 2020). We also used a decision tree algorithm (*tree* function in *tree* package, Ripley, 2023) to find multiple breakpoints in ND and NED seasonal time series separately. Then, we filtered these multiple breakpoints by keeping only those that were identified by the two algorithms in both ND and NED time series, with a difference of less than 3 days. Breakpoints identified between July 15th and August 15th were not considered as being related to a migration event and were removed. Finally, we visually checked the accuracy of the breakpoints identified by both approaches, and when more than one breakpoint was identified, we chose the most appropriate (according to our interpretation of the GPS locations) among them (concerning 18% of the breakpoints).

We calculated the overlap between individual winter and summer utilization distributions (UD) each year to classify animals as migrant or resident (Igota et al., 2004). Seasonal UD were computed on a 50 m resolution grid using all locations available for a given season except those recorded during the +/− 7 days around the breakpoints previously identified. For both periods, we calculated the overlap between the volume of the kernel of winter and summer UDs using the *kerneloverlap* function (method VI, *adehabitatHR* package, Calenge, 2023). We considered that an animal was migrant for the given season if the overlap between seasonal UDs was lower than 20% (threshold determined from preliminary unshown analyses; similar to the range in Cagnacci et al., 2016 in ungulate species) and we considered the corresponding breakpoint as the migration departure date (Figure S2). We also calculated the distance travelled by each ibex during migration as the Euclidean distance between the centroids of the winter and summer locations.

## 2.3 | Drivers of migration phenology

### 2.3.1 | Short-term environmental conditions

We derived four proxies of vegetation phenology: the date of peak of green-up (i.e. peak in vegetation quality; Hamel et al., 2009); the date of peak of vegetation senescence (hereafter called the peak of senescence); the length of spring season, and the length of senescence period (Figure 2; named after Kong et al., 2022). Data were derived from a MODIS NDVI product (NASA-MODIS vegetation, product MOD13Q1, spatial resolution: 250 m, temporal resolution: 16 days) following the methodological workflow described in Kong et al. (Kong et al., 2022; R package *phenofit*). We used weighted Whittaker as rough fitting function, modified bisquare as weighting updating function (Kong et al., 2019) and Beck logistic as fine curve fitting method (Beck et al., 2006). We used the reconstructed daily scale time series of NDVI from the fine fitting to extract phenological metrics ('date of peak of green-up', 'length of spring', 'date of peak of senescence', 'length of senescence') from every growing season for each pixel corresponding to an ibex location. The date of peak of green-up was calculated as the day when the maximum of the first-order derivative function of the time series was reached in each pixel (similar to the date when the Instantaneous Rate of green-up—IRG—is maximum; Bischof et al., 2012). Similarly, the autumn peak of senescence was calculated as the date when the maximum rate of senescence was reached (the rate of decrease in NDVI values is maximum). To estimate the length of spring season and length of senescence period, we calculated the difference in days between the date when NDVI reached a plateau ('peak of season' following Kong et al., 2022) and the date when vegetation greening started ('start of green-up'), and the difference between the date when senescence started and the date when it ended ('vegetation recession date' following Kong et al., 2022), respectively (see also Figure 2). We also derived from the MODIS snow product (NASA-MODIS snow, product MOD10A2, spatial resolution: 500 m, temporal resolution: 8 days, Hall & Riggs, 2021), two seasonal proxies of snow phenology: the date of snowmelt and the date of onset of snow cover (Figure 2). Snowmelt was defined as the first day when a pixel was snow-free during a consecutive 8-day period. The onset of snow cover was defined as the first day when a pixel was covered with snow during two consecutive 8-day periods.

To investigate the effects of the phenological variables on the timing of spring and autumn migrations (Figure 2), we averaged values for each of them across all GPS locations for a given ibex in the week prior to or following migration. Thus, for the spring season, we obtained the average date of peak green-up and length of spring on winter ranges of ibex, and the date of snowmelt on their summer ranges. For autumn migration, we obtained the average date of peak vegetation senescence, length of the senescence period, and date of onset of snow cover on the summer ranges of ibex, that is, the week before their autumn migration. In general, we expected animal migration to be primarily influenced by the local conditions they encountered rather than by those in distant areas (i.e. local resources rather than anticipated future foraging opportunities), with one notable exception being the timing of snowmelt. Indeed, we included snowmelt as the date when snow melted in the locations used by ibex during the week after spring migration. The rationale behind this stems from the fact that snowmelt or snow presence in summer ranges, thus at higher elevation, could also affect the timing of migration. Indeed, in mountain landscapes, snow cover provides a relevant visual cue for informing animals on remote environmental conditions (Berger et al., 2022), and in particular, forage that may emerge soon after snowmelt (the correlation coefficient between snowmelt in summer ranges and peak of green-up in summer ranges was 0.65). However, we expected the date of snowmelt on summer ranges to be more influential on the timing of migration for ibex performing short migrations, as animals can better perceive snow conditions at their destination than ibex performing long-distance migrations.

### 2.3.2 | Seasonal environmental conditions

Temperature and precipitation were derived for each population over the period of monitoring, from a microclimate model that integrated ERA5 hourly weather data produced by the Copernicus Climate Change service at ECMWF (spatial resolution 30 km × 30 km). A digital elevation model (30 m) was used for downscaling the atmospheric data at the population scale (*micro_era5* function in *NicheMapR* package, Kearney et al., 2020). Hourly temperature and daily precipitation were predicted at a height of 1 m on flat terrain for a spatial location and elevation corresponding to the centroid of all ibex GPS locations of a given population (min altitude = 1938 m, max altitude = 2928 m). Then, we calculated for each population year the mean winter temperature and cumulative snowfall (sum of daily precipitation when average daily temperature <0°C) during winter (November–March) and the mean summer temperature and cumulative precipitation throughout the summer period (July–August).

To investigate the influence of temperature on migration timing, we determined the dates when daily mean temperatures reached a threshold of 10°C (spring) and −5°C (autumn) for each population-season. In preliminary analyses, we tested various temperature thresholds (spring: 5, 10, 15°C; autumn: 5, 0, −5°C), but retained only those that most closely aligned with ibex migration timing as the other thresholds occurred too early or too late (i.e. weeks/months before/after migrations) and were unlikely to influence migration departure (see Appendix S4 for further analysis on the effect of temperature on spring migration timing).

The correlations between the short-term environmental drivers and seasonal drivers were all <0.5 except for mean winter temperature and cumulative snow precipitation during winter (−0.7; Figure S5).

### 2.3.3 | Individual characteristics

We grouped individuals in age classes that reflect reproductive status and body growth allocation (Brambilla, Von Hardenberg, et al., 2022; Toïgo et al., 2002; Willisch et al., 2012). Those age-related factors could influence the timing of migration and how individuals tracked the growing vegetation (Brivio et al., 2014). The choice of using age class instead of exact age was done to have a sample size large enough in each class. For females, we considered three age classes: 2–3 years old (non-reproductive, highest body growth allocation, $n=86$), 4–9 years old (highest proportion of reproductive females, limited body growth, $n=65$) and 10+ years old (intermediate proportion of reproductive females due to reproductive senescence beyond 12 years-old, adult size, $n=32$, Rughetti et al., 2015). For males, we considered three different age classes: 2–5 years old (non-reproductive, highest body growth allocation, $n=89$); 6–9 years old (intermediate proportion involved in rutting activities, medium body growth allocation, $n=157$); and 10+ years old (high rut involvement, adult size, $n=33$).

### 2.3.4 | Statistical analyses

We tested the effect of environmental and individual covariates on the timing of spring migration (measured as Julian date) by fitting linear mixed models. The initial model included the following explanatory variables: the mean winter temperature in interaction with cumulative winter snow precipitation, the date of peak green-up in interaction with sex and age classes, the length of spring season in interaction with the date of peak green-up, the date when the 10°C threshold was reached, and the date of snowmelt on summer range in interaction with migration distance (Figure 2). We fitted all possible combinations of these covariates using the dredge function in the MuMin package (Barton, 2023). The date of autumn migration was modelled as a function of the date of peak senescence in interaction with sex and age class, the date of peak senescence in interaction with the length of the senescence period, the date of onset of snow cover, the date when the −5°C temperature was reached, an interaction between the mean temperature during summer and cumulative rainfall during summer, and the migration distance. All those models also included as random effects on the intercept individual identity nested in population to account for within-individual and within-population dependency. Our particular sampling from many ibex populations distributed across a large area and monitored during different years could introduce a blend of spatial variation (among populations) and temporal variation (between years) in covariates. Therefore, we ensured in a dedicated analysis (see Appendix S6) that our models accurately captured the relationship between temporal variation in covariates and migration timing, rather than solely reflecting the spatial differences in environmental conditions among populations. Indeed, migration timing could locally coincide with environmental conditions and vary from one population to another due to local adaptations within a given population, without individuals being able to adjust their migration timing to inter-annual variations in phenological events (see Hagen et al., 2021; Peláez et al., 2020; Plard et al., 2013 for an example on the phenology of parturition in roe deer).

We conducted model selection using Akaike information criterion with second-order adjustment, AICc, to correct for small sample bias. When the difference in AICc (ΔAICc) is greater than 2, there is considerable support for a real difference between models (Burnham & Anderson, 2004). Based on the models with a ΔAICc <2, we selected the final model as the most parsimonious model (least number of parameters) in the set of models with ΔAICc <2. We tested all final models for multicollinearity using variance inflation factors (VIF) and in no cases did any VIF exceed a value of two

(Zuur et al., 2010). We performed all analyses using R 4.2.2 (R Core Team, 2024).

## 2.4 | Individual behavioural plasticity

First, we focused on the subset of migration dates identified in individual ibex tracked during at least two (up to 5) seasonal migrations (average of 2.3 migrations in spring, on 27 females and 45 males and average 2.2 migrations in autumn, on 18 females and 37 males) to estimate the slopes of the relationships between interannual changes in individual migration dates (Δmigration dates, 33 and 19 observations for males and females in spring, 29 and 9 for males and females in autumn) and interannual changes in seasonal and/or local environmental conditions previously selected in the best models (see Results and Charmantier et al., 2008 for a similar approach). These slopes can be considered direct estimates of behavioural plasticity. We estimated them by fitting a linear mixed-effects model for each season (and sex in spring) with interannual changes in migration dates as the response variable and interannual changes in seasonal and/or short-term environmental conditions as predictors. We included individual identity nested in population as random effects in these models. We compared the slopes of these models from longitudinal analyses to those of the previous models (transversal analyses) to assess if relationships at the population scale could be explained by behavioural plasticity in migration timing. Based on individuals with repeated measures, we also estimated the mean between-year differences in migration timing for males and females separately, as well as the mean between-year differences in the date of peak green-up and date of onset of snow cover, the two covariates having the most influence on migration timing for spring and autumn respectively (see Section 3).

# 3 | RESULTS

We identified 211 migration dates in spring and 250 migration dates in autumn; 50% of individuals were classified as migrants in both seasons (Figure S1 for details). The median Euclidean distance and median altitudinal difference between winter and summer ranges were 3035 m (SD = 3333) and 442 m (SD = 239), respectively (Figure S11). The average spring migration occurred around June 6 (SD = ±16 days), whereas the average migration in autumn was November 1 (SD = ±23 days; Figure S12).

## 3.1 | Drivers of migration phenology

### 3.1.1 | Spring migration

The selected model included as explanatory variables the date of peak green-up in interaction with sex, the length of the spring season, and the date of snowmelt (Table 2; marginal and conditional

**TABLE 2** Set of linear mixed-effects models used to investigate variation in migration dates with environmental and individual characteristics at both seasons.

| Season | Initial model | Models | *K* | Log(likelihood) | AICc | ΔAICc |
|---|---|---|---|---|---|---|
| Spring | peakGU*sex*age + snowM*distance + peakGU*SpringL + snowT*tempW + T10 | peakGU*sex + snowM + SpringL + snowT | 10 | −838.1 | 1697.3 | 0 |
| | | peakGU*sex + snowM + SpringL + snowT + distance | 11 | −837.1 | 1697.5 | 0.3 |
| | | peakGU*sex + snowM + SpringL + snowT + distance + T10 | 12 | −836.2 | 1697.9 | 0.7 |
| | | peakGU*sex + snowM + SpringL + snowT + T10 | 11 | −837.3 | 1697.9 | 0.7 |
| | | **peakGU*sex + snowM + SpringL** | **9** | **−839.5** | **1698.0** | **0.7** |
| | | peakGU*sex + snowM + SpringL + tempW | 10 | −838.5 | 1698.1 | 0.8 |
| | | peakGU*sex + snowM + SpringL + distance | 10 | −838.6 | 1698.3 | 1.0 |
| | | peakGU*sex + snowM + SpringL + distance + snowT + distance*snowM | 12 | −836.4 | 1698.4 | 1.1 |
| | | Null model | 4 | −866.7 | 1741.7 | 44.4 |
| Autumn | peakSe*sex*age + SenescenceL*peakSe + OnsetSnow + tempS*Rainfall + T-5 + distance | **SenescenceL + OnsetSnow** | **6** | **−1114.1** | **2240.6** | **0** |
| | | SenescenceL + OnsetSnow + tempS | 7 | −1113.6 | 2241.7 | 1.1 |
| | | SenescenceL + OnsetSnow + peakSe | 7 | −1113.9 | 2242.4 | 1.7 |
| | | SenescenceL + OnsetSnow + distance | 7 | −1114.0 | 2242.5 | 1.9 |
| | | Null model | 4 | −1127.0 | 2262.3 | 21.7 |

*Note*: For clarity, only models with ΔAICc <2 were provided, in addition to the null model. The variables selected from this set of models using likelihood ratio tests are in bold type. We added individual identity and population as random effects in each model.

Abbreviations: distance, migration distance; K, number of parameters; OnsetSnow, date of onset of snow cover; peakGU, date of peak of green-up; peakSe, date of peak of vegetation senescence; SenescenceL, length of senescence period; SnowM, Date of snowmelt; snowT, total snow precipitation during winter; SpringL, length of spring season; T10, date of 10°C mean daily temperature in spring; tempS, average temperature during summer; tempW, average temperature during winter.

**TABLE 3** Parameters included in the most supported models at both seasons describing variation in migration date with environmental and individual characteristics.

| Season | Parameters | Estimates [95% CI] | *p*-values |
|---|---|---|---|
| Spring | Intercept (M) | 31.78 [4.14; 59.7] | 0.03 |
| | Sex (F) | 50.56 [10.26; 91.51] | 0.02 |
| | PeakGU (M) | 0.64 [0.45; 0.82] | <0.0001 |
| | PeakGU:Sex (F) | −0.34 [−0.61; −0.08] | <0.05 |
| | SnowM | 0.13 [0.05; 0.21] | <0.01 |
| | SpringL | 0.13 [0.04; 0.22] | <0.01 |
| Autumn | Intercept | 180.53 [122.13; 237.62] | <0.0001 |
| | SenescenceL | 0.25 [0.10;0.39] | <0.01 |
| | OnsetSnow | 0.38 [0.18;0.57] | <0.001 |

*Note*: Covariates were not scaled. We added individual identity and population as random effects in both models.

Abbreviations: CI, confidence interval; F, females; M, males; OnsetSnow, date of onset of snow cover; peakGU, date of peak of green-up; SenescenceL, length of senescence period; SnowM, date of snowmelt; SpringL, length of spring season.

$R^2 = 0.26$ and 0.77, respectively). Vegetation green-up was the most influential variable affecting spring migration, with 2.7 and 3.1 times stronger effects than the date of snowmelt and the length of the spring season, respectively (Appendix S10, Table S3). Males timed migration to coincide with the peak of green-up on their winter range more closely than females, with a 6.4 versus 3.0 days positive shift in migration for a 10-day variation in the peak of green-up, respectively. In springs characterized by an average peak of green-up (~30 May), both sexes migrated approximately 5 days after the peak. However, when the peak of green-up occurred early (23 April, day 113), females migrated up to 30 days after the peak of green-up, and males up to 20 days after. Conversely, in springs with a late peak of green-up (5 July, day 186), females migrated up to 22 days earlier than the peak of green-up, and males up to 8 days earlier (Table 3 and Figure 3a). By contrast, ibex migrated only 1.3 days later when the length of the spring increased by 10 days (Figure 3b), or when snow melted 10 days later (Figure 3c). Although present in the set of models with ΔAICc <2, the distance ($\beta = -0.004$, $p = 0.11$), interaction between distance and date of snowmelt ($\beta = 0.00002$, $p = 0.16$), the mean temperature during winter ($\beta = 1.10$, $p = 0.10$), cumulative snow precipitation during winter ($\beta = -0.01$, $p = 0.07$) and the date when the 10°C temperature was reached ($\beta = 0.09$, $p = 0.28$) were not statistically significant. Age class was not present in the set of models with ΔAICc <2.

### 3.1.2 | Autumn migration

The selected model for autumn migration included as explanatory variables the length of the senescence period and date of onset of snow cover (Table 2; marginal and conditional $R^2 = 0.11$ and 0.41, respectively). In both sexes, autumn migration occurred later when the onset of snow cover was delayed (rate = 3.8 days per 10-day shift) or when the length of the senescence period was longer (rate = 2.5 days per 10-day shift; Table 3; Figure 3d,e). Although present in the set of models with ΔAICc <2, the date of peak of senescence ($\beta = 0.07$, $p = 0.57$), the mean temperature during summer ($\beta = -0.98$, $p = 0.33$) and the migration distance ($\beta = 0.00015$, $p = 0.69$) were not statistically significant. Similarly, as for the spring model, age class was not present in the set of models with ΔAICc <2.

## 3.2 | Individual behavioural plasticity

The mean difference between successive migration dates within individuals was 13.0 days (SD = 12.3) for males and 10.0 days (SD = 6.6) for females in spring. In autumn, the mean difference was 18.3 days (SD = 17.1) for males and 29.8 days (SD = 17.9) for females. In parallel, the average inter-annual variation in the date of peak green-up and the date of onset of snow cover was 19 days and 21 days across all populations (Figure 1, details in Appendix S9).

The model fitted to investigate year-to-year changes in migration date of a given individual and the corresponding interannual changes in variables previously identified as drivers of migration timing (Table 2) showed that both males and females could adjust their migration dates based on variation in the date of peak of green-up ($\beta = 0.43$ and 0.52, $p < 0.001$ and $p = 0.004$ for males and females respectively, that is, for an increase of 10 days in the date of peak of green-up, males and females adjusted their migration date by 4.3 and 5.2 days, respectively). The length of the spring season ($\beta = 0.10$, $p = 0.061$) and the date of snowmelt ($\beta = 0.17$, $p = 0.057$) were not statistically significant, even if, overall, these slopes were very similar to those provided by the transverval analysis in spring (Figure 4). In contrast with the model fitted with the full dataset, both sexes displayed comparable delays in spring migration departure when the date of peak of green-up increased or decreased (Figures 3a and 4a). In autumn, the slope of the relationship between year-to-year changes in migration date and changes in the date of onset of snow cover and the length of the senescence period were estimated as positive, as reported in the transverval analysis ($\beta = 0.08$ and $\beta = 0.20$ Figure 3d,e), but these effects were not statistically significant ($p = 0.77$ and $p = 0.25$ respectively, Figure 4b).

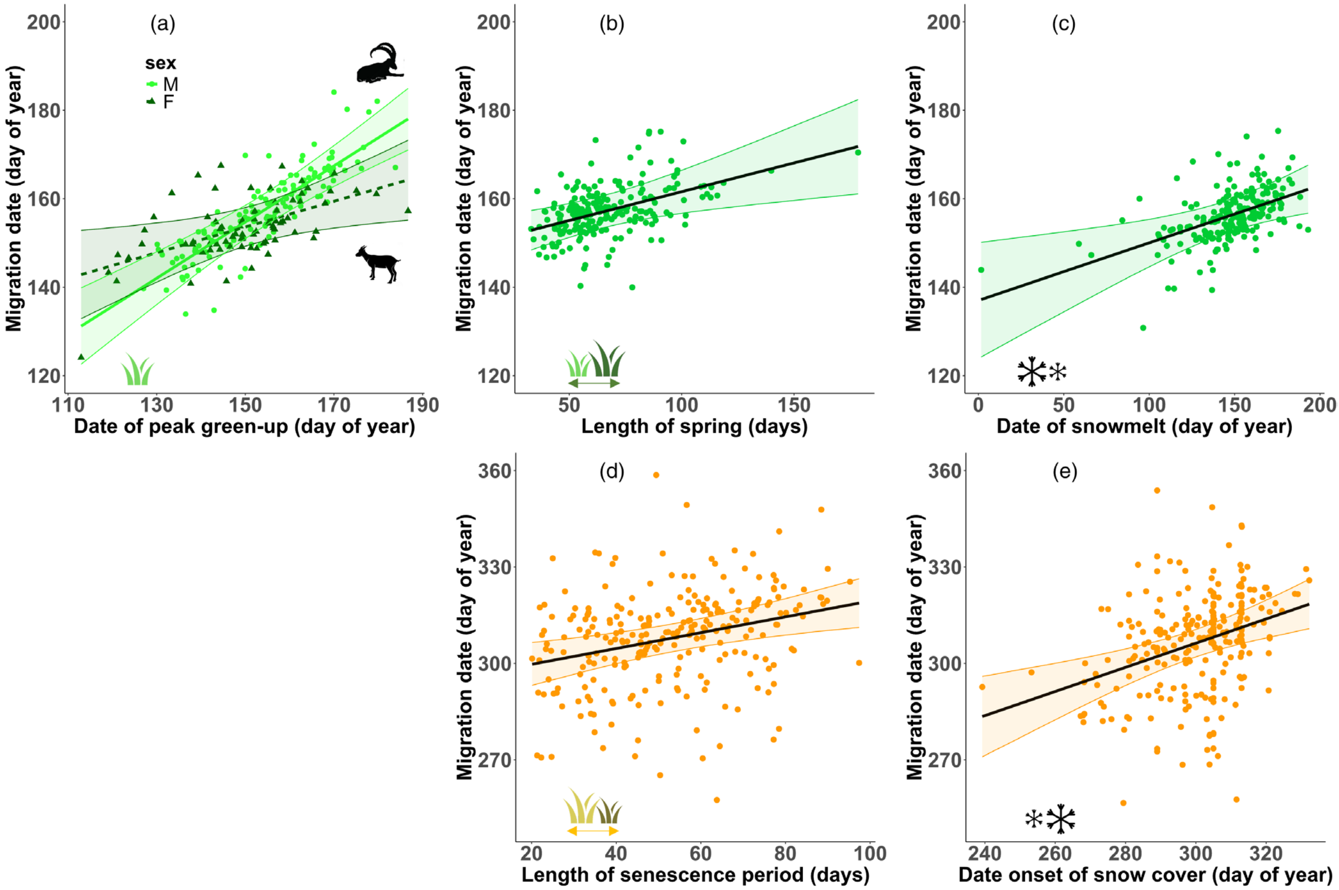

FIGURE 3 Effects of environmental and individual characteristics on Alpine ibex *Capra ibex* migration timing in spring (a: Date of peak of green-up [sex-specific], b: Length of spring, and c: Date of snowmelt; $n = 211$) and autumn (d: Length of the senescence period; e: Date of onset of snow cover; $n = 250$). Solid lines and the shaded areas are the predictions and 95% confidence intervals of the best model (see Table 2), respectively. Dots are the partial residuals accounting for the effects of the other variables in the model.

## 4 | DISCUSSION

Our study shed light on the drivers of migration phenology in a short-distance altitudinal migrant living in alpine mountains. Using GPS data on 406 individuals from 17 populations distributed across the Alps, we revealed that the timing of Alpine ibex migration was mainly linked to the phenology of vegetation, including the timing of the peak of green-up and the length of the spring season for spring migration, and the length of the senescence season for autumn migration. The timing of snowmelt and the onset of snow cover also played a significant role in shaping spring and autumn migrations, respectively. By contrast, ibex migration phenology was not related to the seasonal weather conditions encountered during the whole season preceding migrations. While individuals exhibited the ability to adjust their timing of migration in response to vegetation phenology and snow dynamics, the extent of these adjustments was lower than the magnitude of these interannual changes in environmental conditions. This is particularly true for females, which were only half as able as males to adjust their spring migration to match the peak of vegetation green-up. This difference could be related to sex-specific levels of behavioural plasticity, with females likely being less plastic than males, questioning the ability of individuals with specific needs and constraints to cope with ongoing climate change.

Vegetation phenology is a key factor shaping the phenology of migration across a diversity of taxa, from invertebrate to vertebrate species (Candino et al., 2022; Lee et al., 2024; Sigrist et al., 2022; Van der Graaf et al., 2006; van Toor et al., 2021). Likewise, snow conditions are a major driver of animal migrations, and more generally, ecosystem functioning in alpine and arctic areas (Curk et al., 2020; Laforge et al., 2021). In spring, ibex migration was influenced by the date of peak green-up on winter ranges and was delayed with increasing length of the spring season and when snowmelt on summer ranges happened later (Figure 3a–c). Combined with existing knowledge on Alpine ibex migration and spatial ecology (Chauveau, Garel, Toïgo, Anderwald, Beurier, et al., 2024; Herfindal et al., 2019), these findings suggest that ibex 'jump' the spring green wave (sensu Bischof et al., 2012). Once the highest quality of vegetation has passed in winter ranges, ibex migrate rapidly while trading off foraging with low perceived risk of predation and limited energy expenditure (Chauveau, Garel, Toïgo, Anderwald, Beurier, et al., 2024). When reaching summer ranges, they can catch a second vegetation green-up,

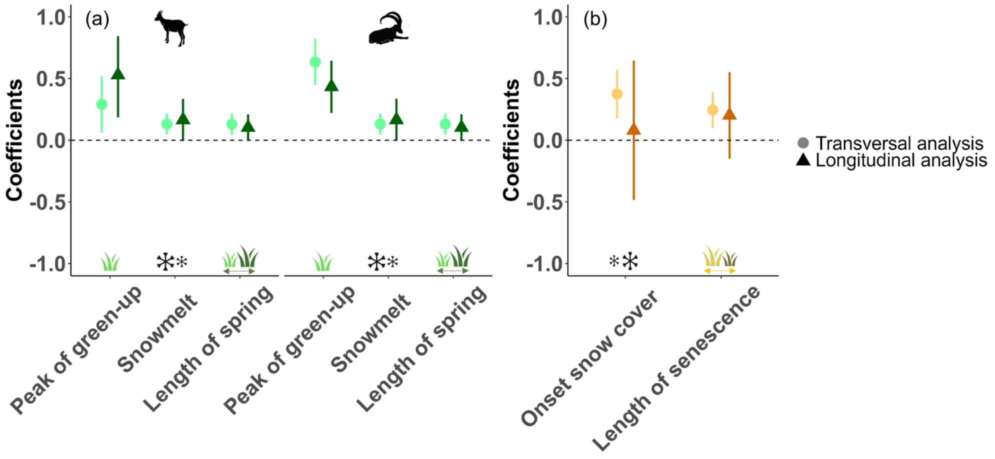

**FIGURE 4** Comparison of coefficients derived from linear mixed-effect models explaining migration departure in response to environmental and individual characteristics during spring (a, left panel for females, right panel for males) and autumn (b) and those obtained from longitudinal analyses (variation in Δmigration dates) assessing behavioural plasticity in migration timing in response to inter-annual changes in environmental drivers. The first analysis is transverval and relied on the full dataset (dots; *n* = 211 individual-year in spring and *n* = 250 in autumn; see Figure 3 and Table 3). The second analysis is longitudinal and relied on individual ibex tracked during at least two seasonal migrations (triangles; *n* = 49 individual-year in spring and *n* = 38 in autumn). Line ranges represent 95% confidence intervals. Peak green-up = date of peak of vegetation green-up, Snowmelt = Date of snowmelt on summer range, Length of spring = length of spring season, Onset snow cover = Date of onset of snow cover on summer range, Length of senescence = Length of senescence period in autumn.

owing to delayed snow and temperature conditions compared with winter ranges (all these variables being correlated; Figure S5). As in other herbivore migrations (e.g. Van der Graaf et al., 2006; in birds, Merkle et al., 2016 in ungulates), tracking and extending access to newly grown, high-quality vegetation should provide large foraging benefits, allowing a prolonged access, in both winter and summer ranges, to forage that is easier to digest and has a higher nutrient content (Albon & Langvatn, 1992; Semenzato et al., 2021). In addition, delaying autumn migration with increasing length of the senescence period (Figure 3e) may provide crucial energetic and growth benefits to this alpine capital breeder, which depends on fat reserves accumulated during spring and summer for overwintering (Pettorelli et al., 2007). As in other alpine and arctic migratory species (Monteith et al., 2011; Rickbeil et al., 2019), the onset of snow cover precludes access to vegetation, and timely departure from summer ranges may mitigate the risk of being constrained by snow cover during migration (Richard et al., 2014), knowing that ibex actively avoid snow-covered areas during autumn migration (Chauveau, Garel, Toïgo, Anderwald, Beurier, et al., 2024).

Males and females displayed different responses to the phenology of vegetation during spring, with males better timing their migration with the peak of green-up compared with females (Figure 3a). In this species with strong sexual size dimorphism, females, with higher relative energetic needs and lower digestive capacities than males (Demment & Van Soest, 1985), would rather be expected to favour forage quality and hence to track vegetation green-up more closely than males (Forage Selection Hypothesis; Main et al., 1996; Short, 1963; Watson & Staines, 1978). This could be the case during early springs when females remained on scarce but emerging vegetation within steep rocky cliffs of winter ranges (when spring starts early vegetation grows slowly; Bliss, 1971, Figure 3a) while males migrated earlier, possibly to benefit more rapidly from abundant forage in alpine grasslands essential to gain mass (Van Der Wal et al., 2000). Indeed, the peak of green-up in winter ranges and snowmelt in summer ranges were correlated (Figure S5), indicating that the timing of snowmelt and vegetation greening on summer ranges coincides with the timing of spring green-up on winter ranges (Figure S5; see also Herfindal et al., 2019). By contrast, when spring green-up was late, females migrated earlier than males and long before the peak of green-up, likely because most of them needed to reach safe habitats of summer ranges before parturition, which occurs right after spring migration, from early June to mid-July. This way, females may favour newborn protection against predators rather than benefiting from the green wave, as suggested by the reproductive strategy-predation risk hypothesis (Debeffe et al., 2017; Grignolio, Rossi, Bassano, et al., 2007; Main & Coblentz, 1996). Therefore, our results suggest that the lower plasticity in the spring migration timing of females might be linked to the upcoming occurrence of parturition. However, when restricting the analysis to the females monitored and migrating over multiple springs, we found that they actually timed migration on green-up similarly to males (i.e. closer to peak of green-up), suggesting that more experienced individuals may be able to better synchronize migration to the timing of the green-up. It is worth noting, however, that the sample size for such females was limited (*n* = 19 and 9 for spring and autumn, respectively), potentially rendering this sample non-representative, in particular if the proportion of reproductive females was low compared with the whole dataset. In addition, we did not detect any influence of age (hypothesized as a rough proxy of reproductive status) on the phenology of female spring migration. Comparing three age classes with low, intermediate and high proportions of reproductive females may, however, not fully capture the influence of reproduction, as age is also related to other biological traits, such as experience, movement abilities and social rank. Additionally, females within the same age class do not necessarily reproduce every year. Further investigations should delve deeper, incorporating the actual reproductive status of females (unavailable for most individuals in our dataset), accounting for parturition phenology (Marchand et al., 2021), and exploring the propensity to migrate and to switch between residency and migration. Such studies are crucial to confirm the strong constraint posed by parturition on female migration.

The rates of changes we detected in ibex migration timing were all lower than those required to perfectly match shifts in environmental conditions. This could suggest that ibex may only partially respond to the rapidly changing conditions in alpine mountains, potentially leading to possible trophic mismatch during early springs. This imperfect matching between spring migration and green-up in alpine migrants may also be explained by the fact that migrating too soon during warm and early springs would lead to an early arrival on still snowy summer ranges (similar example in bighorn sheep *Ovis canadensis sierrae*, John et al., 2024). In addition, unlike long-distance migrants that mostly rely on local conditions to decide when to migrate (but see Pandraud et al., 2022), the perception of remote environmental conditions, such as snow cover at higher altitude in alpine species (Figure 3c, see also Berger et al., 2022) may provide relevant visual cues to inform animals on conditions from close summer ranges and contribute also to decisions concerning migration (Winkler et al., 2014) and to imperfect matching with local environmental conditions (Bracis & Mueller, 2017; Mueller et al., 2011). Moreover, there is growing evidence that individuals' decisions concerning migration can be influenced by those from other individuals in gregarious species (Aikens et al., 2022; McComb et al., 2001) but we missed data on social aspects and kin bonds during migration to investigate their influence on individual responses and plasticity. Hence, the behavioural plasticity in ibex migration timing could be limited in the face of rapid climate change, particularly in females; thus, further research is needed to firmly understand the consequence of mismatches resulting from ongoing climate change.

The date of snowmelt in alpine habitats is expected to advance by 10 days by 2050 and 13 days by 2100 under the intermediate IPCC global warming scenario (RCP 4.5; Vorkauf et al., 2021). These potential changes represent large shifts in comparison to the variation observed during our study period. Thus, springs that we considered as warm and early springs (i.e. date <137) could become the norm in the future, leading to differing consequences between sexes, as the shift in migration timing should be lower in female ibex. However, warm and early springs promote slow plant growth and reduce spatial heterogeneity in vegetation phenology, resulting in decreased spatial access to high-quality forage, which ultimately may hamper reproductive success (Post & Forchhammer, 2007). On the other hand, rapid green-up during late springs reduces the temporal access to high-quality vegetation and leads to decreased juvenile growth in alpine ungulates (Herfindal et al., 2006; Pettorelli et al., 2007). Hence, the effects of vegetation phenology on ungulate performance are manyfold, and understanding how vegetation quality and vegetation communities are modified during these warm events will thus be crucial to truly assess the consequences on migration benefits and migrant fitness. Furthermore, the general increase in temperatures, especially in summer, leading to greater thermal stress is a major concern for the species (Brivio et al., 2019; Semenzato et al., 2021). It is therefore essential that future studies on alpine migratory species focus on the benefits of migration in relation to its timing and assess if changes in phenological events driving migration can modify these benefits, and thus the choice to migrate, potentially leading to demographic consequences.

## AUTHOR CONTRIBUTIONS

Victor Chauveau, Pascal Marchand, Mathieu Garel, Carole Toïgo, Aurélie Coulon and Anne Loison conceived and designed the study. All the co-authors participated in managing animal monitoring and GPS data collection. Mathieu Garel processed microclimate and MODIS data. Victor Chauveau, Pascal Marchand and Mathieu Garel designed statistical analyses. Victor Chauveau analysed the data. Victor Chauveau wrote the draft of the manuscript with comments from all the other co-authors. Victor Chauveau, Pascal Marchand, Mathieu Garel, Carole Toïgo, Aurélie Coulon and Anne Loison revised further versions of the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

## DATA AVAILABILITY STATEMENT

Datasets and scripts are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.10304656 (Chauveau, Garel, Toïgo, Anderwald, Apollonio, et al., 2024).

## STATEMENT ON INCLUSION

Our study brings together authors from five different countries, including scientists and wildlife managers based in the countries where the study was carried out. The study was made possible through a collaborative approach at the European scale. Whenever relevant, literature published by scientists from the different regions was cited.

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## SUPPORTING INFORMATION

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

**Appendix S1:** Details on monitoring of ibex populations.

**Appendix S2.** Number of migrants identified per year and population.

**Appendix S3.** Definition of migration and residency based on the identification of breakpoints in movement characteristics and the overlap between seasonal utilization distributions.

**Appendix S4.** Effect of temperature on spring migration timing.

**Appendix S5.** Correlation between environmental variables used in mixed effects linear models.

**Appendix S6.** Disentangling within- and between-populations contributions to variation in migration timing with environmental covariates.

**Appendix S7.** Geographical separation of seasonal ranges.

**Appendix S8.** Distribution of migration dates in spring and autumn.

**Appendix S9.** Variation in peak of green-up and onset of snow cover within and among populations.

**Appendix S10.** Phenology models with scaled covariates.

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