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1 **It's time to go - Drivers and plasticity of migration phenology in a short-**  
2 **distance migratory ungulate**

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54 1 - Recurring events like migrations are an important part of the biological cycles of species.  
55 Understanding the factors influencing the timing of such events is crucial for determining  
56 how species face the pervasive consequences of climate change in highly seasonal  
57 environments.

58 2 - Relying on data from 406 GPS-collared Alpine ibex *Capra ibex* monitored across 17  
59 populations, we investigated the environmental and individual drivers of short-distance  
60 migration in this emblematic mountain ungulate.

61 3 - We found that vegetation phenology, including spring growth and autumn senescence,  
62 along with snow dynamics - snowmelt in spring, first snowfall in autumn - were the main  
63 drivers of the timing of migration. In spring, ibex migration timing was synchronized with the  
64 peak of vegetation growth, but more in males than in females. Specifically, a shift of 10 days  
65 in vegetation growth peak delayed migration by 6.4 days for males and 2.7 days for females.  
66 This led to increased differences in migration timing between sexes when the vegetation  
67 growth peak occurred early or late in the season. In addition, ibex delayed migration timing  
68 when the length of growing season was longer and when the date of snowmelt on ibex  
69 summer range occurred later. Similarly, in autumn, prolonged vegetation senescence and  
70 delayed first snowfall led to later migration.

71 4 - Overall, most of the response to inter-annual variations in vegetation and snow phenology  
72 could be explained by individual behavioral plasticity. Nonetheless, females appear to be less  
73 plastic than males in their timing of spring migration, likely due to the parturition period  
74 following migration forcing them to trade off foraging needs with predation risk. As the  
75 identified drivers of ibex migration are known to be and will continue to be largely impacted  
76 by climate change, the capacity of ibex to respond to such rapid changes could differ between  
77 sexes.

78 **Keywords:** Alpine ungulate; Alps; altitudinal migration; behavioral plasticity; climate  
79 change; migration timing; movement ecology; snow phenology; vegetation phenology

## 80 **INTRODUCTION**

81 The consequences of climate change on ecological systems and processes are ubiquitous,  
82 resulting in changes in the timing of periodic life-history events, behaviors, and species  
83 distribution (Parmesan & Yohe, 2003; Inouye, 2022). Understanding these effects is crucial  
84 to predict future ecological changes and try to mitigate their consequences (Bellard et al.,  
85 2012). In seasonal environments, the biological cycles of animal species are often  
86 synchronized with the timing of other ecological processes (Both et al., 2009). For instance,  
87 the timing of births generally coincides with the burst of food resources, providing favorable  
88 conditions for maximizing newborn survival (Durant et al., 2007; Plard et al., 2015). The  
89 changes in temperature and precipitation, that directly affect plant growth, can have  
90 cascading consequences on the timing of biological events related to plant availability and  
91 quality, such as animal migration and reproduction (Visser et al., 1998; Walther et al., 2002;  
92 Post & Forchhammer, 2008).

93 Given these profound influences of climate change on different ecological processes,  
94 seasonal migration emerges as a critical adaptive strategy of animal species to shifting  
95 environmental conditions. Indeed, movements between distinct seasonal ranges allow  
96 animals to cope with seasonal availability of resources, weather conditions, predation risk or  
97 competition intensity (Dingle & Drake, 2007). Seasonal migration can provide survival and  
98 reproductive benefits (Avagar et al., 2014; Eggeman et al., 2016; van Moorter et al., 2021) but  
99 should persist only if its benefits outweigh its costs (e.g., movement costs, predation;  
100 Klaassen et al., 2014). The net fitness gain of migration strongly depends on its timing. For  
101 instance, in temperate regions, migratory herbivores move across the landscape to maximize

102 energy intake by tracking gradients of plant phenology, i.e., “surfing” or “jumping the green  
103 wave” (common in birds and ungulates: Van der Graaf et al., 2006; Bischof et al., 2012;  
104 Merkle et al., 2016; see also in whales: Abrahms et al., 2019). In alpine mountains, plant  
105 phenology strongly varies along short altitudinal gradients. Hence, herbivores can seasonally  
106 move along altitudinal gradients to benefit from the gradient of plant phenology (Herfindal et  
107 al., 2019), resulting in altitudinal migrations usually shorter than those observed in lowlands  
108 along latitudinal gradients (Sawyer et al., 2019). In autumn, individuals need to migrate  
109 before harsh weather conditions (e.g., snow cover) impede access to forage, reduce mobility  
110 and increase predation risk. In the context of ongoing global warming, the changes in the  
111 timing of phenological events, such as shifts in the availability of resources and local weather  
112 conditions, stand as a real challenge for migratory species. Indeed, a mismatch between  
113 migration timing and environmental conditions could reduce the benefits and increase the  
114 costs of migration, with potentially long-term consequences on fitness and population  
115 dynamics (Middleton et al., 2018; Aikens et al., 2020).

116 Migration also occurs around other important biological events often related to internal  
117 changes (e.g., physiological/hormonal changes related to parturition or mating season) that  
118 may constrain the timing of migration. Individuals with contrasted reproductive status (i.e.,  
119 reproductive vs. non-reproductive females) or of variable age (e.g., males in which rut-  
120 involvement is age-dependent) may have contrasted needs and constraints, and hence variable  
121 costs/benefits to migrate at a given time, resulting in different migration timing in individuals  
122 of different sex or age (Debeffe et al., 2019; Rodgers et al., 2021). Age is also related to  
123 individual knowledge of past conditions and experience in tracking favorable conditions  
124 (Abrahms et al., 2021). Beyond individual characteristics, individuals often cue on changing  
125 environmental factors to accurately time their departure (Le Corre et al., 2016; Xu & Si,  
126 2019; Weller et al., 2022). In spring, increasing temperatures and related events such as

127 snowmelt and vegetation green-up have been identified as common drivers of long-distance  
128 migrations among birds and ungulate species (Wijk et al., 2012; Gurarie et al., 2019; Mallory  
129 et al., 2020). Conversely, the drivers of autumn migration timing have been less studied, yet  
130 factors such as the return of winter weather conditions, such as snow and cold temperatures,  
131 have often been identified at play (Rivrud et al., 2016; Weller et al., 2022, Ortega et al.,  
132 2024). Similarly, our understanding of migration timing and how individuals adjust their  
133 migratory behavior to their needs, constraints, and experience, is far less advanced in short-  
134 distance migratory species, such as those inhabiting alpine ecosystems (Candino et al., 2022).

135 Individuals and populations can respond to changing environmental conditions through  
136 phenotypic plasticity and genetic adaptation, whose relative importance depends on species  
137 biology (Charmantier et al., 2008; Moyes et al., 2011; Plard et al., 2013). Although genetic  
138 adaptation has been shown to play a role in the advance of arrival on summer ranges in bird  
139 species (Buskirk et al., 2012), ongoing climate change is likely occurring too fast for long-  
140 lived species to adapt genetically. Consequently, migratory species rely heavily on  
141 phenotypic plasticity to respond to environmental changes, and their level of plasticity can  
142 potentially be used as an indirect estimate of their resilience to climate change (Stepanian &  
143 Wainwright, 2018; Rickbeil et al., 2019; Xu et al., 2021). At the same time, species ability to  
144 display phenotypic plasticity is sometimes limited (e.g., parturition timing in roe deer, Plard  
145 et al., 2013) and the extent of phenotypic plasticity in cold-adapted alpine species is less  
146 known. On one hand, species living in alpine mountains are expected to be more sensitive to  
147 climate change due to their unique adaptations to face the strong limiting conditions of their  
148 environment (White et al., 2018). On the other hand, phenotypic plasticity may be favored in  
149 such environments as individuals usually need to adjust their behavior to cope with high  
150 temperature variability at daily and seasonal scales along with marked annual fluctuations in  
151 resource availability (Enriquez-Urzelai et al., 2020). The extent of behavioral plasticity of

152 alpine species in tracking the bottom-up processes governing forage and snow conditions still  
153 requires quantification.

154 In this study we thoroughly investigated the factors (Figure 1) affecting the phenology and  
155 temporal plasticity of short-distance migration in a mountain species, the Alpine ibex *Capra*  
156 *ibex*, using GPS data from 17 populations distributed across the Alpine arc. The Alpine ibex  
157 is an iconic species endemic to the Alps. Despite a current wide distribution, almost all ibex  
158 populations were reintroduced from the last few individuals (probably < 100) of the only  
159 remaining population located in the current Gran Paradiso and Vanoise National Parks  
160 (Brambilla et al., 2020). Therefore, Alpine ibex populations are characterized by a very low  
161 genetic diversity, possibly compelling their adaptive potential and behavioral plasticity  
162 (Biebach & Keller, 2009; Robin et al., 2022). Migration occurs in most ibex populations, but  
163 is partial (i.e., each year, some ibex migrate and others are resident, and this choice can  
164 change from year to year) and consists in a short-distance and rapid altitudinal movement (on  
165 average 12 km traveled in 3-6 days; Chauveau et al., 2023). Alpine ibex migration occurs  
166 close to important biological events: parturition, from early June to mid-July, and rut, from  
167 early December to mid-January. In spring, migratory ibex reach summer ranges where they  
168 can reconstitute fat reserves by foraging on good quality vegetation after winter scarcity. This  
169 is particularly important for reproductive females whose ability to meet the high energy  
170 demand for late gestation and lactation during this period largely contributes to juvenile  
171 survival (Post & Forchhammer, 2008; Richard et al., 2017). In autumn, migration allows ibex  
172 to reach winter ranges usually lower in elevation and often consisting in steep south-facing  
173 rocky cliffs where winter weather conditions are milder (Herfindal et al., 2019). As a result,  
174 plasticity in migration timing may be crucial for fitness and ibex ability to cope with ongoing  
175 climate change.

176 Our first objective was to identify the environmental and individual factors influencing the  
177 timing of ibex migration in both seasons (Figure 1). Specifically, we tested whether migration  
178 timing was driven by local environmental conditions such as vegetation phenology, snow  
179 conditions, and local temperatures experienced by ibex (already identified as a key factor for  
180 ibex individual behavior and movements; Aublet et al., 2009; Mason et al., 2017; Herfindal et  
181 al., 2019; Semenzato et al., 2021). At a larger temporal scale, we expected seasonal climatic  
182 conditions experienced during the whole season preceding migration to be a driver of  
183 migration phenology through their effect on ibex body condition (Cooper et al., 2015;  
184 Anderson et al., 2019). We also tested for the importance of sex and age-specific biological  
185 requirements as individual drivers of migration phenology (all our hypotheses and predictions  
186 are detailed in Table 1). Finally, we investigated more deeply the occurrence and the  
187 importance of behavioral plasticity, i.e., the ability of an individual to alter its migration  
188 timing, in response to changes in environmental conditions. We took advantage of repeated  
189 measurements on the same individuals to get a direct estimate of the magnitude of change in  
190 individual migration timing in response to inter-annual differences in environmental  
191 conditions (Charmentier et al., 2008).

## 192 **MATERIALS AND METHODS**

### 193 1) Study area and populations

194 We relied on a GPS dataset collected on 406 Alpine ibex from 17 populations (557  
195 individual-years; 46% females and 54% males; aged from 2 to 18 years old). Those  
196 populations were distributed across the Alps (France, Italy, Switzerland, and Austria). The  
197 first GPS monitoring started in 2003 and the last one ended in 2022 (see Chauveau et al.,  
198 2023 and Table S1; Figure S1 for details). Animals were generally captured during spring or  
199 summer using traps, drop nets or chemical immobilization by tele-injection depending on

200 study areas, and equipped with several types of GPS collars (Vectronic: GPS Plus, Vertex  
201 Plus, or Vertex Lite models; Lotek: 3300S or Litetrack models; Followit: Tellus model). All  
202 models weighed <3% of individual body mass. The GPS devices were programmed to record  
203 ibex locations at variable frequencies and during variable periods (from 1 location per hour  
204 during one year to 1 location per 6 hours during 2-5 years). After one to five years of  
205 monitoring, GPS collars were retrieved by using a drop-off system or during a recapture (a  
206 few collars were retrieved on dead animals). All capture methods were approved by the  
207 governmental authorities of each concerned country.

## 208 2) Identification of migration departure dates

209 We divided GPS tracks of each animal in yearly tracks starting on March 1<sup>st</sup> and ending  
210 February 28<sup>th</sup> or 29<sup>th</sup> of the following year. Tracks lasting less than one year were kept in the  
211 dataset only when the duration was at least 7 months long, centered on spring or autumn  
212 migration, and including a few months before and after (i.e., March-September or August-  
213 February, respectively) to get enough data and temporal variation for running the  
214 segmentation algorithms (see below). Tracks were considered as migratory if they led to  
215 significant changes in terms of distance (in the x/y plan) and/or elevation between seasons,  
216 and resulted in low overlap between winter and summer ranges (Igota et al., 2004). For each  
217 individual seasonal track, we calculated two movement time series: (i) the net displacement  
218 (ND) that is the Euclidean distance between the first location of the track and each of the  
219 following locations and provides information about changes in x/y plan (Börger & Fryxell,  
220 2012) and (ii) the net elevation displacement (NED), that is the difference in elevation  
221 between the first location of the track and all the following ones, and provides information  
222 about changes in elevation (Spitz et al., 2017).

223 Migration departure dates (hereafter called “migration dates”) were estimated using two  
224 segmentation algorithms able to find significant breakpoints in ND and NED time series (see  
225 examples in Figure S2). We considered these breakpoints to inform on the date when an  
226 animal performed a significant movement, that we defined as the date of migration. We relied  
227 on the divisive hierarchical estimation algorithm to find a unique and common breakpoint to  
228 ND and NED time series at once (*e.divisive* function in *ecp* package, R software 4.2.2, James  
229 et al., 2020, R Core Team, 2023). We also relied on a decision tree algorithm (*tree* function in  
230 *tree* package, Ripley, 2023) to find multiple significant breakpoints in ND and NED seasonal  
231 time series separately. Then, we filtered these multiple breakpoints by keeping only those that  
232 were identified by the two algorithms in both ND and NED time series, with a difference of  
233 less than 3 days. Breakpoints identified between July 15<sup>th</sup> and August 15<sup>th</sup> were not  
234 considered as being related to a migration event and were removed. Finally, we visually  
235 checked the accuracy of the breakpoints identified by both approaches and, when different or  
236 when several breakpoints were identified, we chose the most appropriate (according to our  
237 interpretation of the GPS locations) among them (18% of the breakpoints).

238 We calculated the overlap between individual winter and summer utilization distributions  
239 (UD) each year to classify animals as migrant or resident at both seasons. Seasonal UD were  
240 computed on a 50m resolution grid using all locations available for a given season except  
241 those recorded during the +/- 7 days around the breakpoints previously identified. For both  
242 periods, we calculated the overlap between the volume of the kernel of winter and summer  
243 UD using the *kerneloverlap* function (method VI, *adehabitatHR* package, Calenge, 2023).

244 We considered that an animal was migrant for the given season if the overlap between  
245 seasonal UD was lower than 20% and we considered the corresponding breakpoint as the  
246 migration departure date (Figure S2). We also calculated the distance traveled by an ibex

247 during migration as the Euclidean distance between the centroids of the winter and summer  
248 locations.

### 249 3) Drivers of migration phenology

#### 250 3.1) Local environmental drivers

251 For each pixel of the population distributional ranges (defined with a MCP on all GPS  
252 locations in a population buffered with 5km), we derived four proxies of vegetation  
253 phenology: the date of peak of green-up; the date of peak of vegetation senescence; the length  
254 of spring season, and the length of senescence period (Figure 1; named after Kong et al.,  
255 2022). Data were derived from a MODIS NDVI product (NASA-MODIS vegetation, product  
256 MOD13Q1, spatial resolution: 250m, temporal resolution: 16 days) following the  
257 methodological workflow described in Kong et al., (2022; R package *phenofit*). We used  
258 weighted Whittaker as rough fitting function, modified bisquare as weighting updating  
259 function (Kong et al., 2019) and Beck logistic as fine curve fitting method (Beck et al., 2006).  
260 We used the reconstructed daily scale time series of NDVI from the fine fitting to extract  
261 both phenological metrics from every growing season. The peak of spring green-up was  
262 calculated as the day when the maximum of the first-order derivative function of the time  
263 series was reached in each pixel (similar to the date when the Instantaneous Rate of green-up  
264 - IRG - is maximum; Bischof et al., 2012). Similarly, the autumn peak of senescence was  
265 calculated as the date when the maximum rate of senescence was reached (the rate of  
266 decrease in NDVI values is maximum). To calculate the length of spring season and length of  
267 senescence period we calculated the difference in days between the date when NDVI reached  
268 a plateau ('peak of season' following Kong et al., 2022) and the date when vegetation  
269 greening started ('start of green-up'), and the difference between the date when senescence  
270 started and the date when it ended ('vegetation recession date' following Kong et al., 2022),

271 respectively (see also Figure 1). For each pixel of the population range, we also derived from  
272 the MODIS snow product (NASA-MODIS snow, product MOD10A2, spatial resolution:  
273 500m, temporal resolution: 8 days, Hall & Riggs, 2021), two seasonal proxies of snow  
274 phenology: the date of snowmelt and the date of first snowfalls (Figure 1). Snowmelt was  
275 defined as the first day when a pixel was snow-free during a consecutive 8-day period. The  
276 first snowfall was defined as the first day when a pixel was covered with snow during 2  
277 consecutive 8-day periods.

278 To investigate the effects of the phenological variables on the timing of spring and autumn  
279 migrations (Figure 1), for each individual we extracted and averaged the values of those  
280 variables at the GPS locations of ibex collected during the week before migration (see  
281 Rickbeil et al., 2019 for a similar approach), i.e., on winter ranges for peak of green-up and  
282 length of spring season (spring migration) and on summer ranges for peak of vegetation  
283 senescence, length of senescence period, and first snowfall (autumn migration). In general,  
284 we expected animal migration to be primarily influenced by the local conditions they  
285 encountered rather than those in distant areas (i.e. local resources rather than anticipated  
286 future foraging opportunities), with one notable exception being the timing of snowmelt.  
287 Indeed, we included snowmelt as the date when snow melted in the locations used by ibex  
288 during the week after spring migration. The rationale behind this stems from the fact that  
289 snowmelt in summer ranges occurred much closer to the period of spring migration (on  
290 average 10 days before) than snowmelt in winter ranges (42 days before), making its  
291 influence on animal migration more likely. In addition, in mountain, snow cover provides a  
292 relevant visual cue for informing animals on remote environmental conditions (Berger et al.,  
293 2022), and in particular forage that may emerge soon after snowmelt (the correlation  
294 coefficient between snowmelt in summer ranges and peak green-up in summer ranges was  
295 0.65). As this mechanism is more likely to influence ibex short-distance altitudinal

296 migrations, we included the date of snowmelt in summer ranges in interaction with migration  
297 distance.

### 298 3.2) Seasonal environmental drivers

299 Temperature and precipitation were derived for each population over the period of  
300 monitoring, from a micro-climate model that integrated the atmospheric climate-forcing data  
301 from the National Center for Environmental Predictions (ERA5 6-hourly weather data, spatial  
302 resolution 30 km x 30 km). A digital elevation model (30m) was used for downscaling the  
303 atmospheric data at the population scale (*micro\_era5* function in *NicheMapR* package,  
304 Kearney et al., 2020). Hourly temperature and daily precipitation were predicted at a height  
305 of 1m on flat terrain for a spatial location and elevation corresponding to the centroid of all  
306 ibex GPS locations of a given population (min altitude=1938m, max altitude=2928m). Then,  
307 we calculated for each population-year the mean winter temperature and cumulative snowfall  
308 (sum of daily precipitation when average daily temperature < 0°C) during winter (November-  
309 March) and the mean summer temperature and cumulative precipitation throughout the  
310 summer period (July-August).

311 We used temperature data to determine the date for which a daily mean temperature of 10°C  
312 and -5°C were reached in each population and each year in spring (see Appendix S4 for  
313 further analysis on the effect of temperature on spring migration timing) and autumn,  
314 respectively. These temperature thresholds were determined in preliminary analyses, as they  
315 generally matched ibex migration periods.

316 The correlations between the local environmental drivers and seasonal drivers were all <0.5  
317 except for mean winter temperature and cumulative snow precipitation during winter (-0.7)  
318 (Figure S5).

### 319 3.3) Individual characteristics

320 We grouped individuals in age classes that reflect reproductive status, body growth  
321 investment and foraging experience (e.g., knowledge of the distribution and phenology of  
322 resources; Toïgo et al., 2002, Willisch et al., 2012, Brambilla et al., 2022), i.e. factors that  
323 could influence the timing of migration and how individuals tracked the growing vegetation  
324 (Jesmer et al., 2018; Abrahms et al., 2021). For females, we considered three age classes: 2-3  
325 years-old (non-reproductive, highest body growth investment, very low experience, n=86), 4-  
326 9 years-old (highest proportion of reproductive females, limited body growth, intermediate  
327 experience, n=65) and 10+ years-old (reproductive senescence, adult size, high experience,  
328 n=32). For males, we considered three different age classes: 2-5 years-old (non-reproductive,  
329 highest body growth investment, low experience, n=89); 6-9 years-old (intermediate  
330 proportion involved in rutting activities, medium body growth investment, intermediate  
331 experience, n=157); 10+ years-old (high rut involvement, adult size, high experience, n=33).

#### 332 3.4) Statistical analyses

333 We fitted all possible combinations (using the *dredge* function in *MuMin* package, Bartoń,  
334 2023) of linear mixed models that included the julian day of spring migration as response  
335 variable, and the mean temperature during winter in interaction with cumulative snow  
336 precipitation during winter, the date of vegetation growth peak in interaction with sex and age  
337 classes, the length of spring season in interaction with the date of vegetation growth peak, the  
338 date when the 10°C temperature was reached, and the date of snowmelt on summer range in  
339 interaction with migration distance as explanatory variables (fixed effects; Figure 1). The  
340 date of autumn migration was modeled as a function of the date of senescence peak in  
341 interaction with sex and age classes, the date of senescence peak in interaction with the length  
342 of senescence period, the date of first snowfall, the date when the -5°C temperature was  
343 reached, an interaction between the mean temperature during summer and cumulative rainfall  
344 during summer, and the migration distance. All those models also included as random effects

345 on the intercept individual identity nested in population to account for within-individual and  
346 within-population dependency. Our particular sampling gathering data from many ibex  
347 populations distributed across a large area and monitored during different years could  
348 introduce a blend of spatial variation (among populations) and temporal variation (between  
349 years) in covariates. Therefore, we ensured in a dedicated analysis (see Appendix S6) that our  
350 models accurately captured the relationship between temporal variation in covariates and  
351 migration timing, rather than solely reflecting the spatial differences in environmental  
352 conditions among populations. Indeed, migration timing could locally coincide with  
353 environmental conditions and vary from one population to another due to local adaptations  
354 within a given population, without individuals being able to adjust their migration timing to  
355 inter-annual variations in phenological events (see Plard et al., 2013; Peláez et al., 2020;  
356 Hagen et al., 2021 for an example on the phenology of parturition in roe deer).

357 We conducted model selection using Akaike information criterion with second-order  
358 adjustment, AICc, to correct for small sample bias. When the difference in AICc ( $\Delta AICc$ ) is  
359 greater than 2, there is considerable support for a real difference between models (Burnham  
360 & Anderson, 2004). Based on the models with a  $\Delta AICc < 2$ , we selected final models by  
361 keeping variables present in all models in the set of models with  $\Delta AICc < 2$  using likelihood  
362 ratio tests. We tested all final models for multicollinearity using variance inflation factors  
363 (VIF) and in no cases did any VIF exceed a value of two (Zuur et al., 2010).

#### 364 4) Individual behavioral plasticity

365 We relied on two approaches to investigate the magnitude of individual plasticity in ibex  
366 migration timing.

367 First, we focused on the subset of migration dates identified in individual ibex tracked during  
368 at least two (up to 5) seasonal migrations (32 individuals in spring: 12 F/20 M tracked on

369 average 2 years=72 observations; 25 individuals in autumn, 9 F/16 M tracked on average 2  
370 years=55 observations) to estimate the slopes of the relationships between interannual  
371 changes in individual migration dates ( $\Delta$ migration dates) and interannual changes in seasonal  
372 and/or local environmental conditions previously selected in the best models (see Results and  
373 Charmantier et al., 2008 for a similar approach). These slopes can be considered as direct  
374 estimates of phenotypic plasticity. We estimated them by fitting a linear mixed-effects model  
375 for each season (and sex in spring, see Results) with interannual changes in migration dates  
376 as response variable and interannual changes in seasonal and/or local environmental  
377 conditions as predictors. We included individual identity and population as random effects in  
378 these models. We compared the slopes of these plasticity models to those of the phenology  
379 models to assess if relations at the population scale could be explained by behavioral  
380 plasticity in migration timing.

381 Second, we fitted the models selected as the best for explaining migration timing but for each  
382 sex separately. We used the variances associated with the random effects to estimate  
383 intraclass coefficients related to individual effects as a complementary measure of behavioral  
384 plasticity (McGraw & Wong 1996). An intraclass correlation coefficient close to 1 would  
385 mean that all migration departure dates were similar for a given animal irrespective of  
386 changes in environmental conditions and would therefore suggest a very low level of  
387 plasticity.

## 388 **RESULTS**

389 We identified 211 migration dates in spring and 250 migration dates in autumn (Figure S1 for  
390 details). The median euclidean distance and median altitudinal difference between winter and  
391 summer ranges were 3035 m (SD=3333) and 442 m (SD=239), respectively. The average

392 spring migration occurred around June 6 (SD= $\pm$ 16 days), whereas the average migration in  
393 autumn was November 1 (SD= $\pm$ 23 days; Figure S13).

#### 394 Drivers of migration phenology

##### 395 *Spring migration*

396 The selected model included as explanatory variables the date of peak green-up in interaction  
397 with sex, the length of spring season, and the date of snowmelt (Table 2; marginal and  
398 conditional  $R^2=0.26$  and  $0.77$ , respectively). Vegetation green-up was the most significant  
399 variable affecting spring migration, with 2.7 and 3.1 times more effect than the date of  
400 snowmelt and the length of the spring season, respectively (Table S2). Males timed migration  
401 to coincide with peak green-up more closely than females, with a 6.4 versus 3.0 days positive  
402 shift in migration for a 10 day variation in peak green-up, respectively. In springs  
403 characterized by an average peak green-up ( $\sim$  30 May), both sexes migrated approximately 5  
404 days after the peak. However, when the peak green-up occurred early (23 April, day 113),  
405 females migrated up to 30 days after the peak of green-up, and males up to 20 days after.  
406 Conversely, in springs with a late peak green-up (5 July, day 186), females migrated up to 22  
407 days earlier than the peak of green-up, and males up to 8 days earlier (Table 3 and Figure  
408 2A). By contrast, ibex migrated only 1.3 days later when the length of the spring increased by  
409 10 days (Figure 2B), or when snow melted 10 days later (Figure 2C). Although present in the  
410 set of models with  $\Delta AICc < 2$ , the distance ( $\beta = -0.004$ ,  $p = 0.11$ ), interaction between distance  
411 and date of snowmelt ( $\beta = 0.00002$ ,  $p = 0.16$ ), the mean temperature during winter ( $\beta = 1.10$ ,  
412  $p = 0.10$ ), cumulative snow precipitation during winter ( $\beta = -0.01$ ,  $p = 0.07$ ), and finally the the  
413 date when the  $10^\circ\text{C}$  temperature was reached ( $\beta = 0.09$ ,  $p = 0.28$ ) had no significant effect on  
414 spring migration timing.

##### 415 *Autumn migration*

416 The selected model for autumn migration included as explanatory variables the length of  
417 senescence period and date of first snowfall (Table 2; marginal and conditional  $R^2=0.11$  and  
418  $0.41$ , respectively). In both sexes, autumn migration occurred later when the first snowfall  
419 was delayed (rate = 3.8 days per 10-day shift) or when the length of senescence period was  
420 longer (rate = 2.5 days per 10-day shift; Table 3 and Figure 2D, 2E). Although present in the  
421 set of models with  $\Delta AICc < 2$ , the date of senescence peak ( $\beta=0.07$ ,  $p=0.57$ ), the mean  
422 temperature during summer ( $\beta=-0.98$ ,  $p=0.33$ ) and the migration distance ( $\beta=0.00015$ ,  
423  $p=0.69$ ) had no significant effect on autumn migration timing. Similarly as for the spring  
424 model, age class was not present in the set of models with  $\Delta AICc < 2$ .

#### 425 Individual behavioral plasticity

426 The model fitted to investigate year-to-year changes in migration date of a given individual  
427 and the corresponding interannual changes in variables previously identified as drivers of  
428 migration timing (Table 2) showed that both males and females could adjust their migration  
429 dates based on variations in the date of peak green-up ( $\beta=0.43$  and  $0.52$ ,  $p < 0.001$  and  
430  $p=0.004$  for males and females respectively). The length of spring season ( $\beta=0.10$ , for an  
431 increase of 10 days in the length of spring, individuals adjusted their migration date by 1 day,  
432  $p=0.061$ ) and the date of snowmelt ( $\beta=0.17$ ,  $p=0.057$ ), had no significant effects, even if  
433 overall, these slopes were very similar as those provided by the full dataset in spring (Figure  
434 3). The only exception was for peak green-up with both sexes displaying comparable delays  
435 in spring migration departure when the date of vegetation peak green-up changed (Figures  
436 3A), that contrasted with the lower response in females revealed with the full dataset (Table  
437 3, Figure 2A). In autumn, the slope of the relationship between year-to-year changes in  
438 migration date and changes in the date of first snowfalls and length of senescence period  
439 were positive, as reported on the full dataset ( $\beta=0.08$  &  $\beta=0.20$  Figure 2D, E), but not  
440 significantly different from 0 ( $p=0.77$  and  $p=0.25$  respectively, Figure 3B).

441 Intra-class correlation coefficients between spring migration dates from a given individual  
442 were higher in females (0.65[0.56; 0.74]<sub>95%</sub>) than in males (0.21 [0.13; 0.29]<sub>95%</sub>), suggesting  
443 lower plasticity in the former (values closer to 1 and 95% confidence interval not overlapping  
444 between sexes). In autumn there were no significant differences between sexes (females: 0.28  
445 [0.24; 0.33]<sub>95%</sub>; males: 0.35 [0.29;0.41]<sub>95%</sub>).

## 446 **DISCUSSION**

447 Our study shed light on the drivers of migration phenology in a short-distance altitudinal  
448 migrant living in alpine mountains, a system rarely studied so far. Using GPS data spanning  
449 406 individuals from 17 populations distributed across the Alps, we revealed that the timing  
450 of Alpine ibex migration was mainly linked to the phenology of vegetation, including the  
451 timing of peak green-up and the duration of spring season for spring migration, and the length  
452 of the senescence season for autumn migration. Timing of snowmelt and first snowfall also  
453 played a significant role in shaping spring and autumn migrations, respectively. In addition,  
454 we uncovered from a subset of individuals monitored for several years that these global  
455 responses were largely driven by phenotypic plasticity at the individual scale. Specifically,  
456 individuals exhibited the ability to adjust their timing of migration in response to interannual  
457 changes in environmental conditions. However, the extent of these adjustments in migration  
458 dates was lower than the magnitude of the interannual changes in environmental conditions.  
459 By contrast, ibex migration phenology was not related to environmental conditions  
460 encountered during the season preceding migrations, such as summer and winter  
461 temperature/precipitation. Among individual characteristics, only sex had an effect, with  
462 males timing their spring migration to coincide with the peak of vegetation green-up more  
463 closely than females. This difference could be related to sex-specific levels of phenotypic  
464 plasticity at the individual scale, with females that appeared less plastic than males. Our  
465 findings support the importance of vegetation phenology as a major, common, driver in

466 shaping both short-distance altitudinal migration in mountains and long-distance migrations  
467 in lowlands in herbivore species. However, they also raised questions on the ability of  
468 individuals with specific needs and constraints, particularly female ibex, to cope with  
469 ongoing climate change.

470 Similarly to herbivore long-distance migrations, vegetation phenology was a key factor  
471 shaping the phenology of ibex migration (Albon & Langvatn, 1992; Van Toor et al., 2021;  
472 Candino et al., 2022; Sigrist et al., 2022). In spring, ibex migration was mainly triggered by  
473 the date of peak green-up on winter ranges and was delayed with increasing length of  
474 growing season and when snowmelt on summer ranges happened later (Figure 2A-C).  
475 Combined with existing knowledge on Alpine ibex migration and spatial ecology (Herfindal  
476 et al., 2019; Chauveau et al., 2023), these findings suggest that ibex ‘jump’ the spring green  
477 wave (*sensu* Bischof et al., 2012). Once the highest quality of vegetation is reached in winter  
478 ranges, they migrate rapidly (on average in 3 days). During this migration, animals balance  
479 foraging resources with low perceived risk of predation and limited energy expenditure  
480 (selection of steepest slopes and low elevation changes, see Chauveau et al., 2023) to reach  
481 summer ranges where they may focus again on high-quality vegetation that should emerge  
482 soon, owing to favorable snow and temperature conditions (all these variables being  
483 correlated; Figure S5). This strategy may allow migratory ibex to benefit from a prolonged  
484 access to forage that is easier to digest and with higher nutrient content than plants at later  
485 phenological stages (Albon & Langvatn, 1992; Semenzato et al., 2021). This, in turn,  
486 provides crucial energetic and growth benefits to this alpine capital breeder, which depends  
487 on fat reserves accumulated during spring and summer for overwintering (Pettorelli et al.,  
488 2007). In the same way, a prolonged use of the summer ranges, by delaying migration with  
489 increasing length of senescence period (Figure 2E), provides an extended access to abundant  
490 food resources before winter. This could be important in alpine mountains, where more

491 frequent summer precipitations generally provide abundant forage late in the summer and  
492 increase the length of the senescence period (see the positive correlation between summer  
493 precipitations and the length of senescence period in Figure S5). It could also explain why  
494 such a link was absent in lowland ungulate species, and particularly in income breeders  
495 (Monteith et al., 2011; Rivrud et al., 2016; Debeffe et al., 2019). As the growing season  
496 concludes, the first snowfall puts an end to the access to vegetation, and timely departure  
497 from summer ranges may mitigate the risk of being constrained by snow cover during  
498 migration. This is also well illustrated by the observed behavior of ibex actively avoiding  
499 snow-covered areas during autumn migration (Chauveau et al., 2023, see also Richard et al.,  
500 2014 for an example in mountain goats).

501 Males and females displayed contrasted responses to the phenology of vegetation and  
502 contrasted levels of plasticity during spring. Males timed migration to coincide with peak  
503 green-up (i.e., high quality vegetation) more than two times more closely than females  
504 (Figure 2A). In this species with an important sexual size dimorphism (males >2 times larger  
505 than females, Brambilla et al., 2022), females, with higher relative energetic needs and lower  
506 digestive capacities than males (Demment & Van Soest, 1985), would rather be expected to  
507 favor forage quality, and hence to track vegetation green-up more closely than males (Forage  
508 Selection Hypothesis; Short, 1963; Watson & Staines, 1978; Main et al., 1996). This could be  
509 the case during early springs where females remained on scarce but emerging vegetation  
510 within steep rocky cliffs of winter ranges (when spring starts early vegetation grows slowly;  
511 Bliss, 1971, Figure 2A) while males migrated earlier, possibly to benefit more rapidly from  
512 abundant forage in alpine grasslands. Indeed, peak green-up in winter ranges and snowmelt in  
513 summer ranges were correlated, indicating that the timing of snowmelt and vegetation  
514 greening on summer ranges coincides with the timing of spring green-up on winter ranges  
515 (Figure S5; see also Herfindal et al. 2019). By contrast, when spring green-up was late,

516 females migrated earlier than males and several tens of days before peak green-up, probably  
517 to reach safe habitats of summer ranges before parturition, that occurs right after spring  
518 migration, from early June to mid-July. This way females may favor newborn protection  
519 against predators rather than benefiting from the green wave, supporting the reproductive  
520 strategy-predation risk hypothesis (Main & Coblentz ,1996; Grignolio et al., 2007; Debeffe et  
521 al., 2017). Our findings suggest that the lower plasticity in the spring migration timing of  
522 females is mostly linked to the timing of parturition, although we did not detect any influence  
523 of age (hypothesized as a rough proxy of reproductive status). However, age, that is also  
524 related to many other biological traits such as experience, movement abilities, social rank,  
525 may only poorly inform about the reproductive status of females. Moreover, the gregarious  
526 behavior of ibex could reduce individual differences within sexes. When restricting the  
527 analysis to the females migrating over multiple springs, we found that they actually timed  
528 migration similarly as males, which raises questions on the actual level of plasticity in female  
529 migration phenology. Yet, the sample size for such females was limited (n=49 individual-  
530 years), potentially rendering this sample non-representative, as factors like reproductive  
531 status, parturition phenology, propensity to migrate and individual plasticity in migration  
532 timing may be intricately interconnected (Aikens et al., 2021; Laforge et al., 2021). Further  
533 investigations should delve deeper, incorporating the actual reproductive status of females  
534 (unavailable for most individuals in our dataset), accounting for parturition phenology  
535 (Marchand et al., 2021), and exploring the propensity to migrate and to switch between  
536 residency and migration. Such studies are crucial to confirm the strong constraint posed by  
537 parturition on female migration.

538 The rates of changes we detected in ibex migration timing were all lower than the rate that  
539 would be needed to perfectly match changes in environmental conditions. This could suggest  
540 that such responses may only partially allow ibex to respond to rapidly changing conditions

541 in alpine mountains, leading to possible trophic mismatch (particularly during early springs)  
542 and questioning the resilience of this species to face ongoing climate change. However, in the  
543 context of short-distance altitudinal migration, snow cover provides a relevant visual cue for  
544 informing animals on remote environmental conditions (Figure S5; Berger et al., 2022). In  
545 this case, the anticipated conditions in summer ranges could be as influential as those  
546 encountered in winter ranges in determining migration timing (Rickbeil et al., 2019;  
547 Pandraud et al., 2022; Berger et al., 2022). Indeed, there is growing evidence that migratory  
548 ungulates trade-off perception and memory of when and where beneficial resources may  
549 occur to decide migrating (Mueller et al., 2011, Bracis & Mueller, 2017). In addition, in an  
550 alpine ungulate species jumping the green wave, the benefits from migration during an early  
551 spring may mostly stem from individuals' ability to arrive on time and effectively exploit the  
552 growing vegetation in alpine grasslands from summer ranges. In these areas, forage is not  
553 only of high quality, as in winter range when vegetation emerges, but also far more abundant  
554 than in steep rocky cliffs used to face harsh winter conditions. Therefore, quantifying the  
555 exposure to high-quality vegetation before and after migration, depending on spring  
556 conditions and individuals' plasticity in migration timing, is needed to better assess the  
557 benefit of migration. Temporal plasticity in ibex migration timing highlights a potential for  
558 resilience in this alpine species facing rapid climate change, at least in males. But further  
559 research is still needed to firmly conclude on the consequence of ongoing climate change in  
560 terms of mismatches.

561 More generally, as climate change impact on vegetation phenology is expected to lead to  
562 earlier snowmelt and more advanced vegetation growth in the next decades (Ernakovich et  
563 al., 2013; Yang et al., 2017), or even delayed vegetation senescence (Wu et al., 2022; Spera  
564 et al., 2023), ibex might respond to these changes thanks to behavioral plasticity. The date of  
565 snowmelt in alpine habitats is expected to advance by 10 days in 2050 and 13 days in 2100

566 under RCP4.5, the intermediate GIEC scenario (Vorkauf et al., 2021). These potential  
567 changes represent significant shifts in comparison to our study period. Thus, springs that we  
568 considered as warm and early springs (i.e., date <137) could become the norm in the future.  
569 Ibex appeared to adjust their migration timing to match the peak green-up also during warm  
570 springs. However, rapid changes in plant productivity during warm springs reduce the  
571 availability of good quality vegetation, leading to reduced juvenile growth in alpine ungulates  
572 (Pettorelli et al., 2007). Understanding how vegetation quality and vegetation community  
573 could be modified during these warm events will be crucial to really assess the consequences  
574 on migration benefits. Females could still benefit from the peak green-up on their winter and  
575 summer ranges, but this could occur significantly earlier and not match with the peak of  
576 parturitions, though a close match between reproduction timing and peak energy income can  
577 be less crucial for capital breeders (Hogg et al., 2017). Furthermore, the general increase in  
578 temperatures, especially in summer, leading to greater thermal-stress is a major concern for  
579 the species (Semenzato et al., 2021). It is therefore essential that future studies on alpine  
580 migratory species focus on the benefits of migration in relation to its timing and assess if  
581 changes in phenological events driving migration can modify these benefits, and thus the  
582 choice to migrate, potentially leading to demographic consequences.

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## 606 **CONFLICT OF INTEREST STATEMENT**

607 The authors declare no competing interests.

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968 **TABLES**

969 **TABLE 1:** Predictions of the effect of environmental factors on the timing of Alpine ibex  
 970 migration in spring and autumn. WR= Winter range, M= Males, F= Females, SR= Summer  
 971 range.

Season	Environmental drivers	Differences Sex & Age	Predictions	Sources
<b>Spring</b>	Peak of green-up in WR	M > F Old M > Young M	M & F migrate around the peak of green-up, but F are less synchronized because of parturition following migration. Older ibex (more experienced) better synchronized with peak green-up.	Main & Coblenz, 1996; Debeffe et al., 2017 Grignolio et al., 2007; 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 winter ranges.	Herfindal et al., 2006; Pettorelli et al., 2005; Garel et al., 2011
	Date of snowmelt in SR		Ibex delay migration when later snowmelt on their SR.	Pandraud et al., 2022; Berger 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; Semenzato et al., 2021
	Winter severity: winter snowfall and winter temperatures		Winter severity affects ibex body condition with consequences on migration timing.	Signer et al., 2011 Herfindal et al., 2019
	Distance		Ibex migrating longer distances migrate earlier.	Le Corre et al., 2016 Gurarie et al., 2019
<b>Autumn</b>	Peak of senescence in SR	M > F 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 Cameron et al., 2021

	Length of senescence period in SR		Ibex migrate later when the vegetation senescence period is extended.	
	Date of first snowfall in SR		Ibex migrate after the first snowfall.	Jones et al., 2014 Le Corre et al., 2016 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.	Rivrud et al., 2016 Weller et al., 2022 Ortega et al., 2024
	Summer severity: Summer precipitations and temperatures		Hot and dry summers affect ibex body conditions and migration timing.	
	Distance		Ibex migrating longer distances migrate earlier to avoid costly movement in snow.	Le Corre et al., 2016 Rivrud et al., 2016

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974 TABLE 2: Set of linear mixed-effects models used to investigate variation in migration dates  
975 with environmental and individual characteristics at both seasons. For clarity, only models  
976 with  $\Delta AICc < 2$  were provided, in addition to the null model. The variables selected from this  
977 set of models using likelihood ratio tests are in bold type. We added individual identity and  
978 population as random effects in each model. K = number of parameters, peakGU = date of  
979 peak green-up, SnowM = Date of snowmelt, SpringL = length of spring season, snowT =  
980 total snow precipitation during winter, distance = migration distance, T10 = date of 10°C  
981 mean daily temperature in spring, tempW = average temperature during winter, SenescenceL  
982 = length of senescence period, snowfall = date of first snowfall, tempS = average temperature  
983 during summer, peakSe = date of peak of vegetation senescence.

Season	Model	K	Log(likelihood)	AICc	$\Delta AICc$
<b>Spring</b>	<b>peakGU*sex + snowM + SpringL + snowT</b>	10	-838.1	1697.3	0
	<b>peakGU*sex + snowM + SpringL + snowT + distance</b>	11	-837.1	1697.5	0.3
	<b>peakGU*sex + snowM + SpringL + snowT + distance + T10</b>	12	-836.2	1697.9	0.7
	<b>peakGU*sex + snowM + SpringL + snowT + T10</b>	11	-837.3	1697.9	0.7
	<b>peakGU*sex + snowM + SpringL</b>	9	-839.5	1698.0	0.7
	<b>peakGU*sex + snowM + SpringL + tempW</b>	10	-838.5	1698.1	0.8
	<b>peakGU*sex + snowM + SpringL + distance</b>	10	-838.6	1698.3	1.0
	<b>peakGU*sex + snowM + SpringL + distance + snowT + distance*snowM</b>	12	-836.4	1698.4	1.1
	Null model	4	-866.7	1741.7	44.4
<b>Autumn</b>	<b>SenescenceL + snowfall</b>	6	-1114.1	2240.6	0
	<b>SenescenceL + snowfall + tempS</b>	7	-1113.6	2241.7	1.1
	<b>SenescenceL + snowfall + peakSe</b>	7	-1113.9	2242.4	1.7
	<b>SenescenceL + snowfall + distance</b>	7	-1114.0	2242.5	1.9
	Null model	4	-1127.0	2262.3	21.7

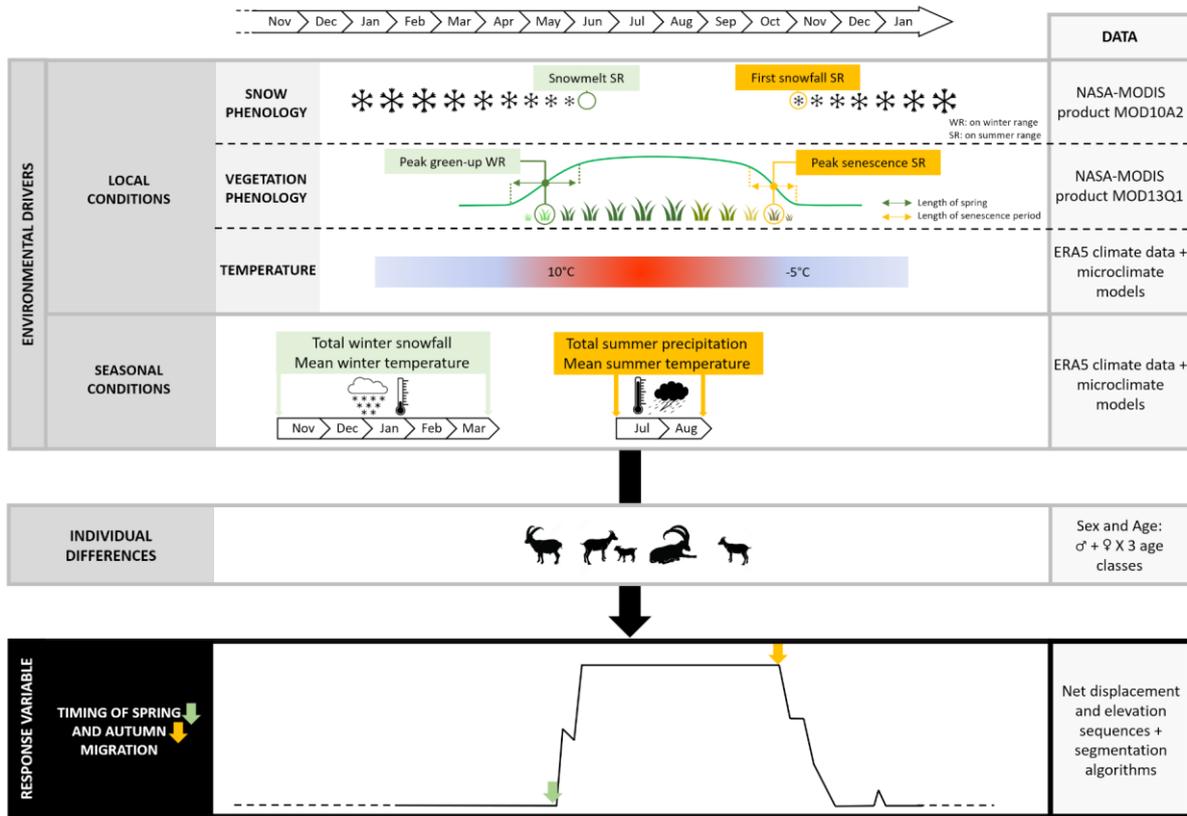
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985 TABLE 3: Parameters included in the most supported models at both seasons describing  
 986 variation in migration date with environmental and individual characteristics. Covariates  
 987 were not scaled. We added individual identity and population as random effects in both  
 988 models. CI= Confidence interval, M=Males, F=Females, peakGU = date of peak green-up,  
 989 SnowM = Date of snowmelt, SpringL = length of spring season, SenescenceL = length of  
 990 senescence period, Snowfall = date of first snowfall.

Season	Parameters	Estimates [95% CI]	p-values
<b>Spring</b>	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
<b>Autumn</b>	Intercept	180.53 [122.13; 237.62]	<0.0001
	SenescenceL	0.25 [0.10;0.39]	<0.01
	Snowfall	0.38 [0.18;0.57]	<0.001

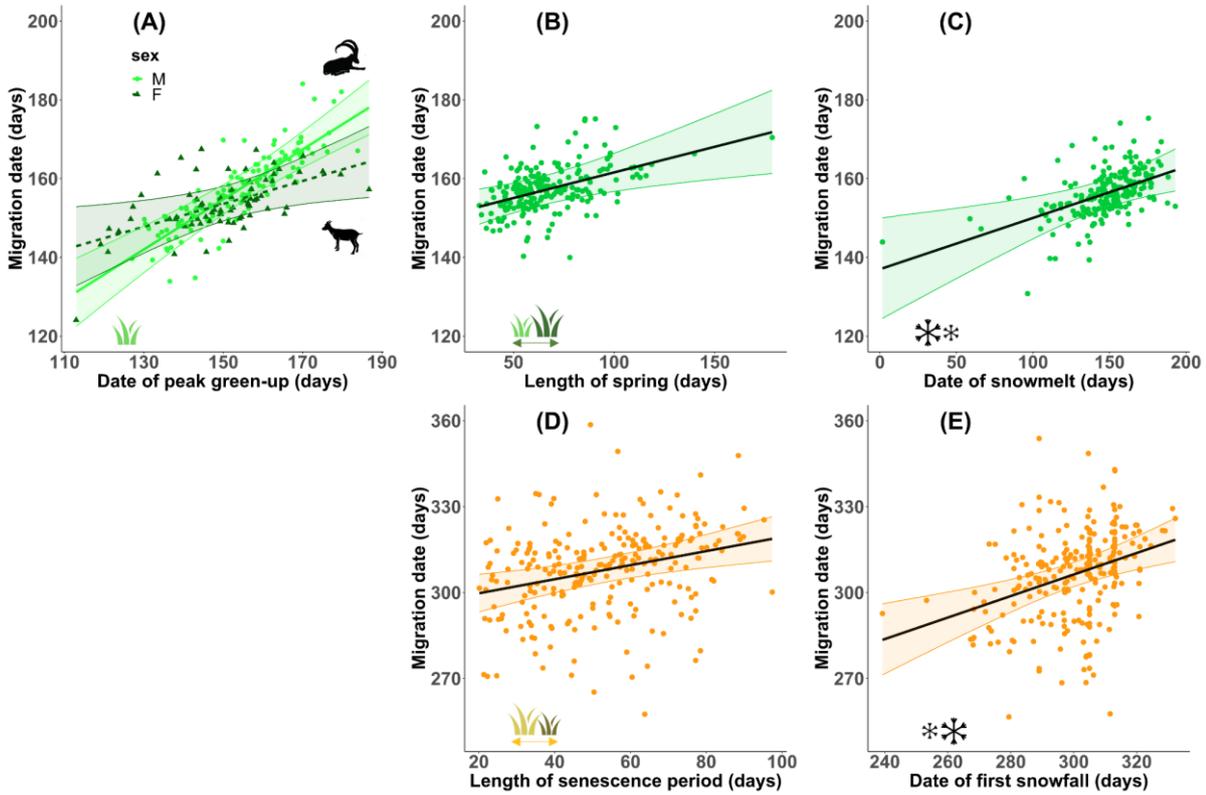
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992 **FIGURES**



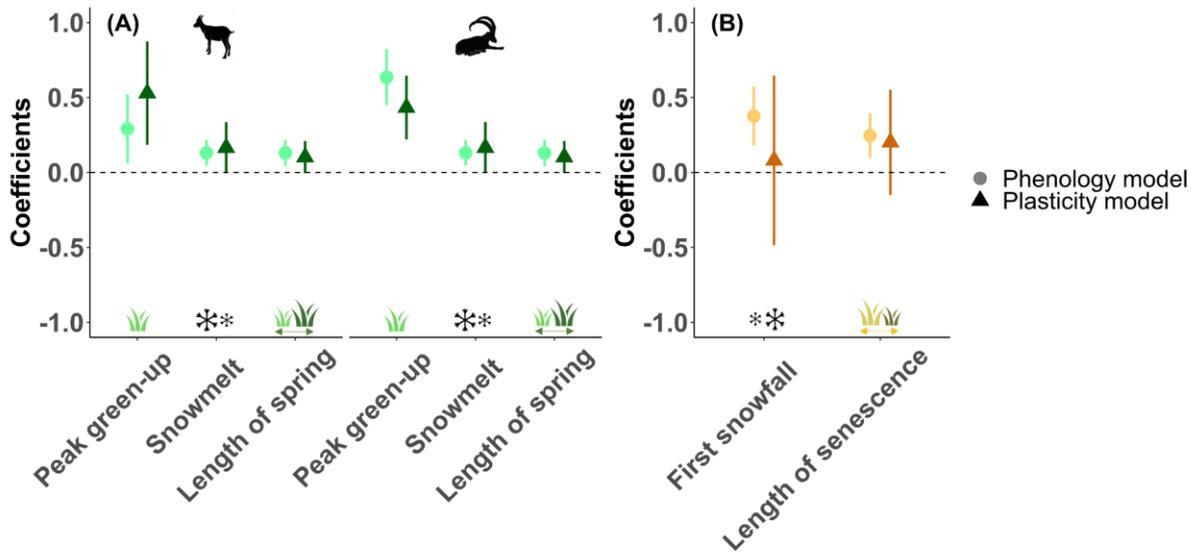
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994 **FIGURE 1:** Conceptual framework summarizing the environmental (seasonal and local) and  
 995 individual drivers hypothesized to affect the timing of spring and autumn migrations in  
 996 Alpine ibex *Capra ibex*. The type of data used to test each hypothesis is listed in the column  
 997 to the right.



998

999 FIGURE 2: Effects of environmental and individual characteristics on Alpine ibex *Capra*  
 1000 *ibex* migration timing in spring (A: date of peak green-up [sex-specific], B: date of snowmelt,  
 1001 and C: length of spring; n=211) and autumn (D: length of the senescence period; E: date of  
 1002 first snowfall; n=250). Solid lines and the shaded areas are the predictions and 95%  
 1003 confidence intervals of the best model (see Table 2), respectively. Dots are the partial  
 1004 residuals accounting for the effects of the other variables in the model.



1005 FIGURE 3: Comparison of coefficients derived from linear mixed-effect models explaining  
 1006 migration departure in response to environmental and individual characteristics during spring  
 1007 (A, left panel for females, right panel for males) and autumn (B) and those obtained from  
 1008 plasticity models (variation in  $\Delta$ migration dates) assessing behavioral plasticity in migration  
 1009 timing in response to inter-annual changes in environmental drivers. The first analysis relied  
 1010 on the full dataset (dots; n=211 individual-year in spring and n=250 in autumn; see Figure 2  
 1011 and Table 3) and the second relied on individual ibex tracked during two seasonal migrations  
 1012 or more (triangles; n=49 individual-year in spring and n=38 in autumn). Line ranges represent  
 1013 95% confidence intervals. Peak green-up = date of peak of vegetation growth, Snowmelt =  
 1014 Date of snowmelt on summer range, Length of spring = length of spring season, First  
 1015 snowfall = Date of first snowfall on summer range, Length of senescence = Length of  
 1016 senescence period in autumn.