



HAL
open science

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

Victor Chauveau, Mathieu Garel, Carole Toïgo, Pia Anderwald, Marco Apollonio, Bruno Bassano, Mathieu Beurier, Michel Bouche, Alice Brambilla, Francesca Brivio, et al.

► To cite this version:

Victor Chauveau, Mathieu Garel, Carole Toïgo, Pia Anderwald, Marco Apollonio, et al.. It's time to go - Drivers and plasticity of migration phenology in a short-distance migratory ungulate. 2024. hal-04608168

HAL Id: hal-04608168

<https://hal.science/hal-04608168>

Preprint submitted on 11 Jun 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

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

3 Chauveau Victor^{1*}, Garel Mathieu², Toigo Carole², Anderwald Pia³, Apollonio Marco⁴,
4 Bassano Bruno⁵, Beurier Mathieu², Bouche Michel⁶, Brambilla Alice^{5,7}, Brivio Francesca⁴,
5 Bunz Yoann⁶, Cagnacci Francesca^{8,9}, Canut Marie¹⁰, Cavailhes Jérôme¹¹, Champly Ilka¹²,
6 Filli Flurin³, Frey-Roos Alfred¹³, Gressmann Gunther¹⁴, Grignolio Stefano^{4,15}, Herfindal
7 Ivar¹⁶, Jurgeit Florian¹⁴, Martinelli Laura¹⁷, Maurino Luca¹⁸, Papet Rodolphe⁶, Petit Elodie¹⁹,
8 Ramanzin Maurizio²⁰, Semenzato Paola^{20,21}, Vannard Eric⁶, Coulon Aurélie^{22,23}, Loison
9 Anne¹, Marchand Pascal²⁴

10 1- Laboratoire d'Ecologie Alpine (LECA), UMR 5553, Université Grenoble Alpes,
11 Université Savoie Mont-Blanc, Centre National de la Recherche Scientifique (CNRS), Le
12 Bourget-du-Lac, France

13 2- Office Français de la Biodiversité (OFB), Direction de la Recherche et de l'Appui
14 Scientifique - Service Anthropisation et Fonctionnement des Ecosystèmes Terrestres, Gières,
15 France

16 3- Swiss National Park, Chastè Planta-Wildenberg, Runatsch 124, 7530 Zernez, Switzerland

17 4- Department of Veterinary Medicine, University of Sassari, via Vienna 2, Sassari 07100,
18 Italy

19 5- Alpine Wildlife Research Centre, Gran Paradiso National Park, Valsavarenche (AO), Italy

20 6- Parc national des Écrins, Domaine de Charance, 05000 Gap, France

21 7- Department of Evolutionary Biology and Environmental Studies, University of Zurich,
22 Zurich, Switzerland

23 8- Animal Ecology Unit, Research and Innovation Centre, Fondazione Edmund Mach,
24 Trento, Italy

- 25 9- NBFC, National Biodiversity Future Center, Palermo 90133, Italy
- 26 10- Parc national du Mercantour, 23 rue d'Italie, CS 51316, 06006 Nice Cedex 1
- 27 11- Parc national de la Vanoise, 135 rue du Dr Julliand, 73000 Chambéry, France
- 28 12- Asters, CEN de Haute-Savoie, 84 route du Viéran, PAE de Pré-Mairy, 74370 Pringy,
- 29 France
- 30 13- Institute of Wildlife Biology and Game Management, University of Natural Resources
- 31 and Life Sciences, Vienna. Gregor Mendel- Str. 33, 1180 Vienna, Austria
- 32 14- Tyrol National Park Authority, Kirchplatz 2, 9971 Matrei i. O., Tyrol, Austria
- 33 15- Department of Life Sciences and Biotechnology, University of Ferrara, via Borsari 46,
- 34 44121 Ferrara, Italy
- 35 16- Gjærevoll Centre for Biodiversity Foresight Analyses, Norwegian University of Science
- 36 and Technology, N-7491 Trondheim, Norway
- 37 17- Ente di gestione Aree Protette Alpi Marittime, Piazza Regina Elena 30, 12010 Valdieri,
- 38 Italy
- 39 18- Ente di gestione Aree Protette Alpi Cozie, Via Fransuà Fontan, 1 - 10050 Salbertrand
- 40 (TO), Italy
- 41 19- Office Français de la Biodiversité, 90 impasse Les Daudes, 74320 Sevrier, France
- 42 20- Department of Agronomy, Food, Natural resources, Animals and Food, University of
- 43 Padova. Viale dell'Università 16, 35020 Legnaro, Italy
- 44 21- DREAM-Italia, Via Enrico Bindi n. 14 – 51100 Pistoia, Italy
- 45 22- Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national
- 46 d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, CP
- 47 135, 57 rue Cuvier 75005 Paris, France
- 48 23- CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France.

49 24- Office Français de la Biodiversité (OFB), Direction de la Recherche et de l'Appui
50 Scientifique - Service Anthropisation et Fonctionnement des Ecosystèmes Terrestres,
51 Juvignac, France
52 * Corresponding author: victor.chauveau@etu.univ-smb.fr

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 (Avgar 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 1st and ending
210 February 28th or 29th 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 15th and August 15th 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 (Δ 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°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]_{95%}) than in males (0.21 [0.13; 0.29]_{95%}), 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]_{95%}; males: 0.35 [0.29;0.41]_{95%}).

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.

583 **ACKNOWLEDGEMENTS**

584 We thank all the professionals and interns involved in the monitoring of GPS-collared ibex
585 on all study sites. We thank F. Couilloud and les Services Départementaux de la Haute-
586 Savoie et de l'Isère from the Office Français de la Biodiversité, and L. Gautero, V. Roggero,
587 A. Rivelli, E. Piacenza, M. Dotto, A. Menzano. We thank all our partners: Ecrins NP, Gran
588 Paradiso NP, Asters-CEN 74, Vanoise NP, Autonomous Region Aosta Valley, Mercantour
589 NP, Protected areas of Maritime Alps, Protected areas of Cottian Alps – for providing GPS
590 data collected during the Alcotra ITA-FR 1667 LEMED-IBEX program. We warmly thank

591 the Global Initiative for Ungulate migrations and its mapping team, the OFB, ANR MovIt,
592 ANR HUMANI, LECA teams and in particular Philippe Choler for fruitful discussions on
593 early versions of this manuscript.

594 This research and the data collection were founded by the Office Français de la Biodiversité,
595 the Agence Nationale de la Recherche (ANR; Grant/award Numbers: HUMANI #18-CE03-
596 0009, Mov-It #16-CE02-0010), the Interreg Alcotra ITA-FR 1664 LEMED-ibex, 2000-2006
597 Alcotra ITA-FR (PN Gran Paradiso and PN Vanoise), 2007-20013 Interreg ITA-Suisse
598 (GREAT project PN Gran PARadiso and PN Suisse), the Interreg Lemed-Ibex project 2014 -
599 2020. The Stiegl Brewery of Salzburg for the Hohe Tauern National Park. The Swiss
600 National Park. The University of Padova, project n. CPDA094513/09 MIUR ex 60%, projects
601 60A08-2154/14 and 60A08-2017/15; Veneto region, Wildlife and Hunting Service (Regione
602 Veneto-Unità di Progetto Caccia e Pesca); Fondazione Edmund Mach, ordinary funds from
603 Autonomous Province of Trento. The Research Council of Norway, project nr 223257.
604 Mercantour National Park was financed by GMF. The study in Vorarlberg (Austria) was
605 funded by a hunting community (private financing).

606 **CONFLICT OF INTEREST STATEMENT**

607 The authors declare no competing interests.

608 **REFERENCES**

609 Abrahms, B., Hazen, E. L., Aikens, E. O., Savoca, M. S., Goldbogen, J. A., Bograd, S. J.,
610 Jacox, M. G., Irvine, L. M., Palacios, D. M., & Mate, B. R. (2019). Memory and resource
611 tracking drive blue whale migrations. *Proceedings of the National Academy of Sciences*,
612 *116*(12), 5582-5587. <https://doi.org/10.1073/pnas.1819031116>

613 Abrahms, B., Teitelbaum, C. S., Mueller, T., & Converse, S. J. (2021). Ontogenetic shifts
614 from social to experiential learning drive avian migration timing. *Nature Communications*,
615 *12*(1), 7326. <https://doi.org/10.1038/s41467-021-27626-5>

616 Aikens, E. O., Dwinnell, S. P. H., LaSharr, T. N., Jakopak, R. P., Fralick, G. L., Randall, J.,
617 Kaiser, R., Thonhoff, M., Kauffman, M. J., & Monteith, K. L. (2021). Migration distance and
618 maternal resource allocation determine timing of birth in a large herbivore. *Ecology*, *102*(6),
619 e03334. <https://doi.org/10.1002/ecy.3334>

620 Aikens, E. O., Monteith, K. L., Merkle, J. A., Dwinnell, S. P. H., Fralick, G. L., & Kauffman,
621 M. J. (2020). Drought reshuffles plant phenology and reduces the foraging benefit of
622 green- wave surfing for a migratory ungulate. *Global Change Biology*, *26*(8), 4215-4225.
623 <https://doi.org/10.1111/gcb.15169>

624 Albon, S. D., & Langvatn, R. (1992). Plant Phenology and the Benefits of Migration in a
625 temperate Ungulate. *Oikos*, *65*(3), 502-513. <https://doi.org/10.2307/3545568>

626 Anderson, A. M., Duijns, S., Smith, P. A., Friis, C., & Nol, E. (2019). Migration Distance
627 and Body Condition Influence Shorebird Migration Strategies and Stopover Decisions During
628 Southbound Migration. *Frontiers in Ecology and Evolution*, *7*, 251.
629 <https://doi.org/10.3389/fevo.2019.00251>

630 Aublet, J.-F., Festa-Bianchet, M., Bergero, D., & Bassano, B. (2009). Temperature
631 constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia*,
632 *159*(1), 237–247. <https://doi.org/10.1007/s00442-008-1198-4>

633 Avgar, T., Street, G., & Fryxell, J. M. (2014). On the adaptive benefits of mammal migration.
634 *Canadian Journal of Zoology*, *92*(6), 481–490. <https://doi.org/10.1139/cjz-2013-0076>

635 Barton, K. (2023). *MuMIn: Multi-Model Inference. R package version 1.42.1.*

636 Beck, P. S. A., Atzberger, C., Høgda, K. A., Johansen, B., & Skidmore, A. K. (2006).
637 Improved monitoring of vegetation dynamics at very high latitudes: A new method using
638 MODIS NDVI. *Remote Sensing of Environment*, *100*(3), 321–334.
639 <https://doi.org/10.1016/j.rse.2005.10.021>

640 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of
641 climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377.
642 <https://doi.org/10.1111/j.1461-0248.2011.01736.x>

643 Berger, D. J., German, D. W., John, C., Hart, R., Stephenson, T. R., & Avgar, T. (2022).
644 Seeing Is Be-Leaving: Perception Informs Migratory Decisions in Sierra Nevada Bighorn
645 Sheep (*Ovis canadensis sierrae*). *Frontiers in Ecology and Evolution*, *10*, 742275.
646 <https://doi.org/10.3389/fevo.2022.742275>

647 Biebach, I., & Keller, L. F. (2009). A strong genetic footprint of the re-introduction history of
648 Alpine ibex (*Capra ibex ibex*). *Molecular Ecology*, *18*(24), 5046-5058.
649 <https://doi.org/10.1111/j.1365-294X.2009.04420.x>

650 Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B., & Mysterud,
651 A. (2012). A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the
652 Green Wave? *The American Naturalist*, *180*(4), 407-424. <https://doi.org/10.1086/667590>

653 Bliss, L. C. (1971). Arctic and Alpine Plant Life Cycles. *Annual Review of Ecology and*
654 *Systematics*, *2*, 405–438. <https://doi.org/10.1146/annurev.es.02.110171.002201>

655 Börger, L., & Fryxell, J. (2012). Quantifying individual differences in dispersal using net
656 squared displacement. In *Dispersal Ecology and Evolution* (pp. 222–230). Oxford University
657 Pres.

658 Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B., & Visser, M. E. (2009).
659 Climate change and unequal phenological changes across four trophic levels: Constraints or
660 adaptations? *Journal of Animal Ecology*, 78(1), 73–83. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2656.2008.01458.x)
661 2656.2008.01458.x

662 Bracis, C., & Mueller, T. (2017). Memory, not just perception, plays an important role in
663 terrestrial mammalian migration. *Proceedings of the Royal Society B: Biological Sciences*,
664 284(1855), 20170449. <https://doi.org/10.1098/rspb.2017.0449>

665 Brambilla, A., Bassano, B., Biebach, I., Bollmann, K., Keller, L., Toïgo, C., & von
666 Hardenberg, A. (2022). Alpine Ibex *Capra ibex* Linnaeus, 1758. In K. Hackländer & F. E.
667 Zachos (Eds.), *Handbook of the Mammals of Europe* (pp. 1–27). Springer International
668 Publishing. https://doi.org/10.1007/978-3-319-65038-8_32-1

669 Brambilla, A., Von Hardenberg, A., Nelli, L., & Bassano, B. (2020). Distribution, status, and
670 recent population dynamics of Alpine ibex *Capra ibex* in Europe. *Mammal Review*, 50(3),
671 267-277. <https://doi.org/10.1111/mam.12194>

672 Burnham, K. P., & Anderson, D. R. (Eds.). (2004). *Model Selection and Multimodel*
673 *Inference* (Vol. 63). Springer New York. <https://doi.org/10.1007/b97636>

674 Buskirk, J. V., Mulvihill, R. S., & Leberman, R. C. (2012). Phenotypic plasticity alone cannot
675 explain climate-induced change in avian migration timing. *Ecology and Evolution*, 2(10),
676 2430-2437. <https://doi.org/10.1002/ece3.367>

677 Calenge, C. (2023). *adehabitatHR: Home Range Estimation. R package version 0.4.20.*
678 <https://CRAN.R-project.org/package=adehabitatHR>

679 Cameron, M. D., Eisaguirre, J. M., Breed, G. A., Joly, K., & Kielland, K. (2021).
680 Mechanistic movement models identify continuously updated autumn migration cues in
681 Arctic caribou. *Movement Ecology*, 9(1), 1-12. <https://doi.org/10.1186/s40462-021-00288-0>

682 Candino, M., Donadio, E., & Pauli, J. N. (2022). Phenological drivers of ungulate migration
683 in South America: Characterizing the movement and seasonal habitat use of guanacos.
684 *Movement Ecology*, 10(1), 1–14. <https://doi.org/10.1186/s40462-022-00332-7>

685 Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C.
686 (2008). Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild Bird
687 Population. *Science*, 320(5877), 800–803. <https://doi.org/10.1126/science.1157174>

688 Chauveau, V., Garel, M., Toïgo, C., Anderwald, P., Beurier, M., Bunz, Y., Bouche, M.,
689 Cagnacci, F., Canut, M., Cavailles, J., Champly, I., Filli, F., Frey-Roos, A., Gressmann, G.,
690 Herfindal, I., Jurgeit, F., Martinelli, L., Papet, R., Petit, E., ... Marchand, P. (2023).
691 Identifying the environmental drivers of corridors and predicting connectivity between
692 seasonal ranges in multiple populations of Alpine ibex (*Capra ibex*) as tools for conserving
693 migration (p. 2023.03.02.530594). bioRxiv. <https://doi.org/10.1101/2023.03.02.530594>

694 Chauveau, V., Garel, M., Toïgo, C., Anderwald, P., Apollonio, M., Bassano, B., Beurier, M.,
695 Bouche, M., Brambilla, A., Brivio, F., Bunz, Y., Cagnacci, F., ... Marchand, P. (2024). *Data*
696 *from: It's time to go - Drivers and plasticity of migration phenology in a short-distance*
697 *migratory ungulate*. Zenodo Digital Repository. <https://doi.org/10.5281/zenodo.10304656>

698 Cooper, N. W., Sherry, T. W., & Marra, P. P. (2015). Experimental reduction of winter food
699 decreases body condition and delays migration in a long-distance migratory bird. *Ecology*,
700 96(7), 1933–1942. <https://doi.org/10.1890/14-1365.1>

701 Debeffe, L., Maren Rivrud, I., Brekkum, Ø., Meisingset, E. L., & Mysterud, A. (2017).
702 Implications of the forage maturation hypothesis for activity of partially migratory male and
703 female deer. *Ecosphere*, 8(12), e02050. <https://doi.org/10.1002/ecs2.2050>

704 Debeffe, L., Rivrud, I. M., Meisingset, E. L., & Mysterud, A. (2019). Sex-specific differences
705 in spring and autumn migration in a northern large herbivore. *Scientific Reports*, 9(1), 6137.
706 <https://doi.org/10.1038/s41598-019-42639-3>

707 Demment, M. W., & Van Soest, P. J. (1985). A Nutritional Explanation for Body-Size
708 Patterns of Ruminant and Nonruminant Herbivores. *The American Naturalist*, 125(5), 641–
709 672. <https://doi.org/10.1086/284369>

710 Dingle, H., & Drake, V. A. (2007). What Is Migration? *BioScience*, 57(2), 113-121.
711 <https://doi.org/10.1641/B570206>

712 Durant, J., Hjermann, D., Ottersen, G., & Stenseth, N. (2007). Climate and the match or
713 mismatch between predator requirements and resource availability. *Climate Research*, 33,
714 271–283. <https://doi.org/10.3354/cr033271>

715 Eggeman, S. L., Hebblewhite, M., Bohm, H., Whittington, J., & Merrill, E. H. (2016).
716 Behavioural flexibility in migratory behaviour in a long-lived large herbivore. *Journal of*
717 *Animal Ecology*, 85(3), 785–797. <https://doi.org/10.1111/1365-2656.12495>

718 Enriquez-Urzelai, U., Tingley, R., Kearney, M. R., Sacco, M., Palacio, A. S., Tejedo, M., &
719 Nicieza, A. G. (2020). The roles of acclimation and behaviour in buffering climate change

720 impacts along elevational gradients. *Journal of Animal Ecology*, 89(7), 1722–1734.
721 <https://doi.org/10.1111/1365-2656.13222>

722 Ernakovich, J. G., Hopping, K. A., Berdanier, A. B., Simpson, R. T., Kachergis, E. J.,
723 Steltzer, H., & Wallenstein, M. D. (2014). Predicted responses of arctic and alpine
724 ecosystems to altered seasonality under climate change. *Global Change Biology*, 20(10),
725 3256–3269. <https://doi.org/10.1111/gcb.12568>

726 Garel, M., Gaillard, J.-M., Jullien, J.-M., Dubray, D., Maillard, D., & Loison, A. (2011).
727 Population abundance and early spring conditions determine variation in body mass of
728 juvenile chamois. *Journal of Mammalogy*, 92(5), 1112–1117. <https://doi.org/10.1644/10->
729 MAMM-A-056.1

730 Grignolio, S., Rossi, I., Bassano, B., & Apollonio, M. (2007). Predation Risk as a Factor
731 Affecting Sexual Segregation in Alpine Ibex. *Journal of Mammalogy*, 88(6), 1488–1497.
732 <https://doi.org/10.1644/06-MAMM-A-351R.1>

733 Gurarie, E., Hebblewhite, M., Joly, K., Kelly, A. P., Adamczewski, J., Davidson, S. C.,
734 Davison, T., Gunn, A., Sutor, M. J., Fagan, W. F., & Boelman, N. (2019). Tactical
735 departures and strategic arrivals: Divergent effects of climate and weather on caribou spring
736 migrations. *Ecosphere*, 10(12), e02971. <https://doi.org/10.1002/ecs2.2971>

737 Hagen, R., Ortmann, S., Elliger, A., & Arnold, J. (2021). Advanced roe deer (*Capreolus*
738 *capreolus*) parturition date in response to climate change. *Ecosphere*, 12(11), e03819.
739 <https://doi.org/10.1002/ecs2.3819>

740 Hall, D. K. & Riggs, G. A. (2021). *MODIS/Terra Snow Cover 8-Day L3 Global 500m Grid,*
741 *Version 61* [dataset]. NASA National Snow and Ice Data Center DAAC.
742 <https://doi.org/10.5067/MODIS/MOD10A2.061>

743 Herfindal, I., Anderwald, P., Filli, F., Campell Andri, S., & Rempfler, T. (2019). Climate,
744 competition and weather conditions drive vertical displacement and habitat use of an alpine
745 ungulate in a highly topographic landscape. *Landscape Ecology*, *34*(11), 2523–2539.
746 <https://doi.org/10.1007/s10980-019-00902-y>

747 Herfindal, I., Sæther, B.-E., Solberg, E. J., Andersen, R., & Høgda, K. A. (2006). Population
748 characteristics predict responses in moose body mass to temporal variation in the
749 environment. *Journal of Animal Ecology*, *75*(5), 1110–1118. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2656.2006.01138.x)
750 [2656.2006.01138.x](https://doi.org/10.1111/j.1365-2656.2006.01138.x)

751 Hogg, J. T., Dunn, S. J., Poissant, J., Pelletier, F., & Byers, J. A. (2017). Capital vs. Income-
752 dependent optimal birth date in two North American ungulates. *Ecosphere*, *8*(4), e01766.
753 <https://doi.org/10.1002/ecs2.1766>

754 IGOTA, H., SAKURAGI, M., UNO, H., KAJI, K., KANEKO, M., AKAMATSU, R., &
755 MAEKAWA, K. (2004). Seasonal migration patterns of female sika deer in eastern
756 Hokkaido, Japan. *Ecological Research*, *19*(2), 169–178. [https://doi.org/10.1111/j.1440-](https://doi.org/10.1111/j.1440-1703.2003.00621.x)
757 [1703.2003.00621.x](https://doi.org/10.1111/j.1440-1703.2003.00621.x)

758 Inouye, D. W. (2022). Climate change and phenology. *WIREs Climate Change*, *13*(3), e764.
759 <https://doi.org/10.1002/wcc.764>

760 James, N. A., Zhang, W., & Matesson, D. S. (2020). ecp: Non-Parametric Multiple Change-
761 Point Analysis of Multivariate Data. *R Package Version 3.1.1*. [https://cran.r-](https://cran.r-project.org/web/packages/ecp/index.html)
762 [project.org/web/packages/ecp/index.html](https://cran.r-project.org/web/packages/ecp/index.html)

763 Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B.,
764 Hurley, M. A., McWhirter, D. E., Miyasaki, H. M., Monteith, K. L., & Kauffman, Matthew.

765 J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from
766 translocated animals. *Science*, *361*(6406), 1023-1025. <https://doi.org/10.1126/science.aat0985>

767 Jones, J. D., Kauffman, M. J., Monteith, K. L., Scurlock, B. M., Albeke, S. E., & Cross, P. C.
768 (2014). Supplemental feeding alters migration of a temperate ungulate. *Ecological*
769 *Applications*, *24*(7), 1769-1779. <https://doi.org/10.1890/13-2092.1>

770 Kearney, M. R., Gillingham, P. K., Bramer, I., Duffy, J. P., & Maclean, I. M. D. (2020). A
771 method for computing hourly, historical, terrain-corrected microclimate anywhere on earth.
772 *Methods in Ecology and Evolution*, *11*(1), 38–43. <https://doi.org/10.1111/2041-210X.13330>

773 Klaassen, R. H. G., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K.-M.,
774 Bairlein, F., & Alerstam, T. (2014). When and where does mortality occur in migratory
775 birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal*
776 *Ecology*, *83*(1), 176-184. <https://doi.org/10.1111/1365-2656.12135>

777 Kong, D., McVicar, T. R., Xiao, M., Zhang, Y., Peña- Arancibia, J. L., Filippa, G., Xie, Y.,
778 & Gu, X. (2022). *phenofit*: An R package for extracting vegetation phenology from time
779 series remote sensing. *Methods in Ecology and Evolution*, *13*(7), 1508–1527.
780 <https://doi.org/10.1111/2041-210X.13870>

781 Kong, D., Zhang, Y., Gu, X., & Wang, D. (2019). A robust method for reconstructing global
782 MODIS EVI time series on the Google Earth Engine. *ISPRS Journal of Photogrammetry and*
783 *Remote Sensing*, *155*, 13–24. <https://doi.org/10.1016/j.isprsjprs.2019.06.014>

784 Laforge, M. P., Webber, Q. M. R., & Vander Wal, E. (2023). Plasticity and repeatability in
785 spring migration and parturition dates with implications for annual reproductive success.
786 *Journal of Animal Ecology*, *92*(5), 1042–1054. <https://doi.org/10.1111/1365-2656.13911>

787 Le Corre, M., Dussault, C., & Côté, S. D. (2016). Weather conditions and variation in timing
788 of spring and fall migrations of migratory caribou. *Journal of Mammalogy*, 98(1), 260–271.
789 <https://doi.org/10.1093/jmammal/gyw177>

790 Main, M. B., & Coblentz, B. E. (1996). Sexual Segregation in Rocky Mountain Mule Deer.
791 *The Journal of Wildlife Management*, 60(3), 497–507. <https://doi.org/10.2307/3802067>

792 Main, M., Weckerly, F., & Bleich, V. (1996). Sexual Segregation in Ungulates: New
793 Directions for Research. *Journal of Mammalogy*, 77, 449–461.
794 <https://doi.org/10.2307/1382821>

795 Mallory, C. D., Williamson, S. N., Campbell, M. W., & Boyce, M. S. (2020). Response of
796 barren-ground caribou to advancing spring phenology. *Oecologia*, 192(3), 837–852.
797 <https://doi.org/10.1007/s00442-020-04604-0>

798 Marchand, P., Garel, M., Morellet, N., Benoit, L., Chaval, Y., Itty, C., Petit, E., Cargnelutti,
799 B., Hewison, A. J. M., & Loison, A. (2021). A standardised biologging approach to infer
800 parturition: An application in large herbivores across the hider-follower continuum. *Methods*
801 *in Ecology and Evolution*, 12(6), 1017–1030. <https://doi.org/10.1111/2041-210X.13584>

802 Mason, T. H. E., Brivio, F., Stephens, P. A., Apollonio, M., & Grignolio, S. (2017). The
803 behavioral trade-off between thermoregulation and foraging in a heat-sensitive species.
804 *Behavioral Ecology*, 28(3), 908–918. <https://doi.org/10.1093/beheco/arx057>

805 McGraw, K. O., & Wong, S. P. (1996). Forming inferences about some intraclass correlation
806 coefficients. *Psychological Methods*, 1(1), 30–46. <https://doi.org/10.1037/1082-989X.1.1.30>

807 Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D.,
808 Oates, B. A., Sawyer, H., Scurlock, B. M., & Kauffman, M. J. (2016). Large herbivores surf

809 waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*,
810 283(1833), 20160456. <https://doi.org/10.1098/rspb.2016.0456>

811 Middleton, A. D., Merkle, J. A., McWhirter, D. E., Cook, J. G., Cook, R. C., White, P. J., &
812 Kauffman, M. J. (2018). Green-wave surfing increases fat gain in a migratory ungulate.
813 *Oikos*, 127(7), 1060-1068. <https://doi.org/10.1111/oik.05227>

814 Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Klaver, R.
815 W., & Bowyer, R. T. (2011). Timing of seasonal migration in mule deer: Effects of climate,
816 plant phenology, and life-history characteristics. *Ecosphere*, 2(4), 1–34.
817 <https://doi.org/10.1890/ES10-00096.1>

818 Moyes, K., Nussey, D. H., Clements, M. N., Guinness, F. E., Morris, A., Morris, S.,
819 Pemberton, J. M., Kruuk, L. E. B., & Clutton-Brock, T. H. (2011). Advancing breeding
820 phenology in response to environmental change in a wild red deer population. *Global Change*
821 *Biology*, 17(7), 2455–2469. <https://doi.org/10.1111/j.1365-2486.2010.02382.x>

822 Mueller, T., Fagan, W. F., & Grimm, V. (2011). Integrating individual search and navigation
823 behaviors in mechanistic movement models. *Theoretical Ecology*, 4(3), 341–355.
824 <https://doi.org/10.1007/s12080-010-0081-1>

825 Ortega, A. C., Merkle, J. A., Sawyer, H., Monteith, K. L., Lionberger, P., Valdez, M., &
826 Kauffman, M. J. (2024). A test of the frost wave hypothesis in a temperate ungulate. *Ecology*,
827 e4238. <https://doi.org/10.1002/ecy.4238>

828 Pandraud, A., Shrader, A. M., Tshipa, A., Ngwenya, N., & Chamailé-Jammes, S. (2022).
829 Cueing on distant conditions before migrating does not prevent false starts: A case study with
830 African elephants. *Oecologia*, 198, 957-966. <https://doi.org/10.1007/s00442-022-05148-1>

831 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts
832 across natural systems. *Nature*, *421*(6918), 37–42. <https://doi.org/10.1038/nature01286>

833 Peláez, M., Gaillard, J.-M., Bollmann, K., Heurich, M., & Rehnus, M. (2020). Large-scale
834 variation in birth timing and synchrony of a large herbivore along the latitudinal and
835 altitudinal gradients. *Journal of Animal Ecology*, *89*(8), 1906–1917.
836 <https://doi.org/10.1111/1365-2656.13251>

837 Pettorelli, N., Pelletier, F., Hardenberg, A. V., Festa-Bianchet, M., & Côté, S. D. (2007).
838 Early onset of vegetation growth vs. rapid green-up: Impacts on juvenile mountain ungulates.
839 *Ecology*, *88*(2), 381–390. <https://doi.org/10.1890/06-0875>

840 Pettorelli, N., Weladji, R. B., Holand, O., Mysterud, A., Breie, H., & Stenseth, N. C. (2005).
841 The relative role of winter and spring conditions: Linking climate and landscape-scale plant
842 phenology to alpine reindeer body mass. *Biology Letters*, *1*(1), 24–26.
843 <https://doi.org/10.1098/rsbl.2004.0262>

844 Plard, F., Gaillard, J.-M., Bonenfant, C., Hewison, A. J. M., Delorme, D., Cargnelutti, B.,
845 Kjellander, P., Nilsen, E. B., & Coulson, T. (2013). Parturition date for a given female is
846 highly repeatable within five roe deer populations. *Biology Letters*, *9*(1), 20120841.
847 <https://doi.org/10.1098/rsbl.2012.0841>

848 Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A. J. M., Douhard, M., Klein, F., Delorme,
849 D., Warnant, C., & Bonenfant, C. (2015). The influence of birth date via body mass on
850 individual fitness in a long-lived mammal. *Ecology*, *96*(6), 1516–1528.
851 <https://doi.org/10.1890/14-0106.1>

852 Post, E., & Forchhammer, M. C. (2007). Climate change reduces reproductive success of an
853 Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society*
854 *B: Biological Sciences*, 363(1501), 2367–2373. <https://doi.org/10.1098/rstb.2007.2207>

855 R Core Team. (2023). *R: A language and environment for statistical computing*. R
856 Foundation for Statistical Computing. <https://www.R-project.org/>

857 Richard, J. H., Wilmshurst, J., & Côté, S. D. (2014). The effect of snow on space use of an
858 alpine ungulate: Recently fallen snow tells more than cumulative snow depth. *Canadian*
859 *Journal of Zoology*, 92(12), 1067-1074. <https://doi.org/10.1139/cjz-2014-0118>

860 Richard, Q., Toïgo, C., Appolinaire, J., Loison, A., & Garel, M. (2017). From gestation to
861 weaning: Combining robust design and multi-event models unveils cost of lactation in a large
862 herbivore. *Journal of Animal Ecology*, 86(6), 1497–1509. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2656.12736)
863 [2656.12736](https://doi.org/10.1111/1365-2656.12736)

864 Rickbeil, G. J. M., Merkle, J. A., Anderson, G., Atwood, M. P., Beckmann, J. P., Cole, E. K.,
865 Courtemanch, A. B., Dewey, S., Gustine, D. D., Kauffman, M. J., McWhirter, D. E., Mong,
866 T., Proffitt, K., White, P. J., & Middleton, A. D. (2019). Plasticity in elk migration timing is a
867 response to changing environmental conditions. *Global Change Biology*, 25(7), 2368–2381.
868 <https://doi.org/10.1111/gcb.14629>

869 Ripley, B. (2023). tree: Classification and Regression Trees. *R Package Version 1.0-43*.
870 <https://cran.r-project.org/web/packages/tree/index.html>

871 Rivrud, I. M., Bischof, R., Meisingset, E. L., Zimmermann, B., Loe, L. E., & Mysterud, A.
872 (2016). Leave before it's too late: Anthropogenic and environmental triggers of autumn
873 migration in a hunted ungulate population. *Ecology*, 97(4), 1058–1068.
874 <https://doi.org/10.1890/15-1191.1>

875 Robin, M., Ferrari, G., Akgül, G., Münger, X., von Seth, J., Schuenemann, V. J., Dalén, L., &
876 Grossen, C. (2022). Ancient mitochondrial and modern whole genomes unravel massive
877 genetic diversity loss during near extinction of Alpine ibex. *Molecular Ecology*, *31*(13),
878 3548-3565. <https://doi.org/10.1111/mec.16503>

879 Rodgers, P. A., Sawyer, H., Mong, T. W., Stephens, S., & Kauffman, M. J. (2021).
880 Sex- specific migratory behaviors in a temperate ungulate. *Ecosphere*, *12*(3), e03424.
881 <https://doi.org/10.1002/ecs2.3424>

882 Sawyer, H., Merkle, J. A., Middleton, A. D., Dwinell, S. P. H., & Monteith, K. L. (2019).
883 Migratory plasticity is not ubiquitous among large herbivores. *Journal of Animal Ecology*,
884 *88*(3), 450-460. <https://doi.org/10.1111/1365-2656.12926>

885 Semenzato, P., Cagnacci, F., Ossi, F., Eccel, E., Morellet, N., Hewison, A. J. M., Sturaro, E.,
886 & Ramanzin, M. (2021). Behavioural heat-stress compensation in a cold-adapted ungulate:
887 Forage-mediated responses to warming Alpine summers. *Ecology Letters*, *24*(8), 1556-1568.
888 <https://doi.org/10.1111/ele.13750>

889 Short, H. (1963). Rumen Fermentations and Energy Relationships in White-Tailed Deer. *The*
890 *Journal of Wildlife Management*, *27*, 184–195. <https://doi.org/10.2307/3798397>

891 Signer, C., Ruf, T., & Arnold, W. (2011). Hypometabolism and basking: The strategies of
892 Alpine ibex to endure harsh over-wintering conditions. *Functional Ecology*, *25*(3), 537-547.
893 <https://doi.org/10.1111/j.1365-2435.2010.01806.x>

894 Sigrist, B., Signer, C., Wellig, S. D., Ozgul, A., Filli, F., Jenny, H., Thiel, D., Wirthner, S., &
895 Graf, R. F. (2022). Green-up selection by red deer in heterogeneous, human-dominated
896 landscapes of Central Europe. *Ecology and Evolution*, *12*(7), e9048.
897 <https://doi.org/10.1002/ece3.9048>

898 Spera, S. A., Spangler, K. R., Hubert, M. O., & Gorman, M. G. (2023). The effects of climate
899 change on the timing of peak fall foliage in Acadia National Park. *Landscape Ecology*, 38(9),
900 2339–2355. <https://doi.org/10.1007/s10980-023-01703-0>

901 Spitz, D. B., Hebblewhite, M., & Stephenson, T. R. (2017). ‘MigrateR’: Extending model-
902 driven methods for classifying and quantifying animal movement behavior. *Ecography*,
903 40(6), 788-799. <https://doi.org/10.1111/ecog.02587>

904 Stepanian, P. M., & Wainwright, C. E. (2018). Ongoing changes in migration phenology and
905 winter residency at Bracken Bat Cave. *Global Change Biology*, 24(7), 3266–3275.
906 <https://doi.org/10.1111/gcb.14051>

907 Toïgo, C., Gaillard, J.-M., Gauthier, D., Girard, I., Martinot, J.-P., & Michallet, J. (2002).
908 Female reproductive success and costs in an alpine capital breeder under contrasting
909 environments. *Écoscience*, 9(4), 427–433. <https://doi.org/10.1080/11956860.2002.11682730>

910 Van der Graaf, S., Stahl, J., Klimkowska, A., & Drent, J. P. B. (2006). Surfing on a green
911 wave—How plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*.
912 *Ardea -Wageningen-*, 94, 567–577.

913 van Moorter, B., Singh, N. J., Rolandsen, C. M., Solberg, E. J., Dettki, H., Pusenius, J.,
914 Månsson, J., Sand, H., Milner, J. M., Roer, O., Tallian, A., Neumann, W., Ericsson, G., &
915 Mysterud, A. (2021). Seasonal release from competition explains partial migration in
916 European moose. *Oikos*, 130(9), 1548-1561. <https://doi.org/10.1111/oik.07875>

917 van Toor, M. L., Kharitonov, S., Svazas, S., Dagys, M., Kleyheeg, E., Muskens, G., Ottosson,
918 U., Zydalis, R., & Waldenstrom, J. (2021). Migration distance affects how closely Eurasian
919 wigeons follow spring phenology during migration. *Movement Ecology*, 9(1), 1-12.
920 <https://doi.org/10.1186/s40462-021-00296-0>

921 Visser, M. E., Noordwijk, A. J. van, Tinbergen, J. M., & Lessells, C. M. (1998). Warmer
922 springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal*
923 *Society of London. Series B: Biological Sciences*, 265(1408), 1867–1870.
924 <https://doi.org/10.1098/rspb.1998.0514>

925 Vorkauf, M., Marty, C., Kahmen, A., & Hiltbrunner, E. (2021). Past and future snowmelt
926 trends in the Swiss Alps: The role of temperature and snowpack. *Climatic Change*, 165(3), 1–
927 19. <https://doi.org/10.1007/s10584-021-03027-x>

928 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin,
929 J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate
930 change. *Nature*, 416(6879), 389-395. <https://doi.org/10.1038/416389a>

931 Watson, A., & Staines, B. (1978). Differences in the quality of wintering areas used by male
932 and female Red deer (*Cervus elaphus*) in Aberdeenshire. *Journal of Zoology, London*, 186,
933 544–550.

934 Weller, F. G., Beatty, W. S., Webb, E. B., Kesler, D. C., Kremenz, D. G., Asante, K., &
935 Naylor, L. W. (2022). Environmental drivers of autumn migration departure decisions in
936 midcontinental mallards. *Movement Ecology*, 10(1), 1-13. [https://doi.org/10.1186/s40462-](https://doi.org/10.1186/s40462-021-00299-x)
937 [021-00299-x](https://doi.org/10.1186/s40462-021-00299-x)

938 White, K. S., Gregovich, D. P., & Levi, T. (2018). Projecting the future of an alpine ungulate
939 under climate change scenarios. *Global Change Biology*, 24(3), 1136–1149.
940 <https://doi.org/10.1111/gcb.13919>

941 Wijk, R. E. van, Kölzsch, A., Kruckenberg, H., Ebbinge, B. S., Müskens, G. J. D. M., &
942 Nolet, B. A. (2012). Individually tracked geese follow peaks of temperature acceleration

943 during spring migration. *Oikos*, *121*(5), 655-664. <https://doi.org/10.1111/j.1600->
944 [0706.2011.20083.x](https://doi.org/10.1111/j.1600-0706.2011.20083.x)

945 Willisch, C. S., Biebach, I., Koller, U., Bucher, T., Marreros, N., Ryser-Degiorgis, M.-P.,
946 Keller, L. F., & Neuhaus, P. (2012). Male reproductive pattern in a polygynous ungulate with
947 a slow life-history: The role of age, social status and alternative mating tactics. *Evolutionary*
948 *Ecology*, *26*(1), 187–206. <https://doi.org/10.1007/s10682-011-9486-6>

949 Wu, C., Peng, J., Ciais, P., Peñuelas, J., Wang, H., Beguería, S., Andrew Black, T., Jassal, R.
950 S., Zhang, X., Yuan, W., Liang, E., Wang, X., Hua, H., Liu, R., Ju, W., Fu, Y. H., & Ge, Q.
951 (2022). Increased drought effects on the phenology of autumn leaf senescence. *Nature*
952 *Climate Change*, *12*(10), 943-949. <https://doi.org/10.1038/s41558-022-01464-9>

953 Xu, F., & Si, Y. (2019). The frost wave hypothesis: How the environment drives autumn
954 departure of migratory waterfowl. *Ecological Indicators*, *101*, 1018–1025.
955 <https://doi.org/10.1016/j.ecolind.2019.02.024>

956 Xu, W., Barker, K., Shawler, A., Van Scoyoc, A., Smith, J. A., Mueller, T., Sawyer, H.,
957 Andreozzi, C., Bidder, O. R., Karandikar, H., Mumme, S., Templin, E., & Middleton, A. D.
958 (2021). The plasticity of ungulate migration in a changing world. *Ecology*, *102*(4), e03293.
959 <https://doi.org/10.1002/ecy.3293>

960 Yang, B., He, M., Shishov, V., Tychkov, I., Vaganov, E., Rossi, S., Ljungqvist, F. C.,
961 Bräuning, A., & Griebinger, J. (2017). New perspective on spring vegetation phenology and
962 global climate change based on Tibetan Plateau tree-ring data. *Proceedings of the National*
963 *Academy of Sciences*, *114*(27), 6966–6971. <https://doi.org/10.1073/pnas.1616608114>

964 Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid

965 common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14.

966 <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

967

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 |
|---------------|--|-----------------------------|---|---|
| Spring | 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 |
| Autumn | 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 |

972

973

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 | $\Delta AICc$ |
|--------|---|----|-----------------|--------|---------------|
| Spring | 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 | SenescenceL + snowfall | 6 | -1114.1 | 2240.6 | 0 |
| | SenescenceL + snowfall + tempS | 7 | -1113.6 | 2241.7 | 1.1 |
| | SenescenceL + snowfall + peakSe | 7 | -1113.9 | 2242.4 | 1.7 |
| | SenescenceL + snowfall + distance | 7 | -1114.0 | 2242.5 | 1.9 |
| | Null model | 4 | -1127.0 | 2262.3 | 21.7 |

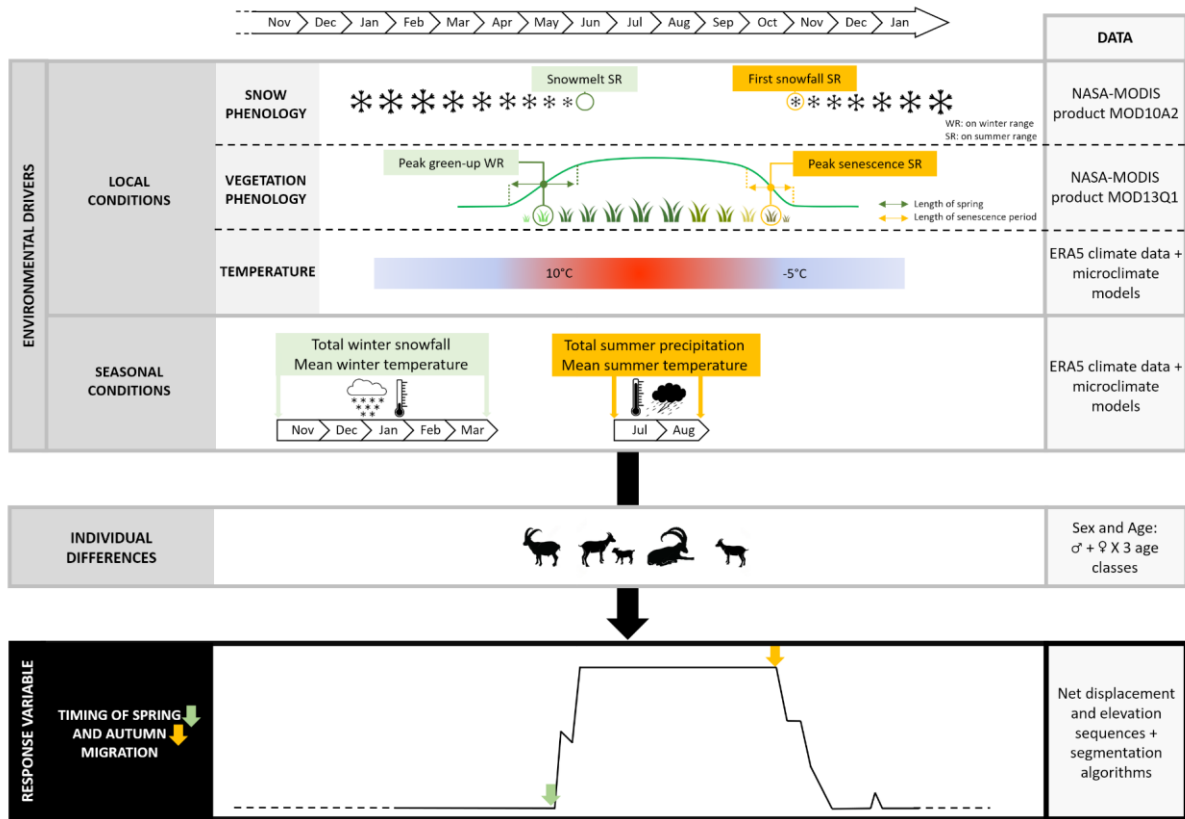
984

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 |
|---------------|----------------|----------------------------|----------|
| 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 |
| | Snowfall | 0.38 [0.18;0.57] | <0.001 |

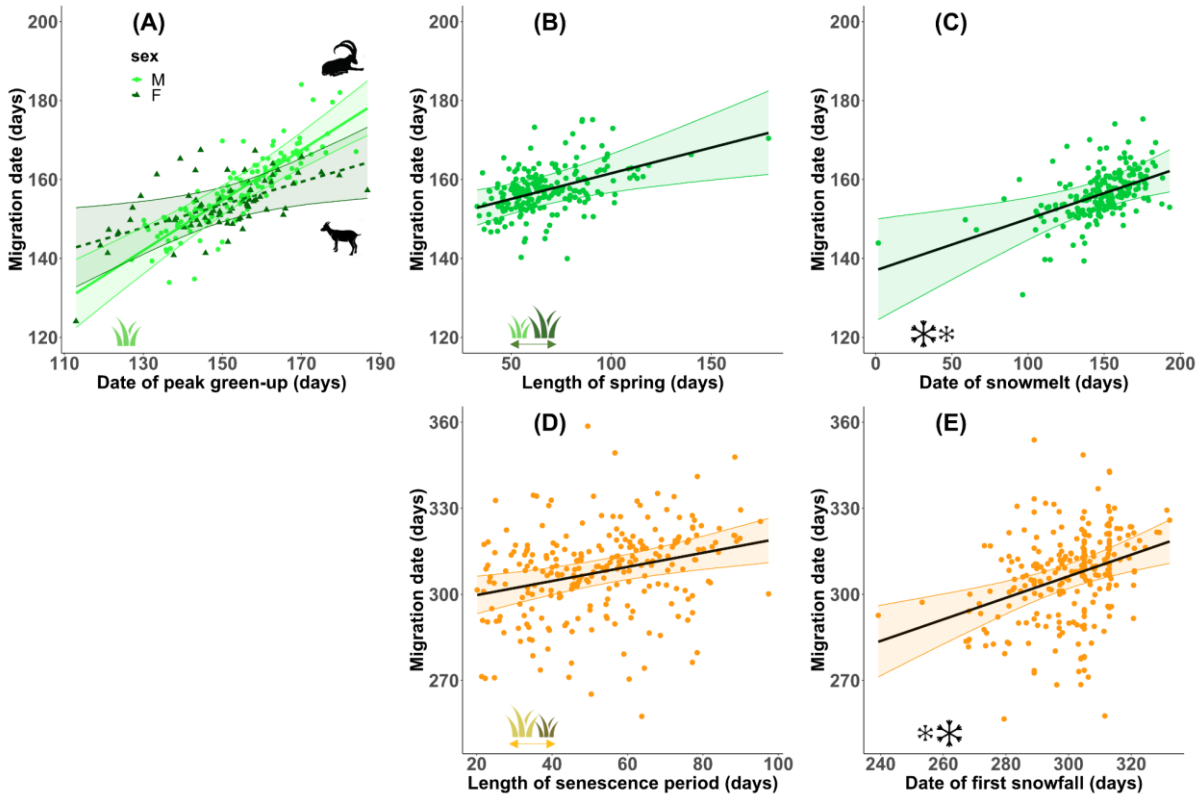
991

992 **FIGURES**



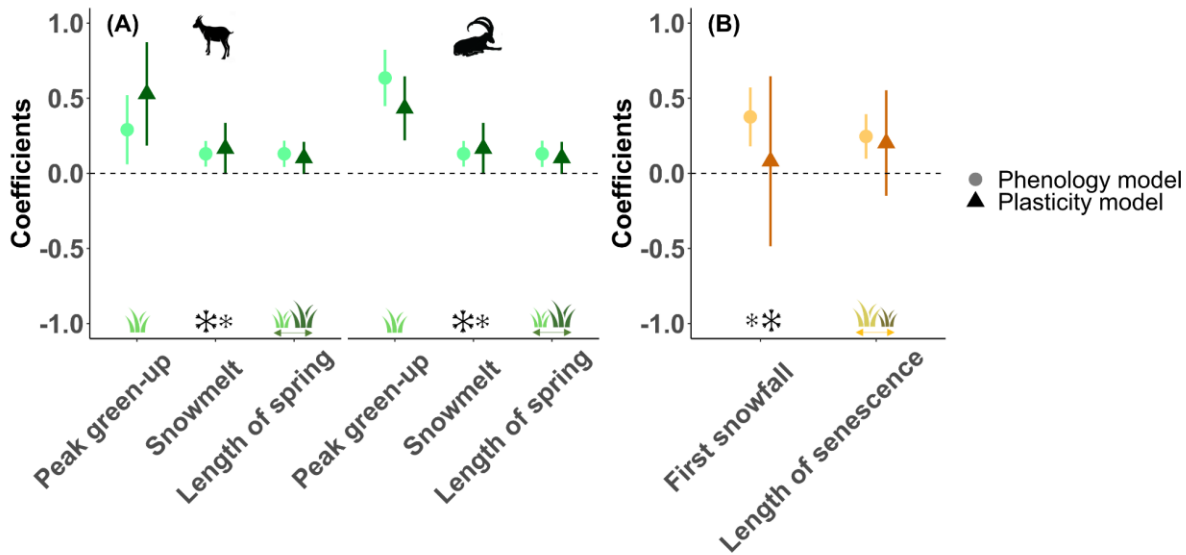
993

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 Δ 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.