

## SUPPORTING INFORMATION

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

#### Appendix S1: Details on monitoring of ibex populations

TABLE S1: Names and periods of monitoring of ibex populations used in the study

Country	Short population name	Population ID and Name in Brambilla et al., 2020	Monitoring period	Number of ibex (year-individuals)	Entity/research group in charge of monitoring
Austria	HTNP	AUSA02 Hohe-Tauern	2006-2008; 2010-2011; 2017-2018	8	Hohe Tauern National Park
	Alberg	AUVO03 AUVO05 Kleinwalsertal-Klostertal Alberg Valluga	2007-2010	7	BOKU Alfred Frey-Roos
France	Bargy	FRV08 Bargy	2013-2020	128	Office Français de la Biodiversité
	Belle	FRV12 Belledonne	2017-2020	84	Office Français de la Biodiversité
	Champy	FRV06 Champagny-Peisey	2018-2020	11	Vanoise National Park

	Maur	FRV01 Maurienne	2018-2020	13	Vanoise National Park
	CBMB	FRV09 Contamines - Beaufortain - Mont-Blanc	2018-2020	20	Asters-CEN Haute Savoie
	Ois	FRV15 Valbonnais- Oisans	2013-2020	22	Ecrins National Park
	Champs	FRU03 Vieux- Chaillol-Sirac	2013-2020	52	Ecrins National Park
	Cerc	FRU02 Cerces- Galibier	2015-2020	27	Ecrins National Park
France - Italy	APAM	FRU10 FRU01 ITCN01 Nord-ouest Mercantour Est Mercantour Alpi Marittime	2018-2020	59	Mercantour NP - Ente di gestione Aree Protette Alpi Marittime

	SPBGP	FRV14 FRV05 ITTO05 Sassière-Prariond Bonneval-sur-Arc PNGP-Valle dell'Orco	2003-2004	14	Vanoise National Park
Italy	Marm	ITTN04 Monzoni-Marmolada	2010-2018	18	Fondazione Edmund Mach – University of Padova - Francesca Cagnacci, Paola Semenzato, Maurizio Ramanzin
	Sesv	ITBZ03 CHGR05 Sesvenna Macun-Terza-Sesvenna	2018-2020	3	Fondazione Edmund Mach – Francesca Cagnacci, Paola Semenzato
	GPNP	ITAO02 Gran Paradiso	2013-2017	32	Gran Paradiso National Park
	Orser	ITTO08 Orseria - Rocciaivre	2018-2019	15	Ente di gestione Aree Protette Alpi Cozie

Switzerland	SNP	CHGR02 Albris	2007-2019	44	Swiss National Park
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Appendix S2: Number of migrants identified per year and population

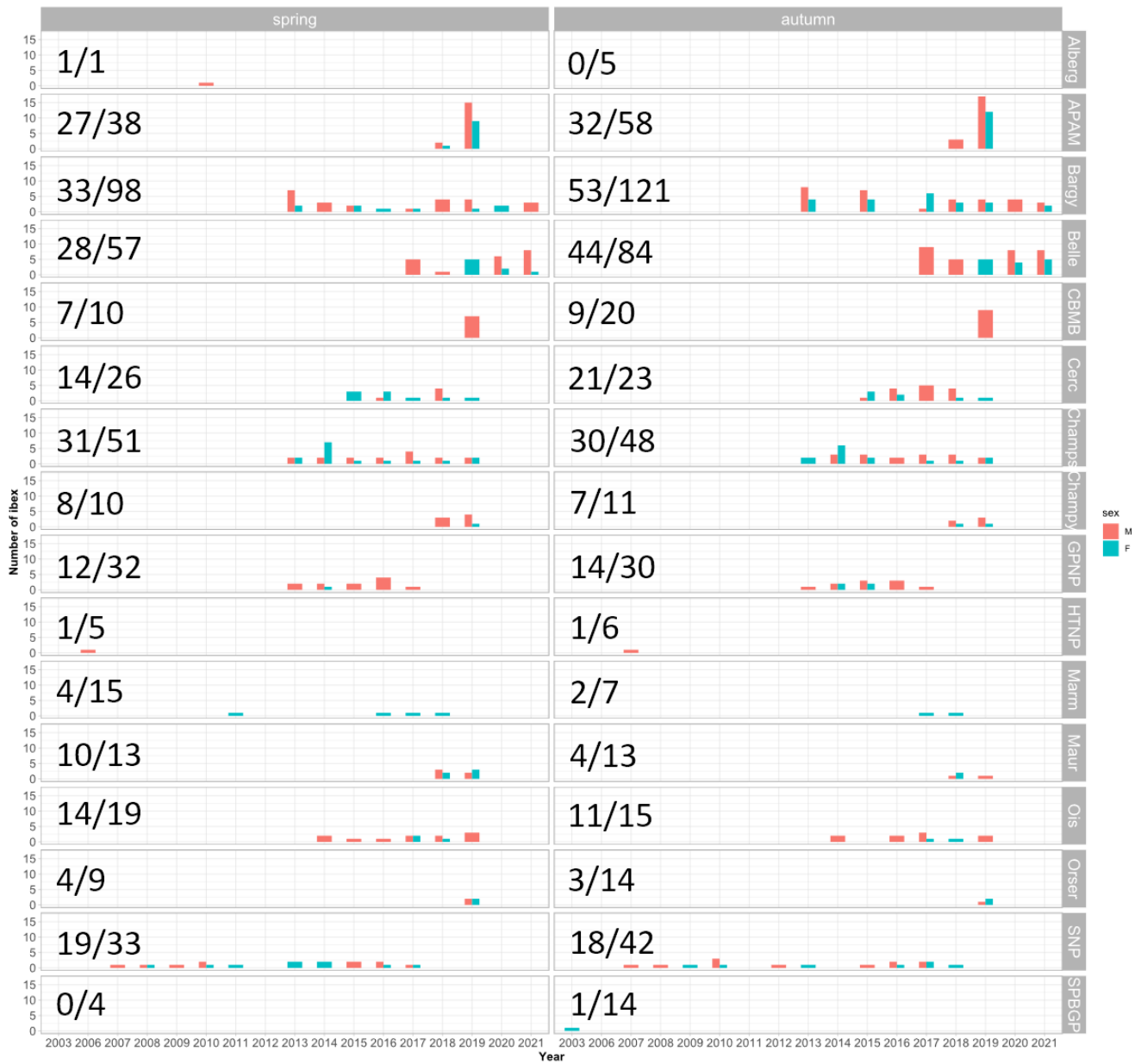


FIGURE S1: Numbers of migrants each year and in each population for spring and autumn seasons. Sex of individuals is displayed in red for males and blue for females.

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

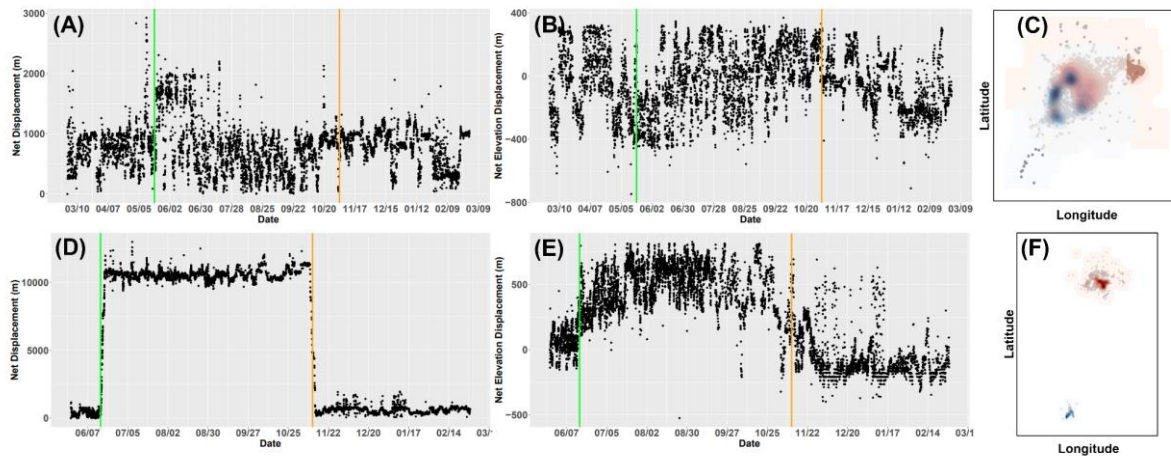


FIGURE S2: Two examples of the metrics derived from ibex GPS data sets to classify seasonal tracks as residency (A, B, C) and migration (D, E, F). The definition was based on a procedure involving two segmentation algorithms to identify common breakpoints (representing potential migration dates, green and orange vertical lines) in Net Displacement (A, D) and Net Elevation Displacement time series (B, E). When the overlap in volume between winter (blue areas) and summer (red areas) utilization distributions was  $>$  or  $< 0.2$ , seasonal tracks were classified as residency (C; overlap = 0.46 here) or migration (F; overlap = 0), respectively. In this latter case, the breakpoint previously identified was considered as the migration date.

#### Appendix S4: Effect of temperature on spring migration timing

In the core of the manuscript, we did not reveal any evidence that the avoidance of thermal stress (i.e., the date when a temperature of 10°C [that generally occurred around migration period] was predicted by microclimate models at the centroid of the population) triggered ibex spring migration to higher altitudes (Table 2). However, because temperature has been repeatedly related to spring elevational movements and more generally the behavior of ibex (Aublet et al., 2009; Mason et al., 2017; Herfindal et al., 2019; Semenzato et al., 2021), we conducted further analyses to better understand those contrasted results. We first investigated whether temperature at the GPS location of animals (available for a limited sample of individuals/populations) could be more informative than the temperature predicted by microclimate models at the centroid of the population (used in the core of the manuscript). We used temperature data collected by GPS collars to investigate the variation in the temperature smoothed over the 4 day period including the 3 days before migration and the day of migration, focusing on the Bargy and Belledonne populations - the two populations for which GPS-collar temperatures were readily available. Second, as ibex might simply not respond to a particular temperature threshold but to relative changes in spring temperatures, we investigated whether the relative changes in temperatures over consecutive days could better explain migration timing than absolute temperature. We calculated the average change in daily temperatures over the 4 day period including the 3 days before migration and the day of migration either (i) using the temperature predicted at the centroid of each population (see Methods, section 3.2) *Seasonal environmental drivers*) or (ii) the temperatures recorded by GPS collars. If ibex timed migration to positive changes in spring temperatures, we expected the distribution of those values to be biased toward positive changes. To compare the results with a null model, we also sampled random migration dates within the distribution of

identified migration dates, for a population and given year, and extracted the average change in daily temperatures during the 4 days preceding these random dates.

Interestingly, the average temperature on the day of spring migration varied largely between years within a population, and could double from a year to another (see Figure S3).

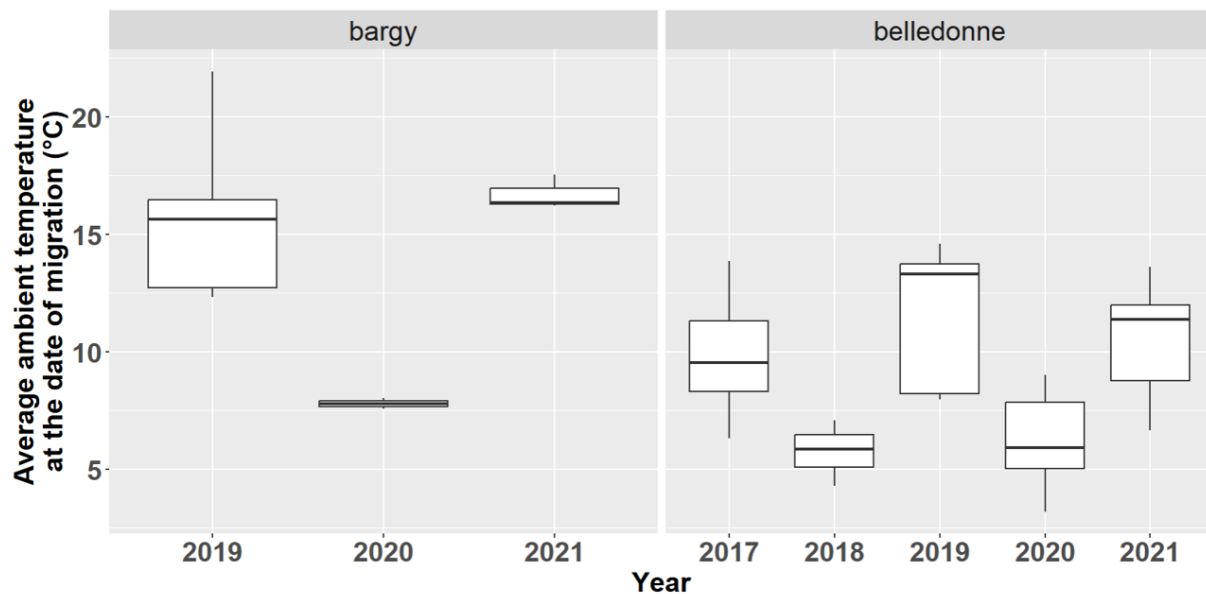


FIGURE S3: Average daily temperature means (smoothed values over 4 days around spring migration dates, i.e. 3 days before + day of migration) the day of spring migration each year of monitoring in Bargy and Belledonne populations. Temperature data were recorded by sensors embedded in the GPS collars of animals. Please note that, in addition to the temperature in each population distribution, the GPS models (and hence the temperature sensors) differed between the two populations, so that a comparison between populations would be biased.

Based on microclimate temperature data calculated at the centroid of the two populations we can observe that migratory events tended to occur more often following a relative increase in temperature over the days preceding migrations, although the difference between both



conditions was, on average, low ( $0.28^{\circ}\text{C}$  [0.07;0.48]95%; Figure S4). When using ambient temperature recorded by GPS collars, the difference was negative but not significant (average difference of  $-0.06^{\circ}\text{C}$  [-0.37;0.27]95%).

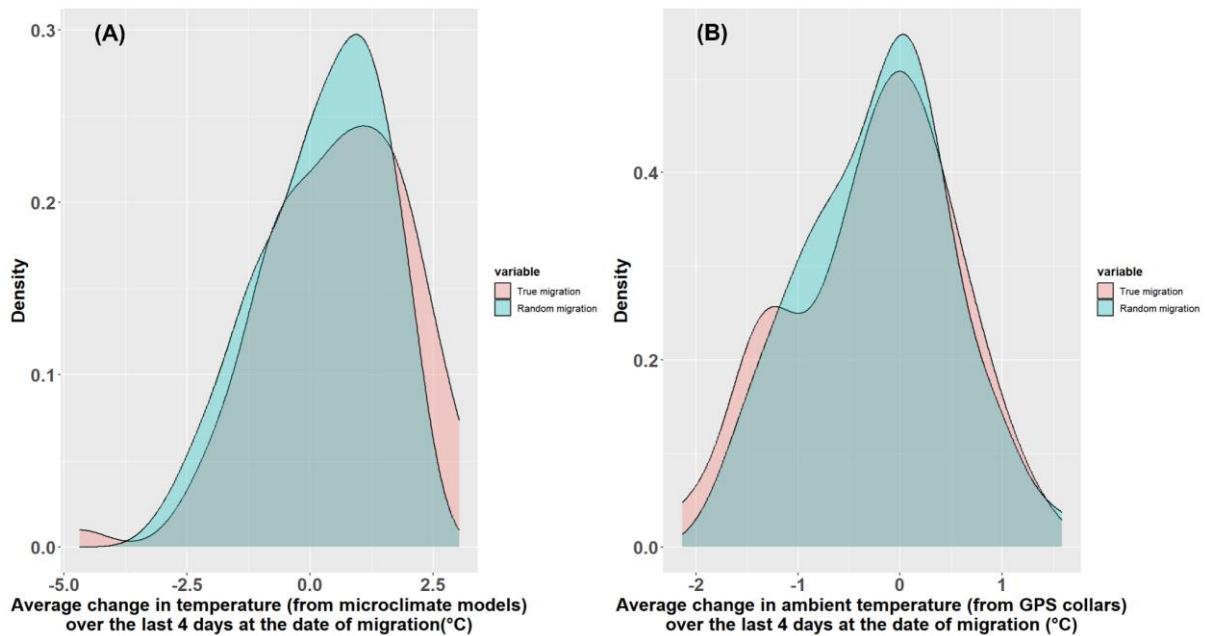


FIGURE S4: Distributions of the average relative changes in daily temperatures over the four days preceding observed migrations (red) and random migrations (blue). The red and blue distributions were significantly different only in the first case (A=temperature data calculated with microclimate models, B=temperature data recorded by GPS collars). The mean of the red distribution is  $0.48[0.28; 0.68]$  in A and  $-0.26[-0.51; -0.01]$  in B. The mean of the blue distribution is  $0.23[0.08; 0.38]$  and  $0.21[0.05; 0.39]$  in B.

Overall, there was no clear indication that temperature, i.e. neither absolute values nor relative changes from day to day, was an important parameter triggering spring migration directly, and its effect may most likely rely indirectly on cascading consequences on vegetation phenology, as we showed in the core of the manuscript (Figure 2A).

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

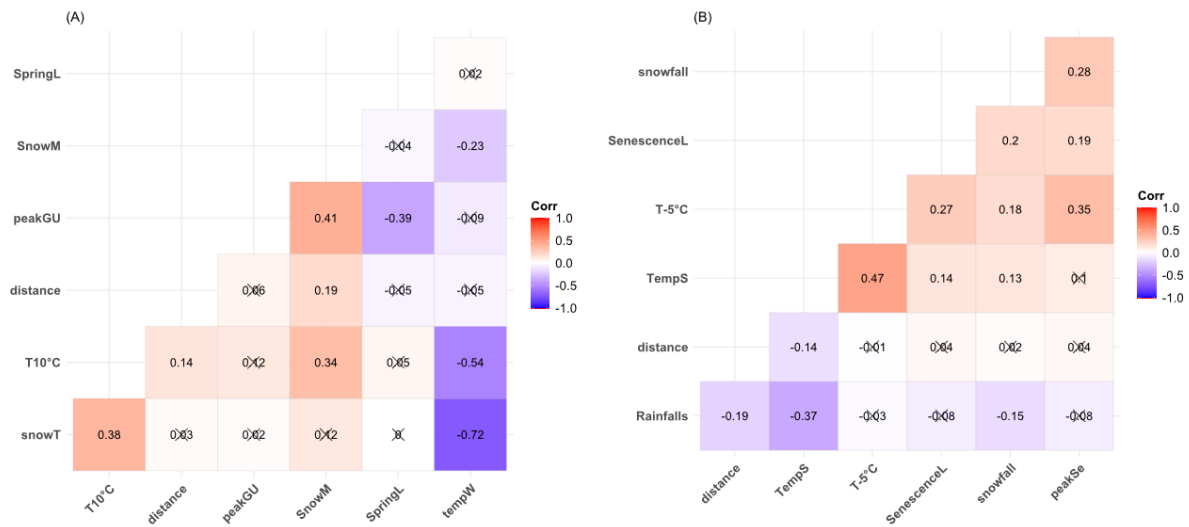


FIGURE S5: Correlation between environmental variables for models investigating Alpine ibex *Capra ibex* migration timing in spring (A) and autumn (B). Non-significant correlations are marked with a cross. peakGU = date of peak green-up on ibex winter range, SnowM = date of snowmelt on summer range, SpringL = length of spring season on ibex summer range, distance = Euclidean distance between winter and summer ranges of ibex, T10°C = date of 10°C mean daily temperature, snowT = Total snow precipitation during winter, TempW = mean winter temperature during winter. Snowfall = date of first snowfall on summer range, peakSe = date of peak of vegetation senescence on ibex summer range, SenescenceL = length of senescence period on ibex summer range, T-5°C = date of -5°C mean daily temperature, Rainfalls = total rainfall precipitation during summer, TempS = mean temperature during summer, distance = Euclidean distance between summer and winter ranges of ibex.

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

Data used in our study came from ibex monitored in different populations using a large area (i.e., the whole alpine arc) and during different years (2003-2022) with contrasted weather conditions (e.g., temperature, precipitation), and hence variable vegetation and snow phenologies between years and populations. Therefore, the global responses we observed combined both individual responses to inter-annual variation in environmental conditions within populations and spatial variation in responses between populations (due to local adaptations to population-specific environmental conditions; Van De Pol & Wright, 2009). Importantly, highlighting global responses to variation in environmental conditions may not preclude the absence of responses to inter-annual variation within populations if global responses mostly reflect population-specific responses to local environmental conditions (see Plard et al., 2013; Pelaez et al., 2020; Hagen et al., 2021 for an example on the phenology of parturition in roe deer). Although the existence of individual plasticity in migration timing (Figure 3) already suggested intra-population responses occurred, and despite limited sample size for some populations (justifying why we chose to present the following results in an appendix rather than in the core of the manuscript), we went further into inter-annual and inter-populations differences in environmental conditions. We also investigated the relative contributions of responses to temporal variation within populations and of responses to spatial variation between populations in the global response we previously reported.

### **Methods**

First, we investigated the differences in the range of environmental covariates between populations and between years within populations. Second, we visually compared the response to peak green-up (i.e. the most important driver of ibex spring migration) we

previously reported and the population-specific responses computed using linear regressions for each population, and for each population and sex, as the global response was sex-specific. Third, we followed the approach proposed by Van De Pol & Wright (2009) to disentangle responses to temporal variation within populations from responses to spatial variation between populations. We performed within-population centering for each environmental covariate by subtracting population means from each individual value, to eliminate any between-population variation and get a new predictor reflecting within-population component only. By contrast, population means for each covariate reflected the between-population component only. We replaced raw values of environmental conditions by those two new predictors in the models investigating variation in migration timing with environmental and individual characteristics, and performed the same model selection procedure as reported in the core of the manuscript (see ‘Statistical analyses’ in Material & Methods).

## **Results**

The ranges of environmental conditions generally overlapped between most populations, suggesting low inter-population differences in conditions encountered (Figures S6 & S7). By contrast, the inter-annual variation in environmental conditions within populations was very high, so that most populations could face similar environmental conditions over time despite important distances between them (Figure S8, see also ranges of values on x axis Figure S9).

Population-specific representations of responses to peak green-up confirmed the delayed migration timing with increasing date of peak green-up in most populations (positive relationships in 13/15 populations; Figure S10), with response magnitude similar to the global response we previously reported. When separating both sexes, we obtained similar results for males, but not for females for which low sample size may be limiting (n=73 from 12

populations; Figure S11) but is in accordance with the lower response to peak green-up shown in the core manuscript.

When disentangling within- and between population components of the responses to environmental conditions in spring, the best model included the within-population component of the date of peak of green-up (Figure S12 & Figure S9). The effect of the within-population variation of the date of peak of green-up on the timing of migration was more pronounced in males compared to females, in accordance with our previous results.

The between-population component of the date of peak of green-up also affected the timing of spring migration date in males but not in females. Thus, as we could expect, males migrated later in populations with a later peak of green-up but they also adjusted their migration timing depending on the inter-annual variations in the date of peak of green-up. This result was also consistent with our analyses on plasticity showing the extent to which individuals responded to inter-annual variations in the date of peak of green-up. On the other hand, female migration timing was not affected by average conditions experienced in their population, but they could adjust their timing between years, though to a lesser extent than males. This absence of effect could be due to a smaller sample size for females ( $n=76$  vs  $n=137$  for males) resulting in poor estimations of average conditions experienced by females in their population, particularly if females were monitored for only 1 year, and increasing the risk of selecting populations with overlapping environmental conditions.

Ibex migrated later in populations with an overall longer length of spring season, but they also migrated later during years with a longer spring. Interestingly, ibex adjusted their date of migration depending on the date of snowmelt on their summer range, but this was not a factor explaining differences of timing between populations. Again, probably because the ranges of date of snowmelt among populations were highly overlapping (Figure S6).

In autumn, ibex adjusted their migration timing depending on the date of first snowfall (effect of the within-population variation component), but this was not a driver explaining differences among populations (Figure S12). Ibex also migrated later during years with a longer period of vegetation senescence (Figure S9). However, in autumn, we detected that the average date of peak of senescence in the population explained differences in the timing of migration among populations.

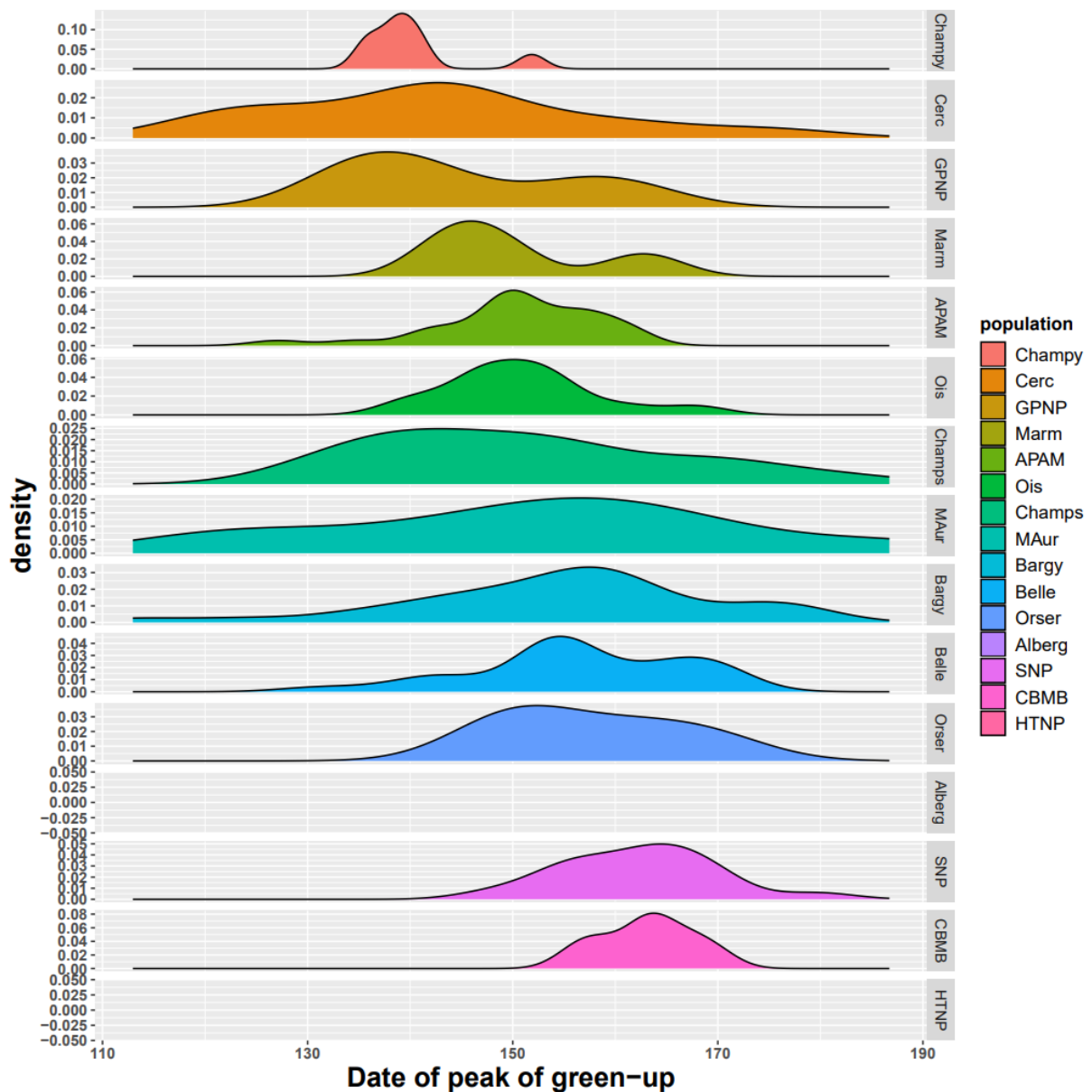
Overall, factors having a between-population effect were factors for which the range differed more between populations. This was the case for the date of peak green-up in spring or the date of peak of vegetation senescence in autumn. Detecting a between-population effect of certain covariates might be difficult, for instance, since most of our data comes from French populations, the date of first snowfall is likely similar between those populations, constraining a detection of a between-population effect. Furthermore, as some populations were monitored for only one year, the average conditions calculated over this period very likely do not represent average conditions in the population area.

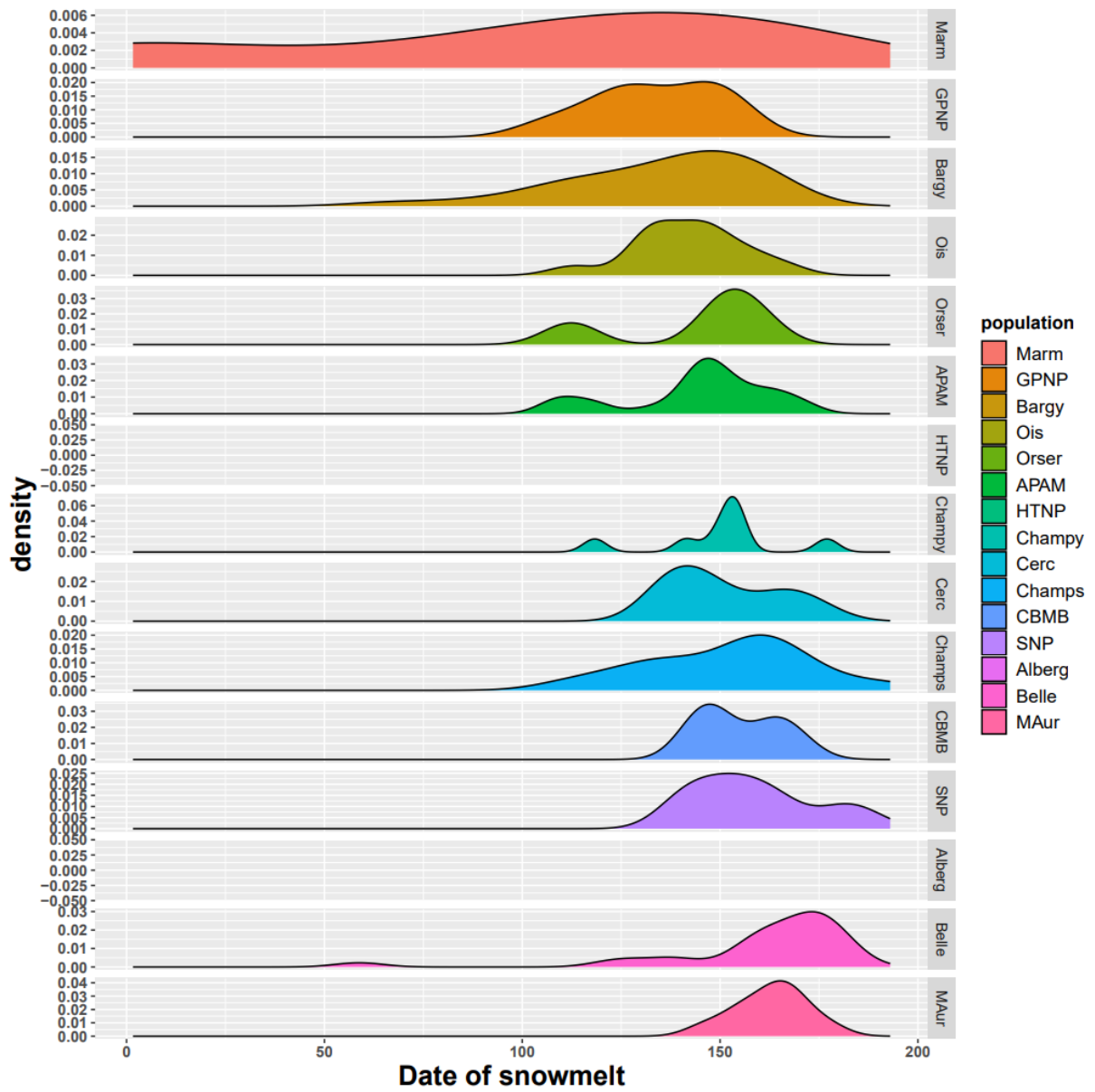
## **Conclusion**

In conclusion, this type of analysis is probably more pertinent when there are larger differences in the range of covariates between populations. Here the temporal variation in covariates was high within populations. This resulted in large overlaps in the ranges of covariates for most populations which prevents detecting inter-population differences.

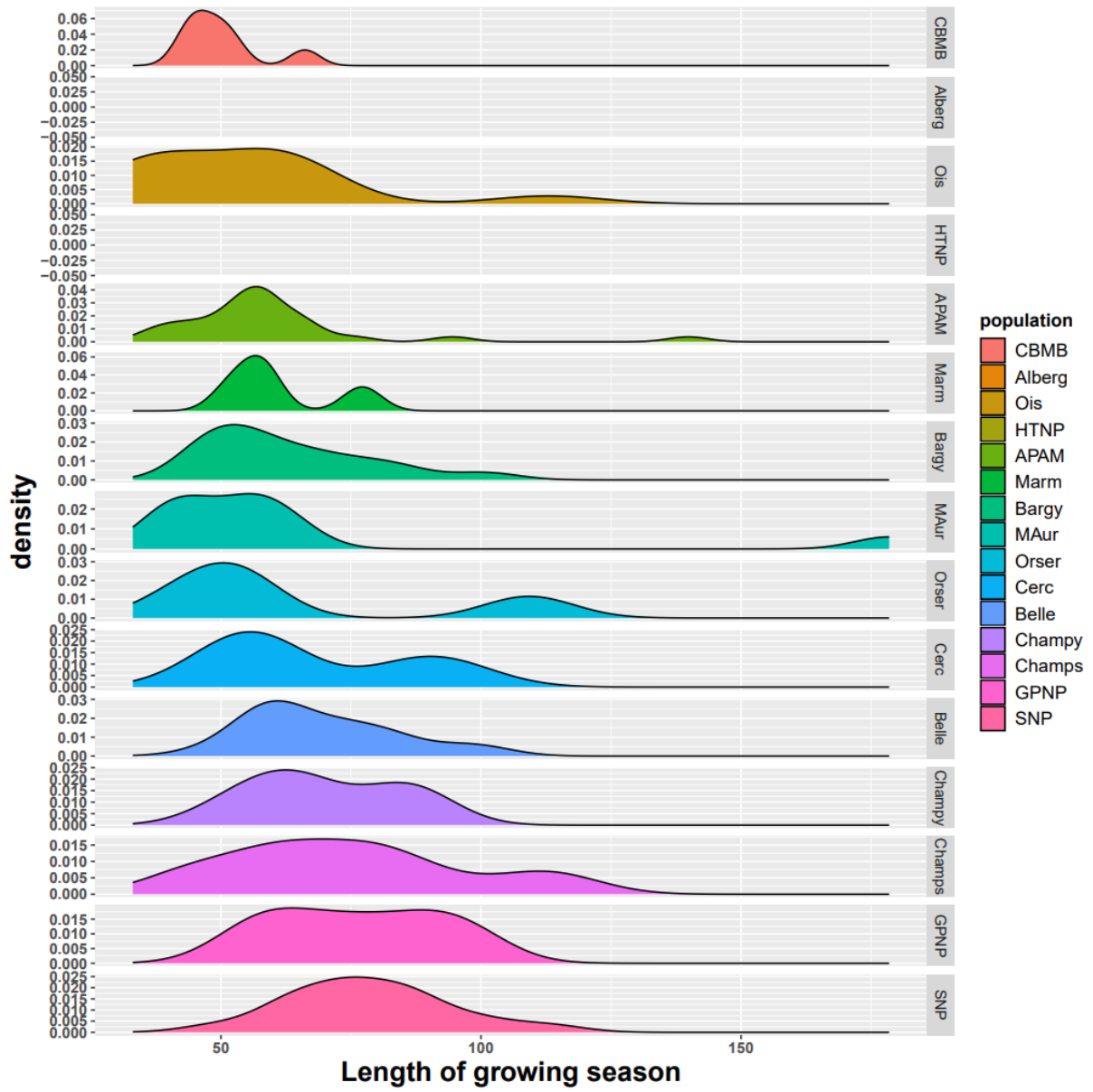
This further analysis confirmed our previous results. The within-population effects assessed here are similar to the relations we previously showed. This is indeed the temporal variation in environmental conditions that affected the timing of migration and not just the average conditions between populations that differed. Although between-population differences in the timing of vegetation phenology also affected the timing of migration, those differences are

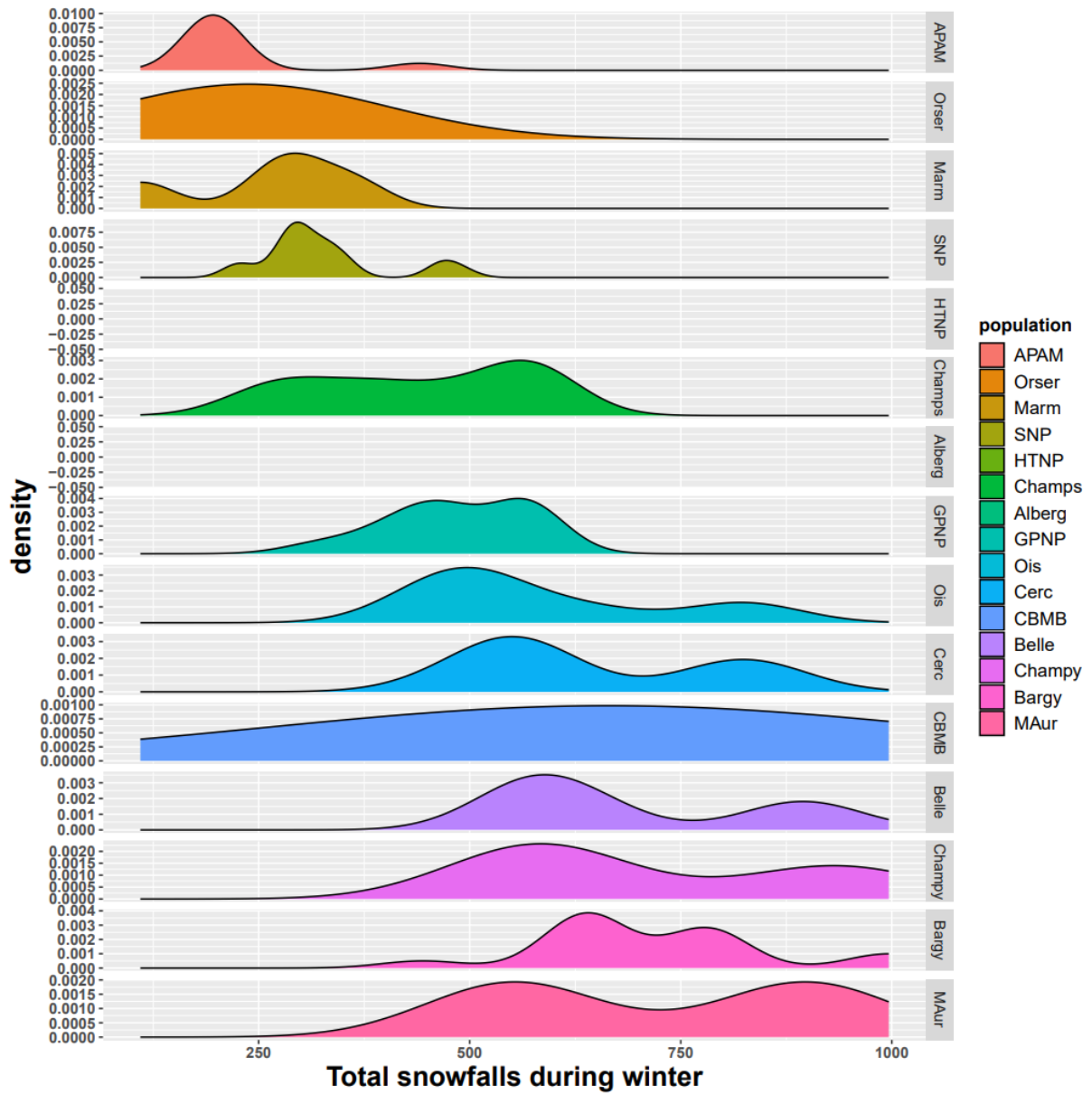
likely not related to local adaptation since almost all ibex populations were reintroduced during the last century. Moreover, analyses in the core manuscript showed that 1) ibex migration timing is affected by different environmental factors in spring and autumn (based on our phenology models) and we also showed 2) that individuals adjusted their migration timing between years, based on inter-annual variation in these environmental factors. So, we can firmly conclude that animals displayed behavioral plasticity.

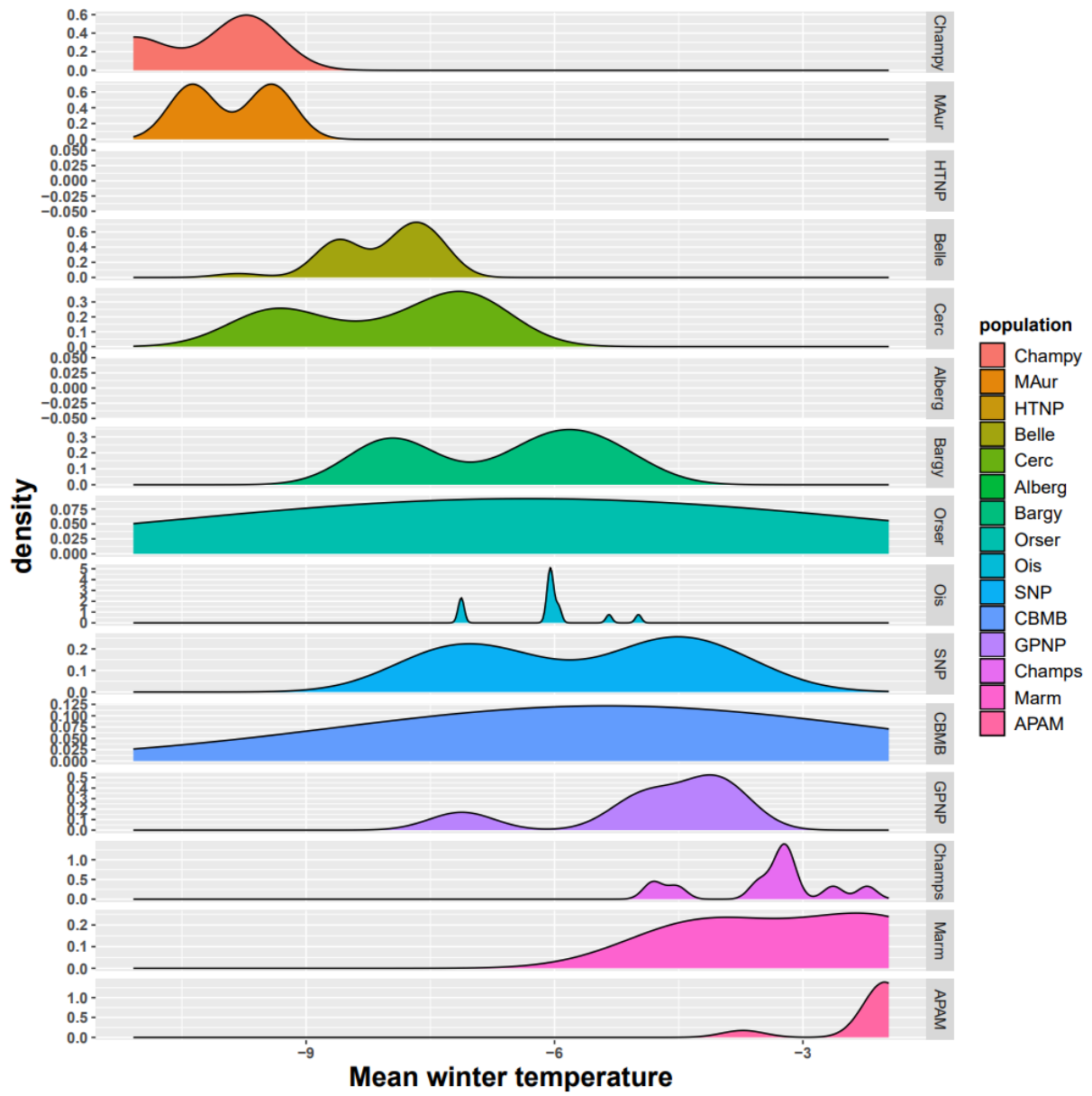


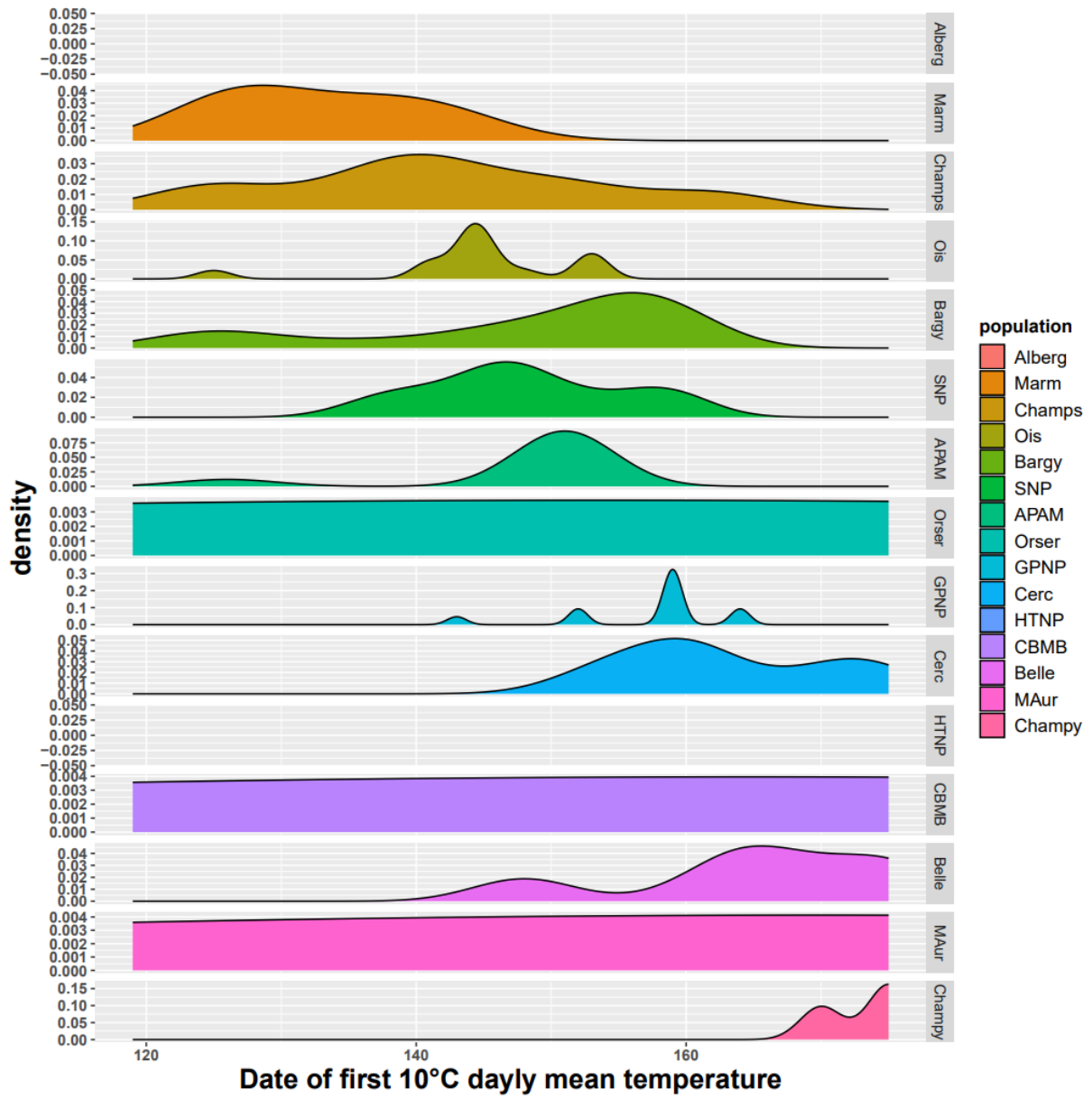












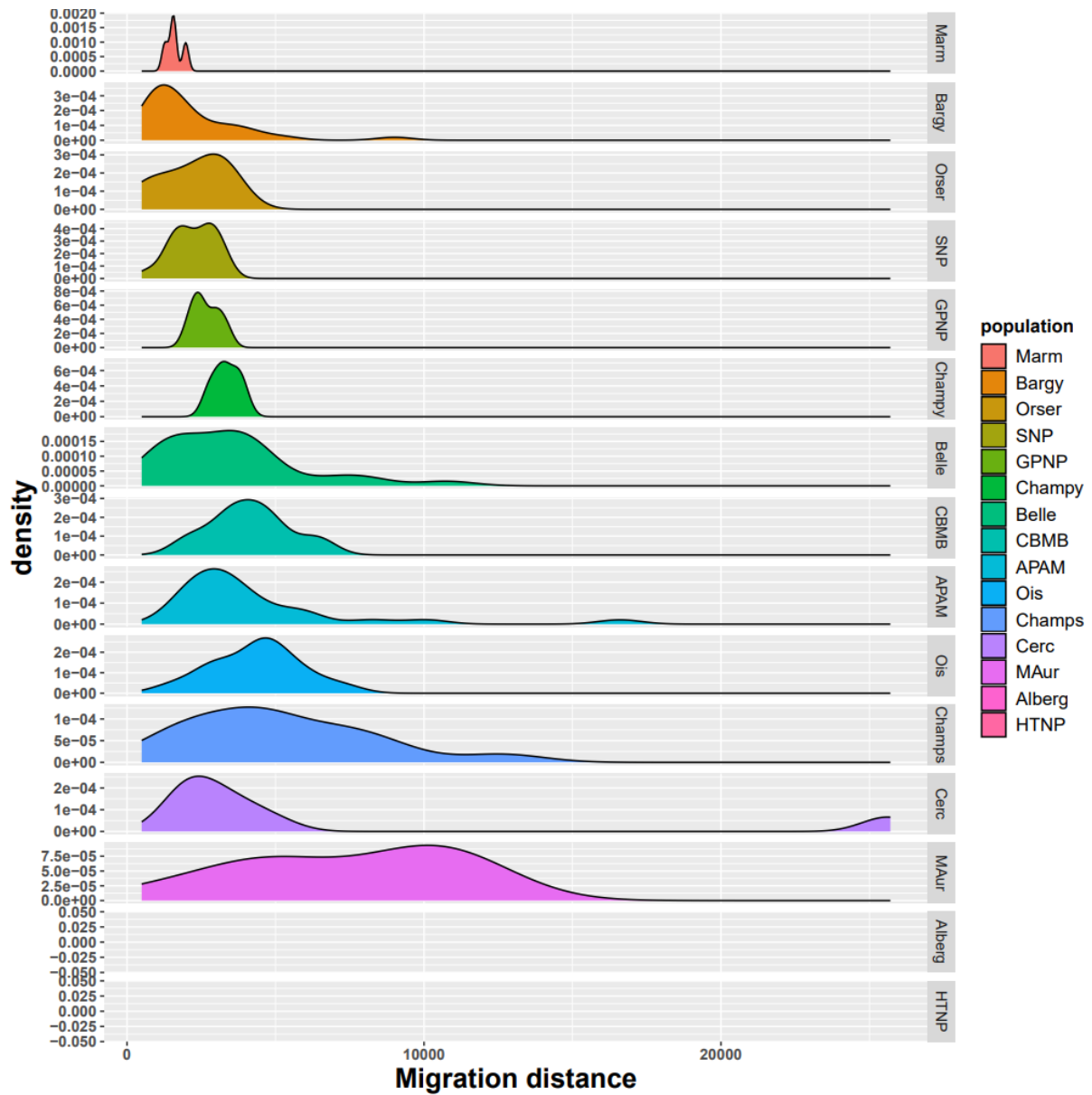
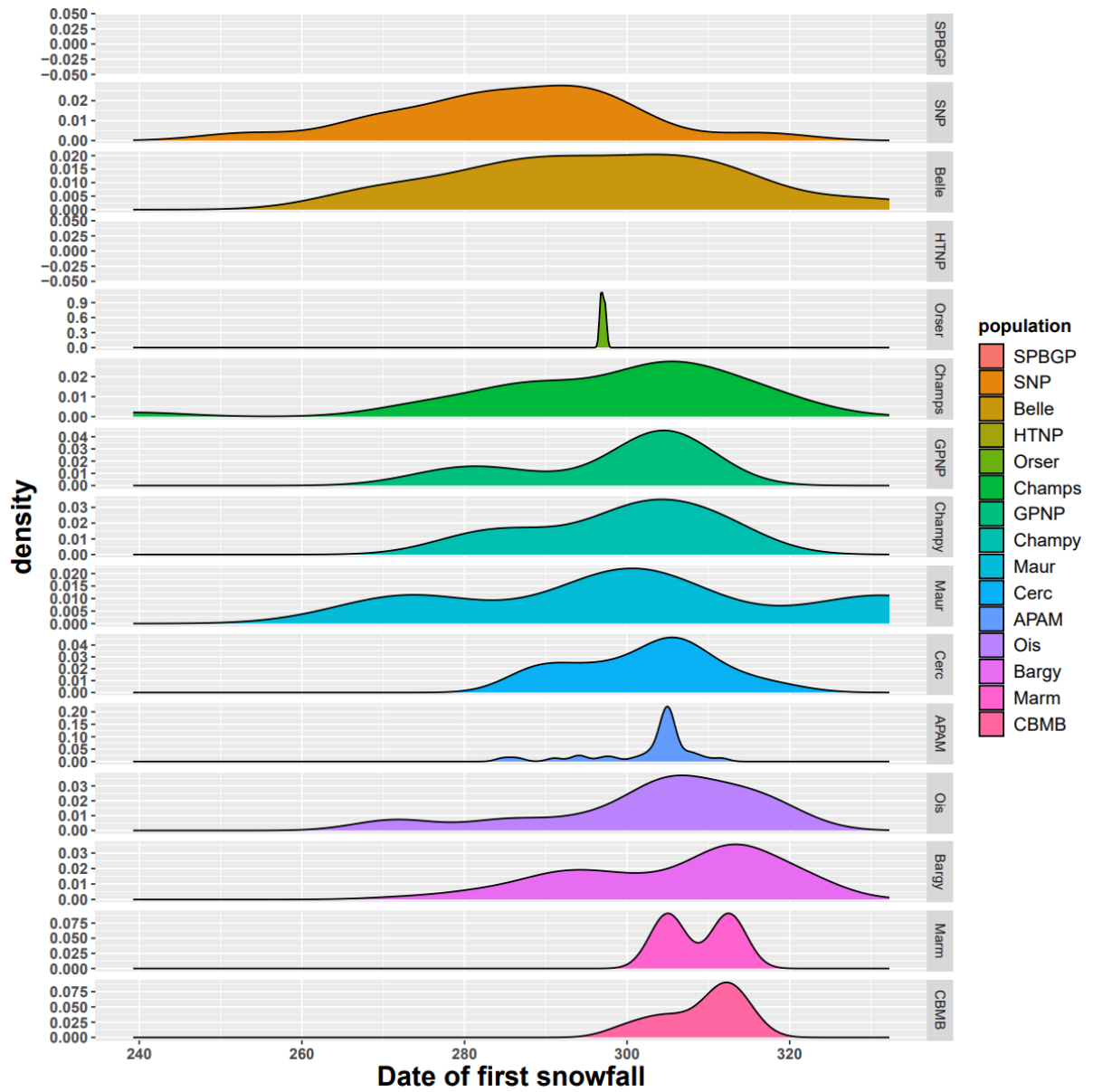
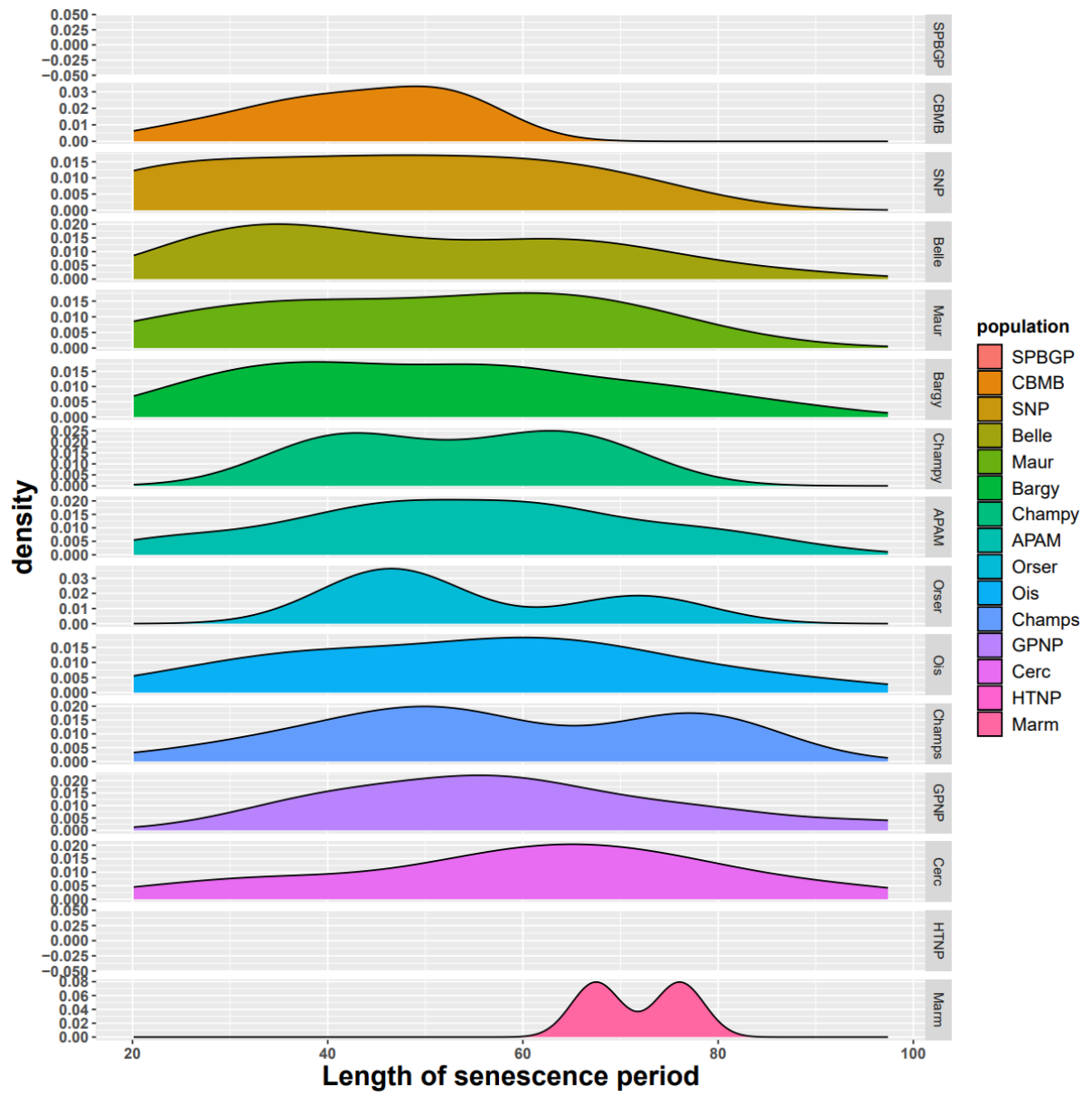
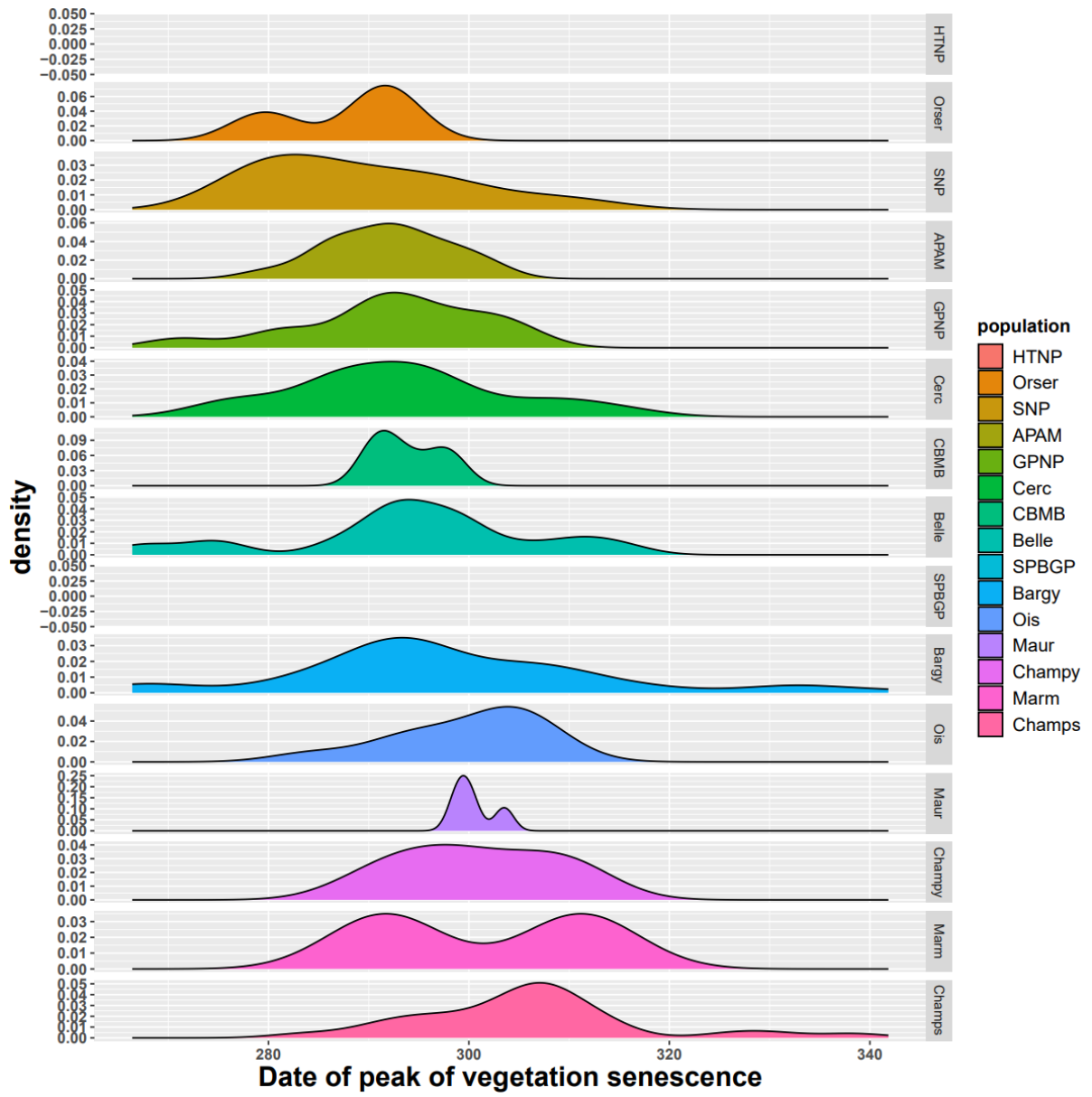


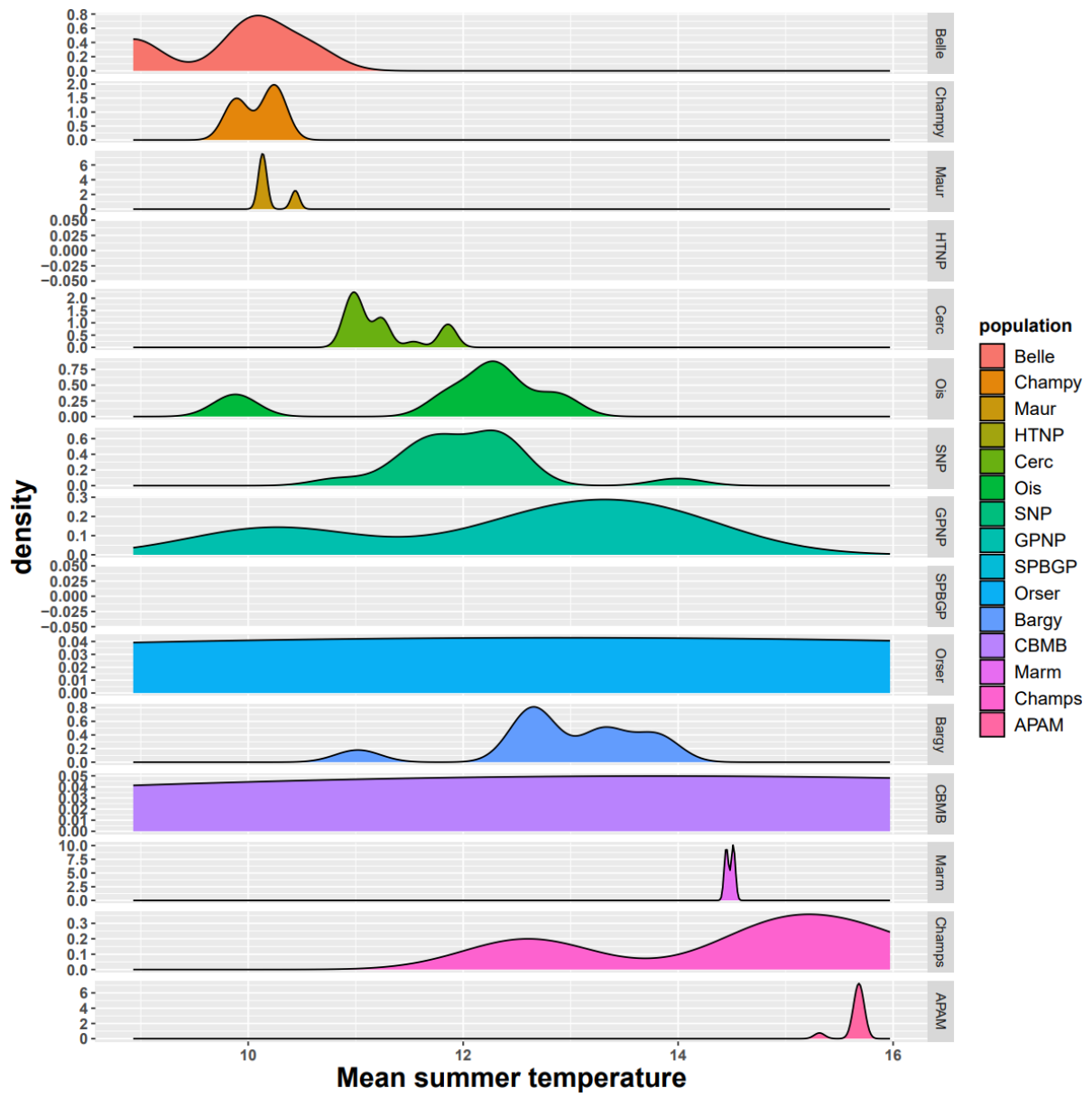
FIGURE S6: Range of measure of the different covariates in each population included in our initial model to test our hypothesis regarding the factors affecting the timing of spring migration in ibex.

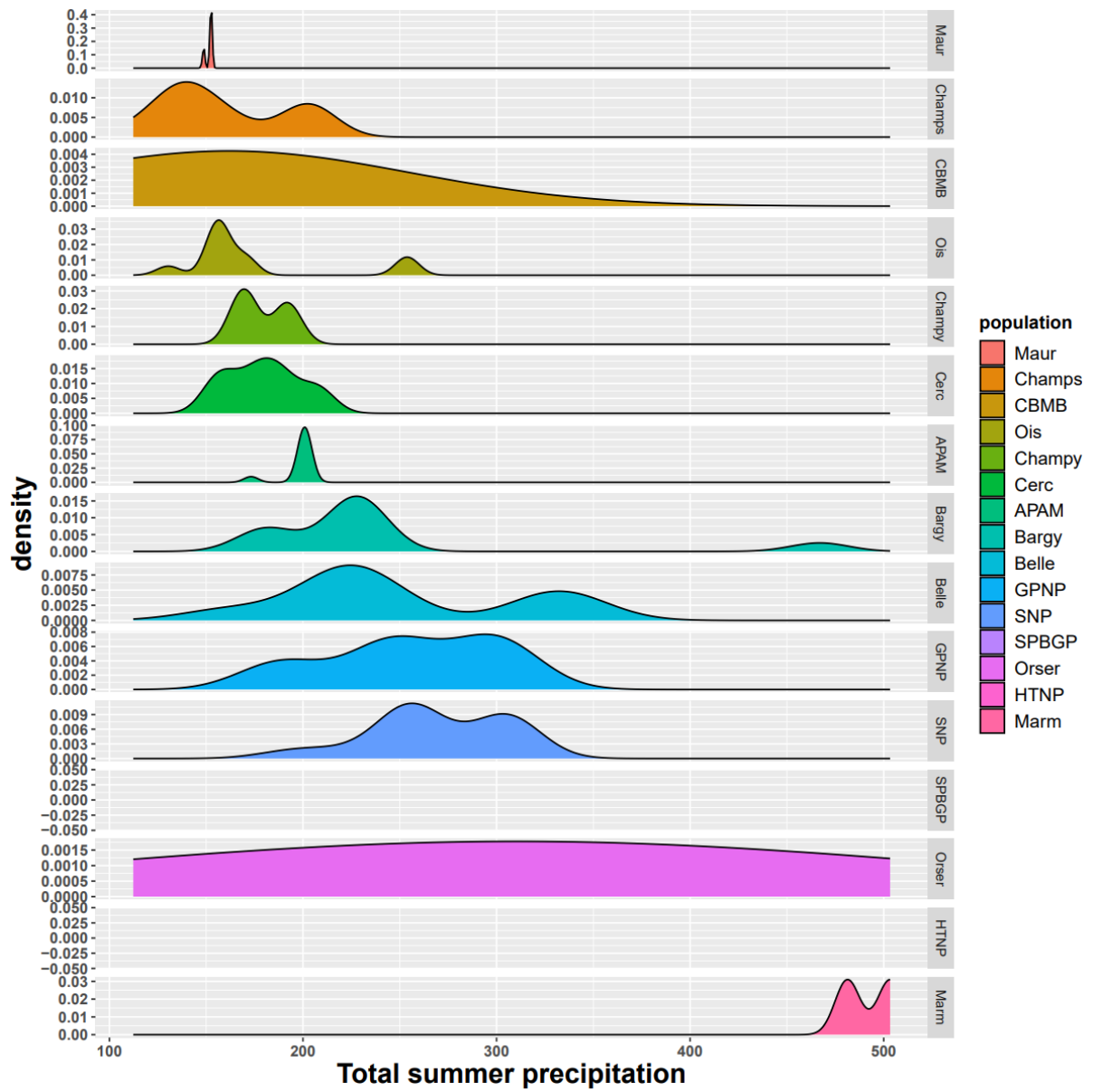


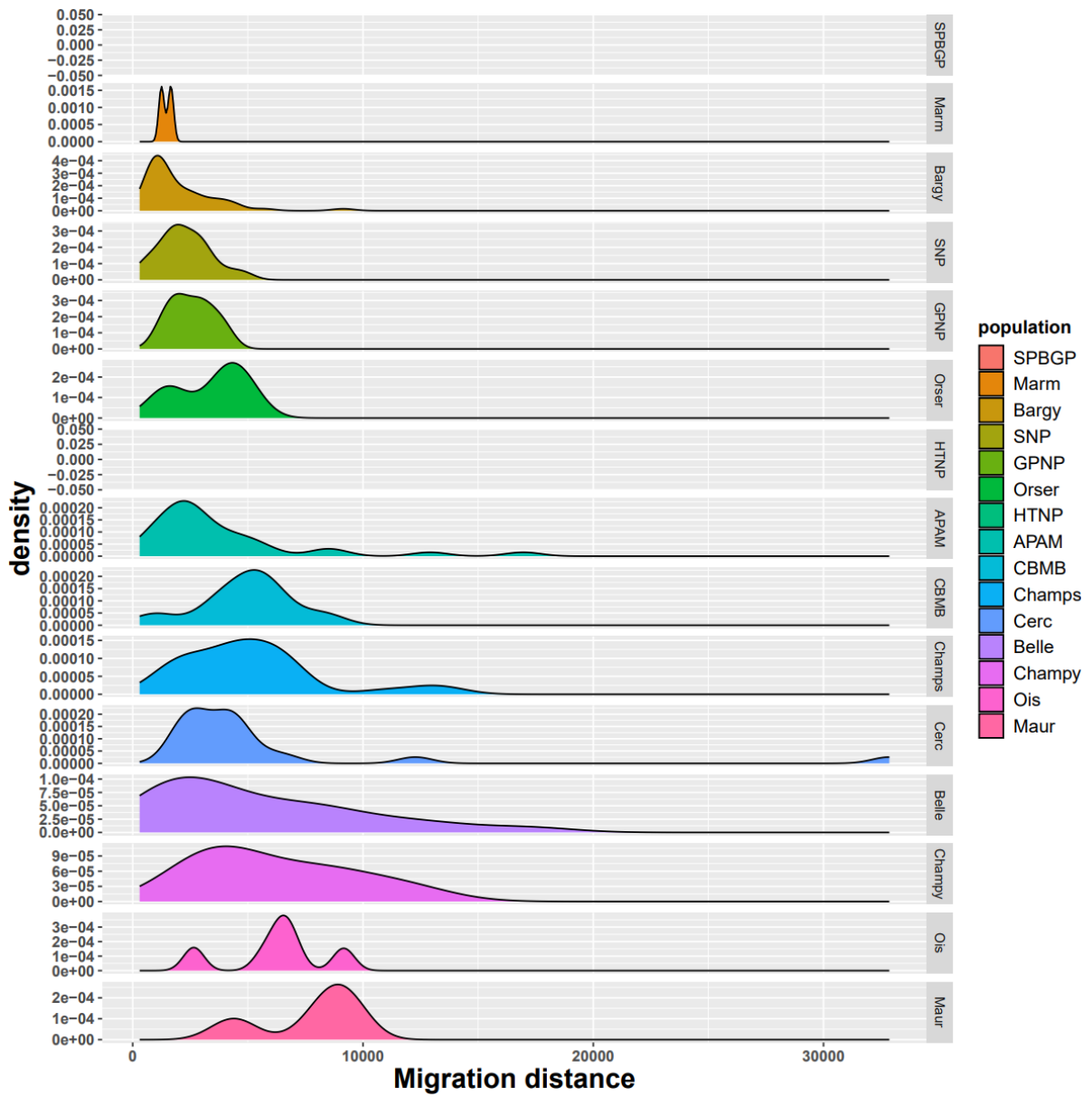












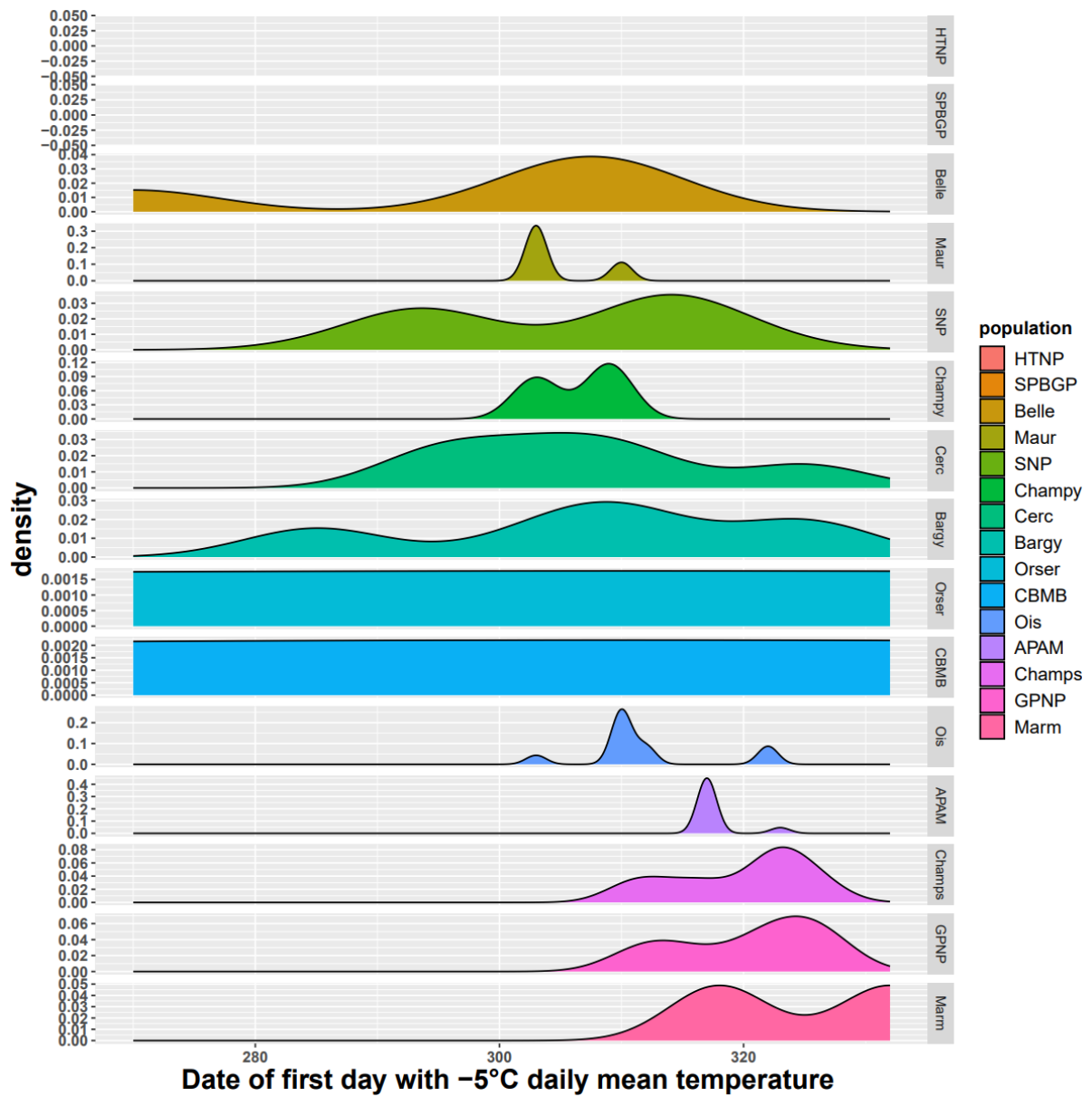
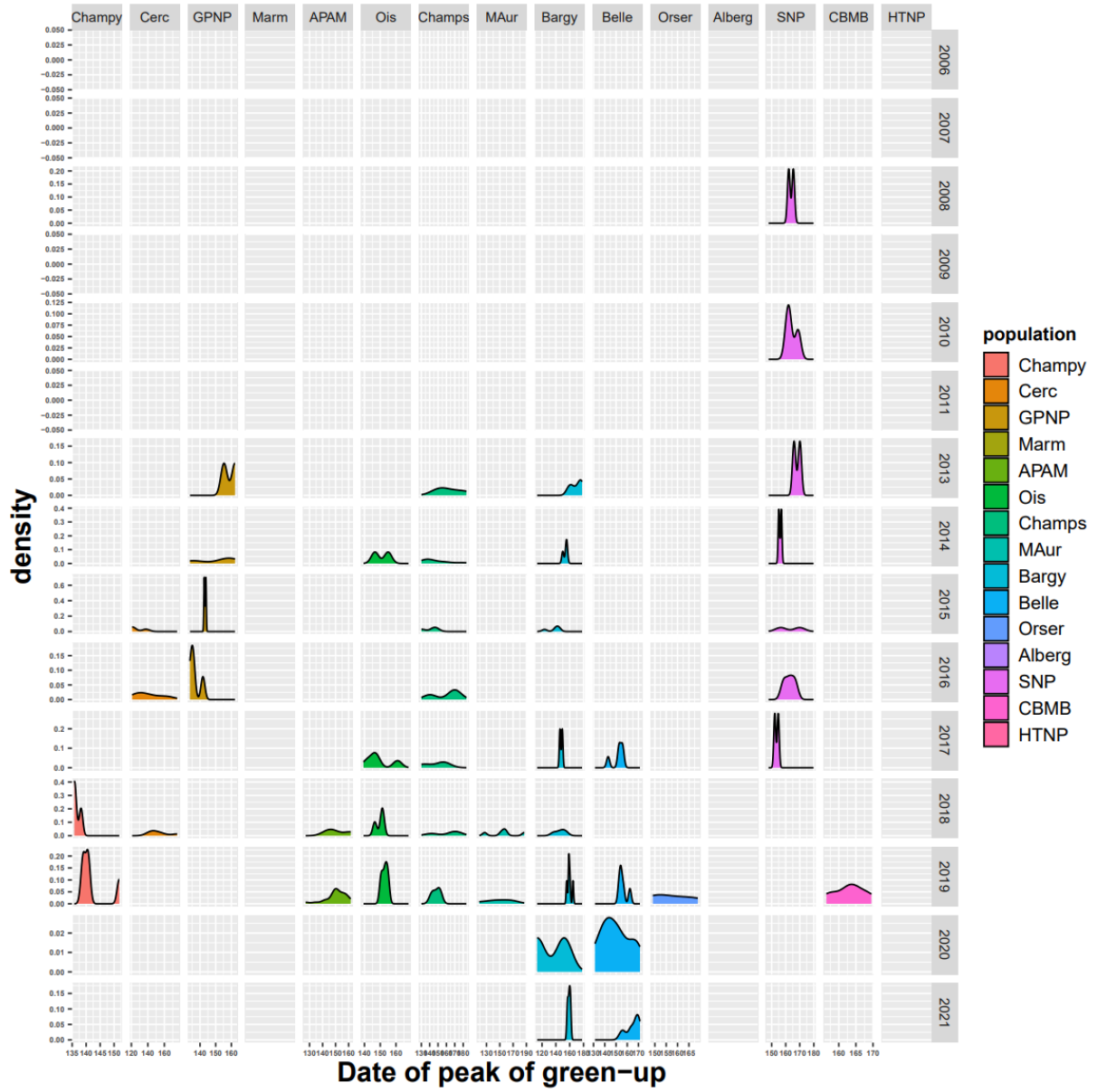


FIGURE S7: Range of measure of the different covariates in each population included in our initial model to test our hypothesis regarding the factors affecting the timing of autumn migration in ibex.



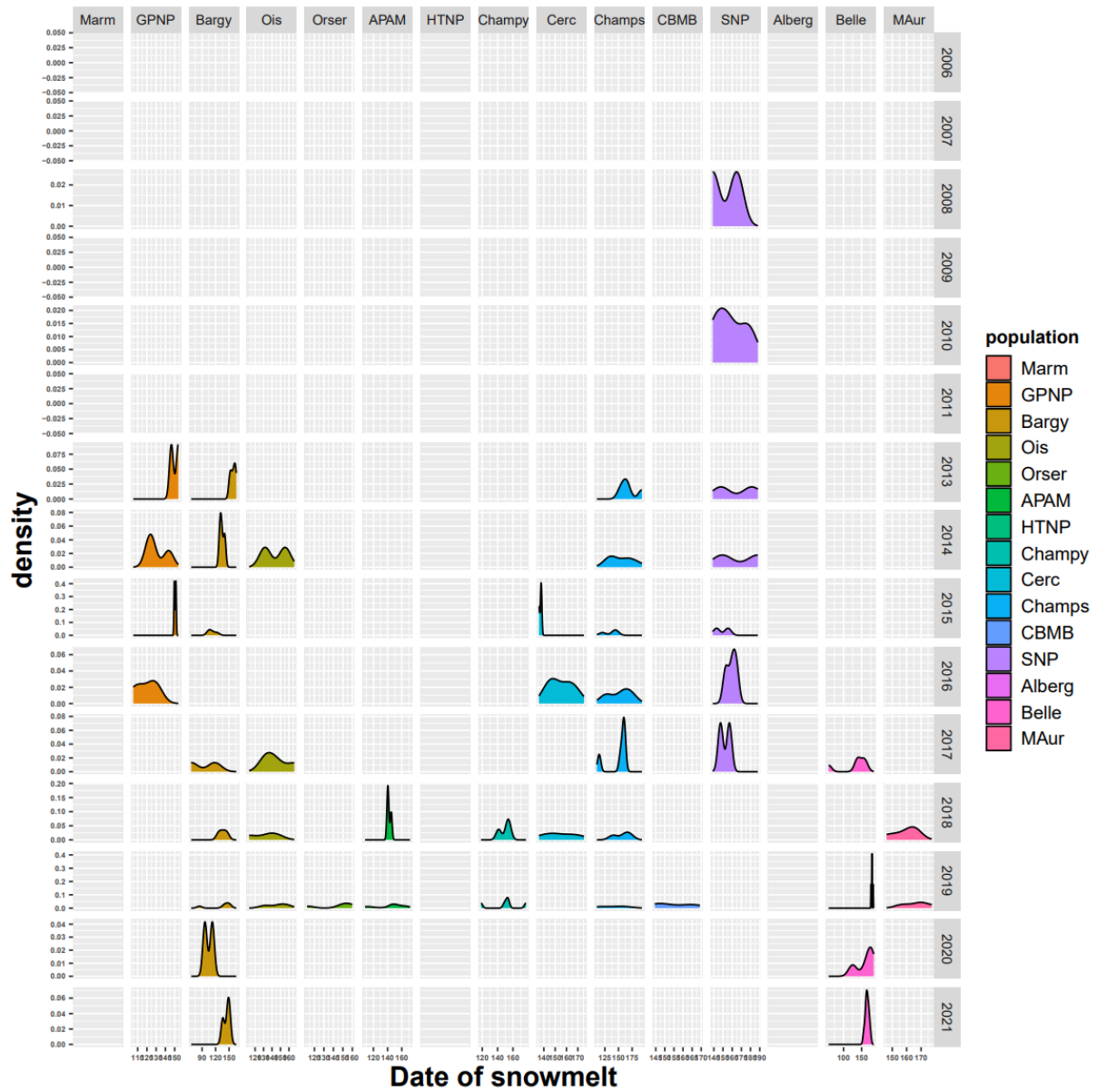


FIGURE S8: Range of measure of two different covariates (Date of peak of green-up and date of snowmelt) in each population and in each year.

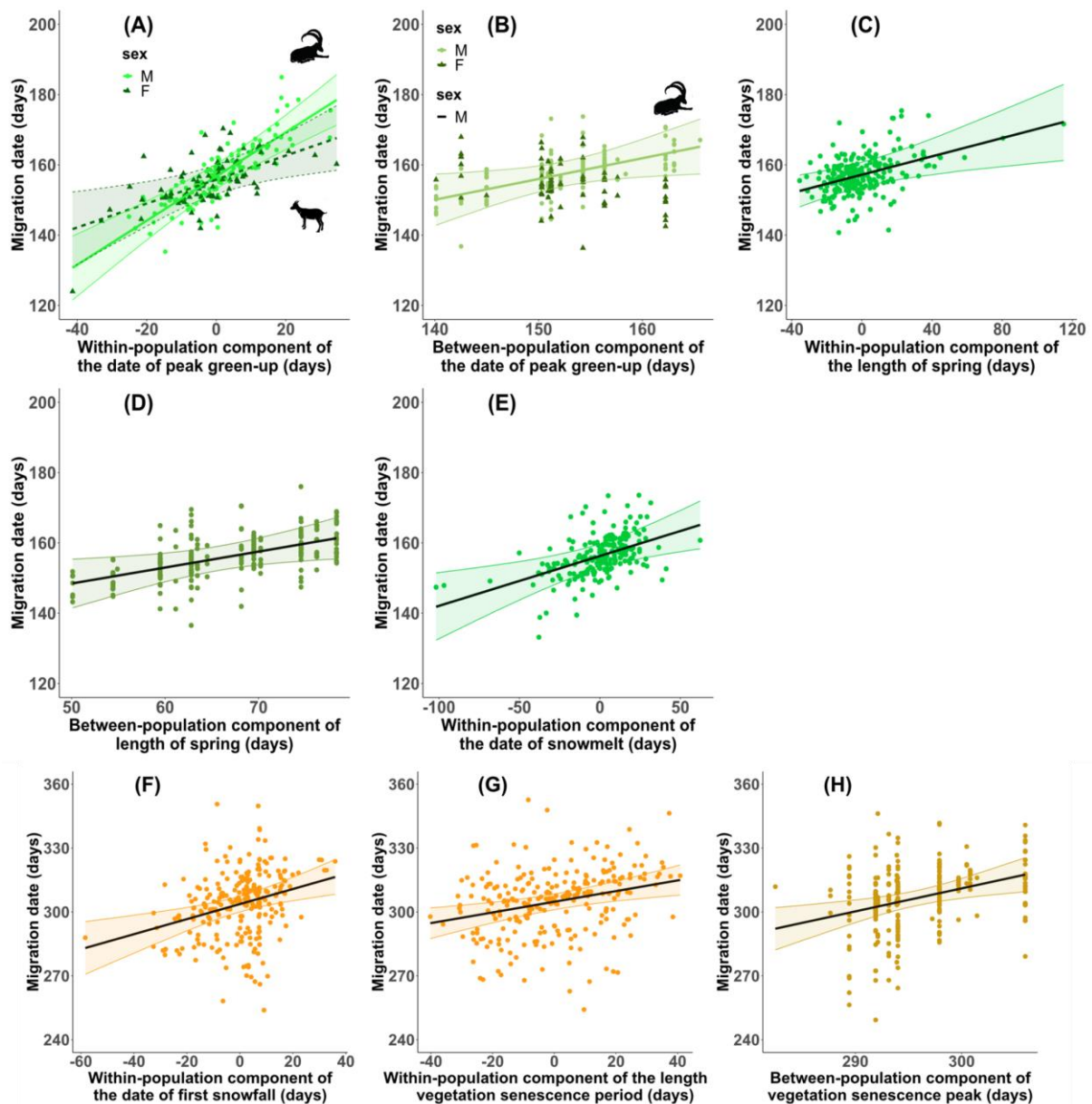


FIGURE S9: Effects of environmental and individual factors on migration departures in spring (A, B, C, D, E, n=211) and autumn (F, G, H, n=250). (A) Effect of the within-population component of the date of peak green-up in relation with sex on spring migration departure. (B) Effect of the between-population component of the date of peak green-up in relation with sex on migration departure. The effect was significant for males but not for females. (C) Effect of the within-population component of the length of spring season on migration departure. (D) Effect of the between-population component of the length of spring

on migration departure. (E) Effect of the within-population component of the date of snowmelt (on summer range) on spring migration departure. (F) Effect of the within-population component of the date of first snowfall on autumn migration departure. (G) Effect of the within-population component of the length of senescence period on autumn migration departure. (H) Effect of the between-population component of the date of peak of vegetation senescence on autumn migration departure. Solid lines and the shaded areas are the predictions and 95% confidence intervals accounting for covariates. Dots are the partial residuals accounting for the effects of the other variables in the model.

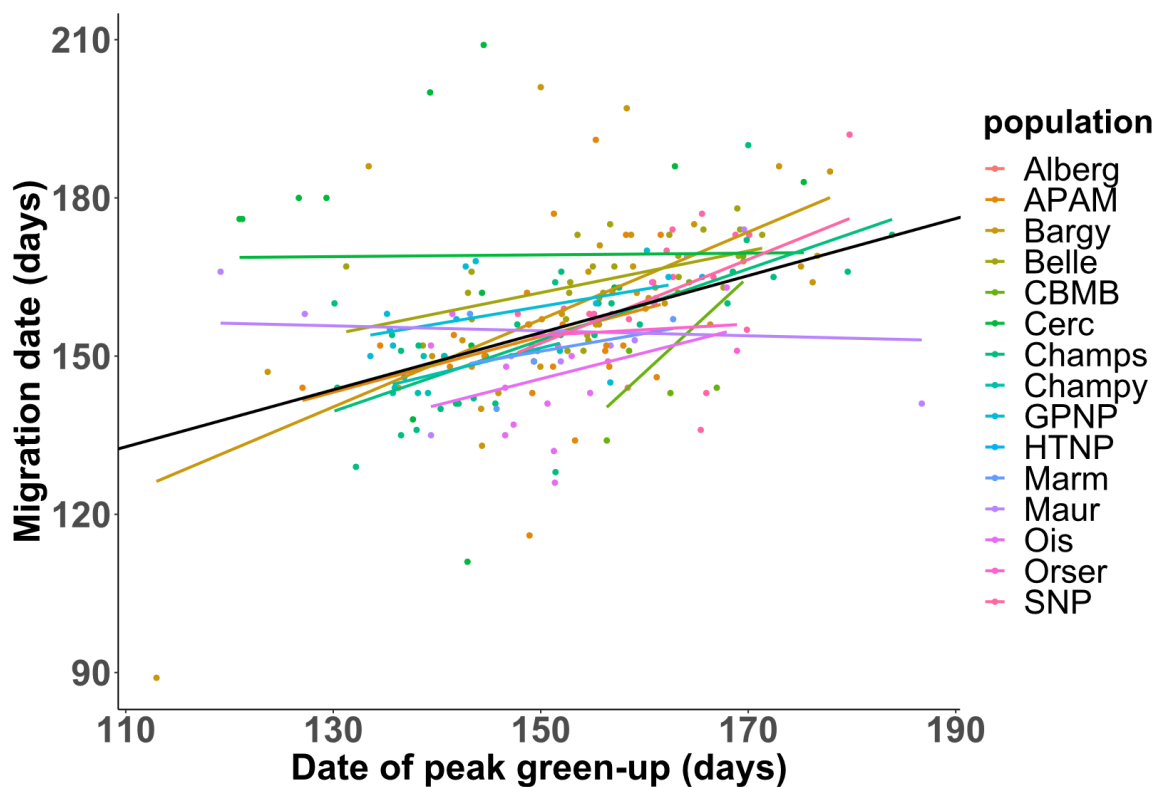


FIGURE S10: Effect of the timing of the date of peak green-up on the timing of migration over all populations (black line) and within each population (colored lines).



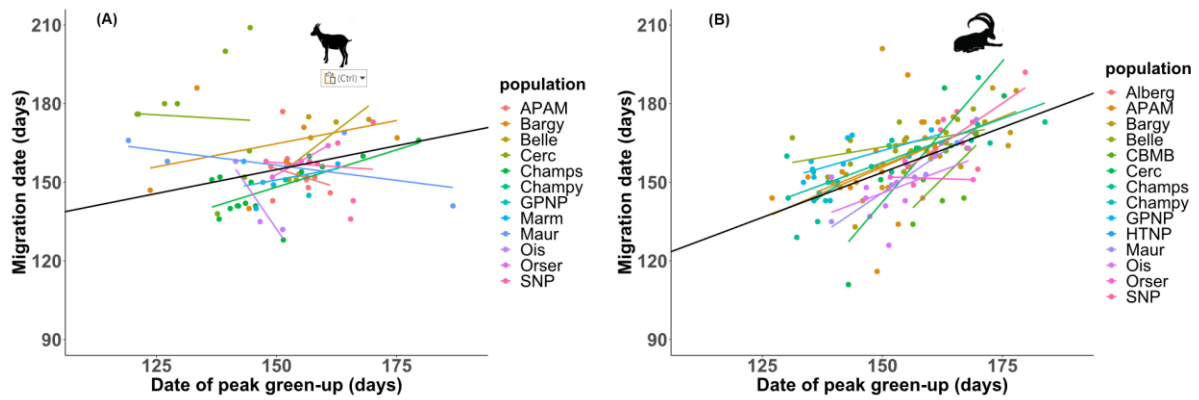


FIGURE S11: Effect of the timing of the date of peak green-up on the timing of migration over all populations (black line) and within each population (colored lines) for female ibex (A, n=76) and for male ibex (B, n=137).

SPRING				AUTUMN			
	mig1				mig2		
Predictors	Estimates	CI	p	Predictors	Estimates	CI	p
(Intercept)	36.59	-54.67 – 127.86	0.430	(Intercept)	-13.64	-220.99 – 193.71	0.897
peakGUw within	0.63	0.43 – 0.82	<0.001	SnowF within	0.35	0.15 – 0.56	0.001
sex [F]	174.00	51.83 – 296.17	0.005	peakS between	1.08	0.38 – 1.78	0.003
peakGUw between	0.59	0.06 – 1.12	0.031	LengthSen within	0.25	0.10 – 0.40	0.001
LengthS between	0.45	0.07 – 0.84	0.022	<b>Random Effects</b>			
LengthS within	0.13	0.04 – 0.22	0.004	$\sigma^2$	306.73		
SnowM within	0.14	0.05 – 0.23	0.002	$\tau_{00\_new\_id}$	125.62		
peakGUw within $\times$ sex [F]	-0.29	-0.57 – -0.01	0.042	$\tau_{00\_pop}$	11.65		
sex [F] $\times$ peakGUw between	-1.16	-1.96 – -0.36	0.005	ICC	0.31		
<b>Random Effects</b>				$N_{new\_id}$	220		
$\sigma^2$	59.32			$N_{pop}$	15		
$\tau_{00\_new\_id}$	104.48			Observations	250		
$\tau_{00\_pop}$	16.30			Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.144 / 0.409		
ICC	0.67						
$N_{new\_id}$	173						
$N_{pop}$	15						
Observations	213						
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.281 / 0.763						

FIGURE S12: Parameters of the best models obtained after model selection on an initial model containing a predictor reflecting within-population variation component or between-

population variation for each covariate. peakGUw=date of peak of green-up on winter range, LengthS=length of spring season on winter range, SnowM=date of snowmelt on summer range, SnowF= date of first snowfall on summer range, peakS= date of peak of senescence on summer range, LengthSen= length of senescence period on summer range.

Appendix S7: Distribution of migration dates in spring and autumn

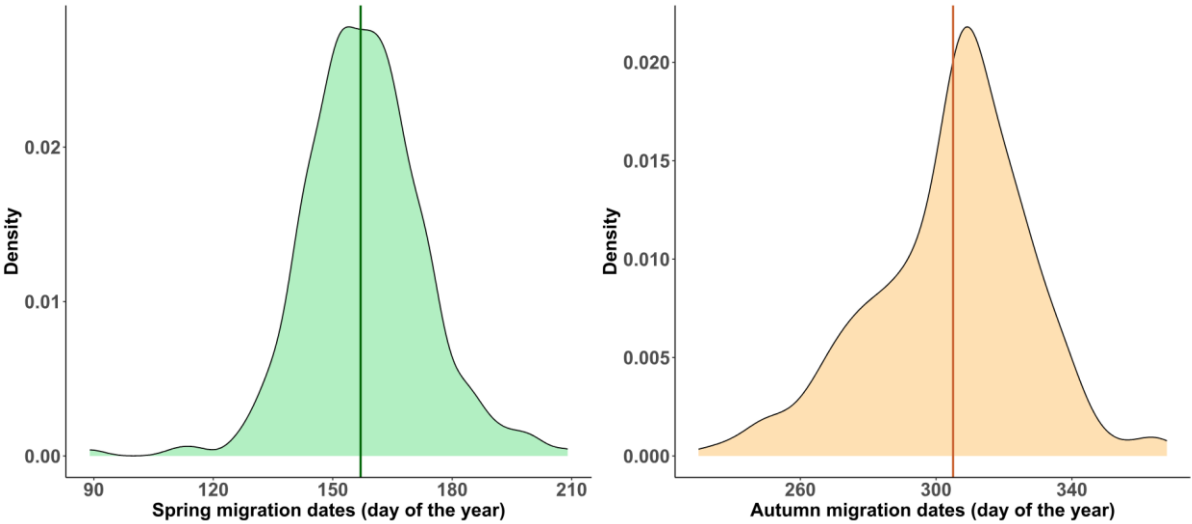


FIGURE S13: Distribution of the migration dates identified in spring and autumn based on 241 migration events in spring and 307 in autumn. The average migration departure occurred on June 6 (green vertical line, day of the year 157, SD=16 days), the average migration departure in autumn was November 1 (brown vertical line, day of the year 305, SD=23 days).

Appendix S8: Phenology models with scaled covariates

TABLE S2: Estimates, 95% confidence intervals (CI) and p-values for the parameters included in the two most supported models at both seasons describing migration date with environmental and individual characteristics. All environmental covariates were scaled to make their effect size comparable. peakGU = date of peak green-up, SnowM = Date of snowmelt, SpringL = length of spring season, SenescenceL = length of senescence period, Snowfall = date of first snowfall. We added individual identity and population as random effects in both models.

Season	Parameters	Estimates [95% CI]	p-values
Spring	Intercept (M)	156.56 [152.80;160.19]	<0.0001
	Sex (F)	-1.99 [-6.08;2.18]	0.34
	PeakGU (M)	8.20 [5.81;10.57]	<0.0001
	PeakGU:Sex (F)	-4.45 [-7.90; -1.04]	<0.05
	SnowM	3.06 [1.07;5.03]	<0.01
	SpringL	2.66 [0.91; 4.42]	<0.01
Autumn	Intercept	306.24 [302.01; 310.92]	<0.0001
	SenescenceL	4.39 [1.76; 7.02]	<0.01
	Snowfall	5.27 [2.56; 8.04]	<0.001

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