ARTICLE

Integrating microclimatic variation in phenological responses to climate change: A 28-year study in a hibernating mammal

Anouch Tamian[1] | Vincent A. Viblanc[1] | F. Stephen Dobson[1,2] |
Peter Neuhaus[3] | Tracey L. Hammer[1,3] | Anna P. Nesterova[4] |
Shirley Raveh[5] | Amy L. Skibiel[6] | David Broussard[7] |
Theodore G. Manno[8] | Nandini Rajamani[9] | Claire Saraux[1]

[1]Département Ecologie, Physiologie et Ethologie, Institut Pluridisciplinaire Hubert Curien, CNRS, Strasbourg, France

[2]Department of Biological Sciences, Auburn University, Auburn, Alabama, USA

[3]Department of Biological Sciences, University of Calgary, Calgary, Canada

[4]FaunaStats, Schiltigheim, France

[5]Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK

[6]Department of Animal, Veterinary and Food Sciences, University of Idaho, Moscow, Idaho, USA

[7]Department of Biology, Lycoming College, Williamsport, Pennsylvania, USA

[8]Science Department, Catalina Foothills High School, Tucson, Arizona, USA

[9]Indian Institute of Science Education and Research, Tirupati, Andhra Pradesh, India

Correspondence
Anouch Tamian
Email: anouch.tamian@iphc.cnrs.fr

Abstract

Phenological shifts associated with directional changes in climate, resulting in earlier spring activities, have been documented in several animal species. However, the extent to which species respond to overall climate change versus local climate variation is rarely studied. In addition, climate data are usually averaged over large spatial scales, even though local heterogeneity in habitats may be high, and species might be more susceptible to changes in local rather than global climate conditions. In this study, we examined the effects of spatio-temporal climate variation and climate change on the phenology of a hibernating mountain rodent, the Columbian ground squirrel (*Urocitellus columbianus*). Over 28 years of research (1992–2019), we studied the relationship between the microclimatic conditions experienced by adult and juvenile ground squirrels from four neighboring meadows, and their dates of emergence from hibernation. We used a microclimate model to calculate microclimate variables (local snow depth, soil temperature, air temperature, wind speed, and humidity) at an hourly scale, a 5-m spatial resolution, and at animal height on the study sites over 28 years.

Vincent A. Viblanc and Claire Saraux contributed equally to the work reported here.

Emergence dates varied with age and sex, among years, as well as among and within meadows, with some areas averaging up to 10 days earlier emergence dates from hibernation than others. While emergence dates tended to be delayed throughout the study period, long-term temporal changes and interannual variability in emergence dates differed among meadows and depended on individual age and sex. Dates of hibernation emergence were correlated with local climate variables considered either during hibernation or during the preceding summer. Ground squirrels emerged earlier in years or at locations when/where snow melted earlier (years: all individuals excluding 2-year-old males, locations: yearlings and older females), and when the previous summer was less windy (≥3-year-old individuals) and more humid (2-year-old males). Two-year-old male ground squirrels also emerged later in locations where snow depth during winter was higher. Using a microclimate model allowed realistic predictions of phenological responses to climate, highlighting its potential for research on animal responses to abiotic change.

KEYWORDS
climate variability, exogenous effects, hibernation, microclimate model, phenology, snow cover, spatial variability

INTRODUCTION

The extent to which animals are able to adapt to current climate change (e.g., earlier springs in the temperate zones) and increasing fluctuations in extreme events (e.g., storms, droughts, late snow falls) is of major concern in terms of biodiversity loss and ecosystem function (Martay et al., 2017; Pires et al., 2018; Walther et al., 2002). In particular, variations in winter and spring onsets occurring in seasonal ecosystems around the world (Kreyling & Henry, 2011; Kunkel et al., 2004; Menzel & Fabian, 1999; Pachauri et al., 2014) are affecting the annual timing, known as phenology, of life cycle events (e.g., reproduction) in many animal species (Charmantier et al., 2008; Cohen et al., 2018; Sparks & Yates, 1997). Phenological shifts are generally consistent with the direction of climate change in most animal species, such as earlier spring activities following earlier spring onsets (Parmesan & Yohe, 2003; Radchuk et al., 2019). The strength of phenological shifts, however, varies greatly within and among species, between trophic levels, and between geographical locations, from little or no changes to marked changes in seasonal timing (Chmura et al., 2019; Parmesan, 2007; Radchuk et al., 2019; Strode, 2003; Thackeray et al., 2016; Visser & Holleman, 2001; Winder & Schindler, 2004; see Parmesan & Yohe, 2003; Root et al., 2003 for a meta-analyses).

Because global climate change is altering phenological cycles (Chmura et al., 2019; Cleland et al., 2007; Menzel, 2002) and because phenological shifts have marked consequences for individual reproduction (e.g., match–mismatch of reproduction and peak resource availability; Durant et al., 2007; Visser & Both, 2005) and population dynamics (Ozgul et al., 2010), it is critical to understand how species phenology responds to fluctuations in climate. The need to distinguish phenological responses to long-term climate change from responses to short-term climate variability complicates this understanding. While climate variability usually considers year-to-year variation in climate, climate change only refers to those variations that persist for longer periods, usually greater than a decade (World Meteorological Organization, 2015). Another layer of complexity is added by the temporal and spatial scales over which inferences are drawn. Numerous studies rely on satellite or weather station data, often collected several kilometers or tens of kilometers from studied populations (Graae et al., 2012; Potter et al., 2013). However, individuals are often more affected by local climate conditions, which are shaped by spatial heterogeneity in habitat topography, soil composition, or sun exposure (Maclean et al., 2017; Suggitt et al., 2011; Zellweger et al., 2019). This is especially true in rugged areas, such as mountain habitats, where heterogeneity is high over relatively small spatial scales (Gultepe, ; Huggett, 1995; Nagy & Grabherr, 2009). Local contrasts in slope angles, sun exposure, soil composition, and vegetation cover can cause climate to vary, through variations in solar radiation, wind exposure, or humidity,

from scales of 1–10 km (i.e., mesoclimates) to scales of 0–100 m (i.e., microclimates) (Barry, 1992). Due to a lack of climate data at a fine resolution (<1 km), few studies have examined phenological responses to microclimatic conditions (James et al., 1984; Paruchuri et al., 2019; Potter et al., 2013; Suggitt et al., 2011; Varner & Dearing, 2014).

In this study, we examined the relationship between the phenology of hibernation and climate in a mountain hibernator, the Columbian ground squirrel (*Urocitellus columbianus*). We focused on hibernation emergence dates (ED) for individual ground squirrels from four neighboring meadows monitored over a period ranging from 18 to 28 years, depending on the meadow. Our objectives were to (1) examine spatial (among and within the four meadows) and temporal (over the years) variation of ground squirrel ED and to (2) determine how this variation might be explained by local and temporal variation in microclimatic conditions (scale of tens of meters, as experienced by the animals). Columbian ground squirrels are colonial ground-dwelling sciurid rodents inhabiting burrow systems in subalpine meadows of the northern regions of the Rocky Mountains. Columbian ground squirrels are an interesting model system to investigate changes in phenology in relation to microclimates. These are relatively long-lived animals (the oldest squirrel in our data set lived up to 14 years) that hibernate for ~8 months of the year, and are only active for a short summer period during which reproduction occurs (Dobson et al., 1992; Murie & Harris, 1982; Young, 1990b). Because of this short active season, phenological shifts may importantly determine animal reproductive success or ability to fatten for winter. A long-term delay in adult female ED (9.4 days over a 20-year period) correlating with lower spring temperature and delayed snowmelt has previously been reported in one of our four study populations (Lane et al., 2012). While this study suggested phenological plasticity in ground squirrel ED, likely due to climate change (Dobson et al., 2016), it only considered adult females from a single population and used wide-scale climate variables to test for their effects on ED (the weather data came from a meteorological station located in a prairie habitat, some 55 km from the study site). Yet, although some emigration occurs (Wiggett et al., 1989), adult ground squirrels are largely highly philopatric and inhabit relatively small home ranges over their lifetimes (female range rarely exceeds 1 km^2 and male range around 4.2 km^2; Arnaud et al., 2012; Festa-Bianchet & Boag, 1982; Harris & Murie, 1984; Murie & Harris, 1978). Thus, these animals are more likely to respond to very local climate conditions than to wide-scale climate variations. In addition, previous studies have shown that adult males emerge

from hibernation first, followed by adult females, and lastly yearlings (Dobson et al., 1992; Murie & Harris, 1982). However, data are lacking on whether different age or sex categories show similar or different phenological plasticity to local climate variation, both within and among neighboring populations (resolution of ~300 m).

To study the relationship between ED and climate, we performed a three-step analysis. First, we analyzed how variable ED was both within and among four different meadows over a 28-year period. We analyzed variation in ED in relation to individual (sex and age) and environmental characteristics (year and hibernation location) that were expected to affect hibernation emergence. Second, although our four study sites are located in the same valley, they present observable variability in slope, topography, and exposure to sun both within and among sites. Thus, we expected local climate variations to occur, affecting variation in ED both among meadows and within different parts of a given meadow. In the absence of local weather stations, we used a microclimate model (see Kearney, 2020; Kearney et al., 2020; Lembrechts & Lenoir, 2020; Maclean, 2020; Saleeba et al., 2020) to predict climate since 1992 on the four study sites, at a 5-m resolution, and at animal height (10 cm above ground, or 1 m below ground, roughly the depth of a ground squirrel hibernaculum; Young, 1990a). We then analyzed climate variation and tested whether we could detect a directional change in local climate patterns over the past 28 years (viz., climate change). Finally, we tested whether variation in ED could be explained by the local climate conditions encountered by the animals. Because emergence from hibernation is strongly related to the energetic state of individuals at the end of hibernation (Fietz et al., 2020; Norquay & Willis, 2014; Williams et al., 2014), there are two theoretical ways that climate could affect ground squirrel EDs: (1) by modifying individual energy expenditure during hibernation (Geiser, 2013; Humphries et al., 2002; Pretzlaff & Dausmann, 2012) and (2) through carryover effects from one active season to the next (Moore & Martin, 2019; Norris, 2005; Saino et al., 2017). On one hand, the energy available and stored by individuals during the active season should affect their ability to fast during hibernation (Columbian ground squirrels are "fat-storing" hibernators, Murie & Boag, 1984, Humphries et al., 2003). On the other, harsh climate conditions during winter could also affect ground squirrel energy expenditure and thus influence individual ability to fast and hibernate (Davis, 1976; Fietz et al., 2020; Humphries et al., 2004).

As the environment is multifactorial by nature, our analyses included several climate variables that could

affect either energy storage before hibernation or energy expenditure during hibernation (as recommended by McGuire et al., 2021). Specifically, we expected areas or years with earlier snowmelt and higher underground temperature to be associated with earlier ED (see Lane et al., 2012). The presence and depth of the snow cover directly impacts soil insulation and ground temperature, potential external cues for hibernating individuals. In addition, we expected carryover effects of climate on ED to occur from one year to the next. During hibernation, ground squirrels rely almost exclusively on body fat (Shaw, 1926). Overwinter survival depends on fat reserves accumulated during the previous season (Murie & Boag, 1984), and low-fat deposition is likely to affect ED the subsequent year. We did not measure body mass before hibernation in our study, but we reasonably expected foraging conditions (length and quality of forage) during the previous summer to directly reflect the amount of fat accumulated and burned during winter (Dobson et al., 1992; Neuhaus, 2000). Thus, we expected unfavorable forage conditions, for example low rainfall reflected by humidity, to be associated with low primary productivity (Dobson et al., 2016; Dobson & Kjelgaard, 1985; Neuhaus et al., 1999), and strong winds to be associated with more time spent by animals in vigilance rather than foraging (Fairbanks & Dobson, 2007). Through the decrease of fur thermal insulation (McCafferty et al., 2017), humidity might also negatively affect the time spent foraging, which should have detrimental effects on the accumulation of fat stores and ultimately on hibernation duration. This may cause individuals to emerge earlier due to the early depletion of overwintering fat stores, or conversely to delay emergence by more pronounced hypometabolism and a longer torpid period until resource availability is high again (i.e., avoiding early arousals when resource availability is low). Juveniles, which are less able to mitigate the survival costs of low-fat energy stores during hibernation, might experience this more than adults (Murie & Boag, 1984). Alternately, more favorable conditions during the previous summer could also allow for longer hibernation periods and later ED in juveniles, allowing them to avoid the period of high territorial aggression displayed by reproducing adults early in the season (Murie & Harris, 1978; Murie & Harris, 2011). Taken together, the joint investigation of summer and winter condition effects on ED in different neighboring populations was expected to provide us with a comprehensive understanding of how these mountain-adapted rodents deal with local heterogeneity in weather conditions, and whether different populations respond differently to long-term changes in climate patterns.

MATERIALS AND METHODS

Emergence date sampling

Study site and population monitoring

Columbian ground squirrels were monitored in the Sheep River Provincial Park in Alberta, Canada (50°38′ N, 114°39′ W), located in the foothills of the Rocky Mountains (Figure 1a). This study area includes four different meadows surrounded by mixed forests (primarily lodgepole pine, white spruce, quacking aspen, and birch trees) and composed of vegetation that is representative of grasslands in montane subregions (Alberta Parks, 2008). We monitored ground squirrel colonies on Meadow A (MA; 3.6 ha, from 1510 to 1535 m, monitored since 1994), Meadow B (MB; 2.6 ha, from 1500 to 1540 m, monitored since 1992, meadow on which the Lane et al., 2012 study was done), Meadow C (MC; 1.7 ha, from 1540 to 1560 m, monitored since 1999), and Meadow DOT (5.7 ha, from 1527 to 1570 m, monitored since 2001). Meadows A, B, and C slopes are southeast facing, whereas Meadow DOT slope is southwest facing.

We collected individual data with comparable methods on all four meadows. Individuals were trapped and permanently marked as pups or when they first appeared in the meadow as immigrant adults with the application of unique metal numbered ear tags (model no. 1, National Band & Tag Co.). Sex was determined based on visual inspection of genitalia (Murie & Harris, 1982). Each year, the meadows were monitored daily from before the first emergences from hibernation (early April each year) to the end of lactation for breeding females. Unfortunately, dates of entry into hibernation were not recorded and we were not able to follow the entire cycle of annual phenology. From mid-April to the end of May each year, ground squirrels were captured within a couple of days of emergence from hibernation (usually on the day of emergence or the following morning) using livetraps (National Live Traps; Tomahawk Co., WI, USA: $13 \times 13 \times 40 \text{ cm}^3$) baited with peanut butter. The first day of observation or capture (usually the same) of a given squirrel was used as a proxy for hibernation ED, typically confirmed by the squirrel's appearance and physical condition (large skin flakes from hibernation lost within few days, large abdominal flaps of skin where fat reserves were accumulated and lost, no defecation upon capture; Murie & Harris, 1982). Emergence was recorded as an ordinal date (number of days after 1 January each year). Emergence data were not collected in 2006 on Meadow DOT, in 2003–2006 on MA, and in 2002–2003 on MC. The location of each initial capture
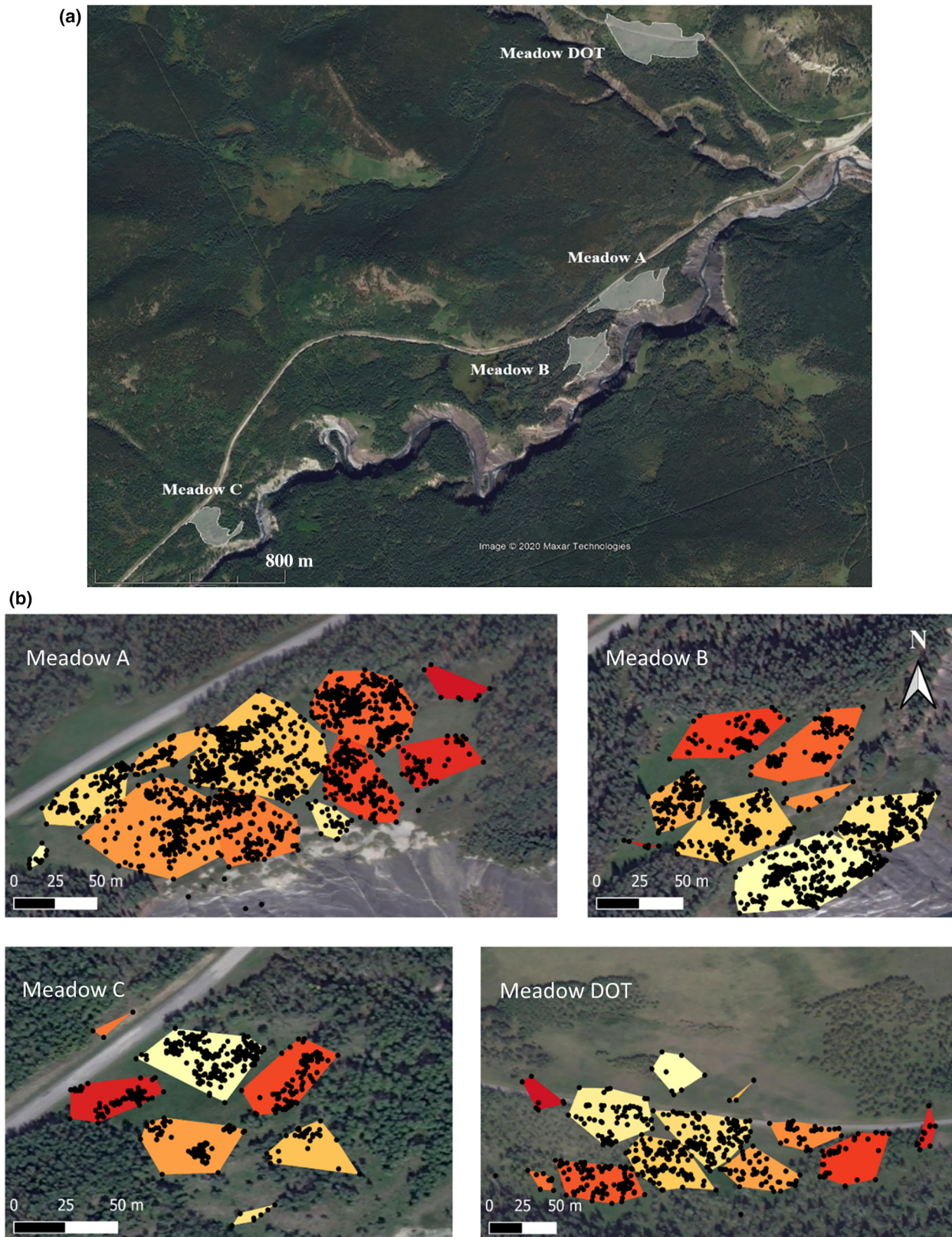
FIGURE 1 Study site composed of meadows and clusters within meadows. (a) The four different meadows where populations were monitored (gray areas on the map). (b) Emergence locations (black dots) grouped into spatial clusters on each meadow. Clusters are represented by minimum convex polygons and colored according to their mean emergence date. Lighter colors correspond to earlier mean emergence date of the cluster (yellow and light orange), and darker colors correspond to later mean emergence date of the cluster (dark orange and red). Mean ordinal emergence date on clusters ranged from 118 to 127 on Meadow A, from 118 to 130 on Meadow B, from 120 to 124 on Meadow C, and from 114 to 124 on Meadow DOT (Map data: Google, Maxar Technologies)

was recorded at a ± 1.0-m resolution, on 10×10 m Cartesian grids of color-flagged wires at each meadow. Hibernacula are usually used by the animals during a few days after emergence until collective burrows are re-excavated for the active season. First capture locations should thus provide a reasonable approximation of the area where individuals hibernated.

Recorded Cartesian coordinates were converted to GPS coordinates using a database of GPS and Cartesian coordinates collected in 2018–2019. We estimated the error associated with the conversion of Cartesian to GPS coordinates at a median ($\pm$SD) of 5.5 (± 3.4) m ($n = 225$ coordinates). Coordinates were collected for 74% of the emergences, 4351/5873. The missing emergence sites were before 1994 on MA, 1999 on MB, 2006 on MC, and 2012 on Meadow DOT. Emergence locations were also not recorded in 2000–2007 on MA. Thus, sample sizes varied among years.

Age classification

Because male Columbian ground squirrels emigrate, and new individuals occasionally leave and arrive on meadows, some individuals on the MA, MB, MC, and Meadow DOT were not known from birth (19% of the cases overall, 455/2436). For these individuals, recorded age resulted from estimates of physical characteristics mainly distinguishing between yearlings, 2-year-olds, and older individuals. To establish meaningful age bins in further analyses, we conducted a preliminary analysis testing how ED varied with age using individuals of known age ($n = 4681$ observations and $N = 1981$ individuals). We ran a linear mixed-effects model (LMM) of ED (dependent variable) as a function of age (independent categorical variable), specifying individual identity as a random factor in the model to account for repeated measures of individuals among years. Tukey's honestly significant differences (HSD) tests were applied for post hoc comparisons. On average, the emergence date of 1-year-old individuals (ordinal date $\pm$ SE $= 126.5 \pm 0.3$ days) was significantly later than all other age categories (Tukey's HSD, $p < 0.001$). For 2-year-old individuals, emergence date (121.7 ± 0.3 days) was significantly earlier than for yearlings ($p < 0.001$), but significantly later than for older age categories (116.7 ± 0.2 days; $p < 0.001$). No other significant differences were found among older age categories (all $p > 0.05$). Thus, individuals aged 3 and older were combined into a unique age category ($\geq$3-year-old) for subsequent analyses allowing us to use all existing ED data ($n = 5873$ observations in total and $N = 2436$ individuals). Sample sizes per meadow, year, and age and sex classes are provided in Appendix S1: Table S1).

Spatial clustering

To evaluate spatial heterogeneity in ED within a meadow, we investigated the spatial autocorrelation of ED. Specifically, we examined whether correlation between ED at two locations depended on the distance between them. To do so, we used variograms (Matheron, 1963) that measured the value of the spatial variance at different distance intervals. For any two data points, we measured their spatial distance and estimated the variance in ED. The variance was then averaged over bins of distance intervals. Empirical variograms were based on all emergence locations, but with pairs of points considered only if points were in the same year and within the same meadow. We modeled variograms using a least square method (Rivoirard et al., 2008). The empirical variogram of ED exhibited spatial structure (i.e., increasing variance when the distance between sampling points increased before leveling off; see Appendix S1: Figure S1), meaning that ED were not random, such that spatially close locations had closer ED than more distant locations. Based on the modeled variogram, we found that variance in ED stabilized at a range of about 40 m. Thus, hibernation emergence locations were grouped into spatially relevant clusters according to their GPS coordinates to understand whether individuals on some parts of the meadow emerged earlier than others.

We built clusters by grouping emergence locations according to an iterative algorithm (adapted from Woillez et al., 2007; see also Saraux et al., 2014). The algorithm started with each location as its own cluster. Each iteration of the algorithm then (1) calculated the distances between the center of gravity of all clusters on the meadow and (2) merged the two closest clusters if the shortest distance among all cluster distances was below a threshold distance of 40 m. The process was reiterated until none of the distances between clusters were lower than 40 m. In total, we defined 11, 8, 7, and 12 clusters for MA, MB, MC, and Meadow DOT, respectively (named differently depending on the meadow), which corresponded to hotspots of ground squirrel emergences in the habitat (compared to zones where ground squirrels were rarely seen emerging). Emergence locations and built clusters were imported into QGIS (3.10.12 long-term released version, QGIS.org, QGIS Geographic Information System, 2021) and presented on a Google satellite map (2021) (see Figure 1b).

Microclimate data

We calculated hourly microclimatic conditions using the Kearney et al. (2020) microclimate model, at a fine-scale

resolution (5 × 5 m grid) for each meadow during the entire monitoring period (from 1992 to 2019). The modeling function (*micro_ncep* from NicheMapR package; Kearney et al., 2020) downscales global atmospheric climate-forcing data (NCEP Reanalysis, historical data from the National Centre for Environmental Predictions, Kalnay et al., 1996, provided by the NOAA/OAR/ESRL PSL, Boulder, CO, USA, from their website at https://psl.noaa.gov/), using terrain-specific corrections, including spatial variations in slopes (from the Mapzen elevation and Mapzen terrain service, via "elevatr" package in R; Hollister et al., 2020), soil composition and hydrological properties (acquired from the "SoilGrids" database in R; Hengl et al., 2017), orientation, and hill shade. The microclimate model increases the quality and resolution of large-scale weather data and has been empirically validated (Kearney, 2020; Lembrechts & Lenoir, 2020; Maclean, 2020; Saleeba et al., 2020). Because Columbian ground squirrels live in open grass meadows with adjacent trees (see Figure 1), we estimated climatic variables without specifying shade due to vegetation cover.

Our model estimated snow depths (in centimeters) on the ground as well as temperatures (in degrees Celsius), wind speed (in meters per second), and relative humidity (in %) at 10 cm above ground (roughly the height of a ground squirrel). In addition, we estimated temperature at various soil depths below ground (0, 2.5, 5, 25, 50, 75, 100, 125, 150, and 200 cm). Hibernating burrows are usually around 70 cm in depth and rarely exceed 1 m (Young, 1990a, 1990b). Soil temperatures at various depths were highly correlated (see Appendix S1: Figure S2). Thus, we used 1-m-deep temperatures as representative of hibernaculum conditions.

There was no reasonably close weather station with records of climate date for the entire study period (the closest one being 58 km away at lower altitude in the plains). In addition, weather stations record temperature and precipitation variables at a standard height of 2 m, which is not representative of what a ground squirrel might experience a few centimeters above ground. Thus, using the microclimate model enabled us to obtain climate data over the entire study period at a high resolution and at the height of the animal, and further allowed us to measure snow cover (see Appendix S1: Figure S3 for a validation of the microclimate model).

To estimate spatial and temporal variation of climate, we averaged the model-generated time series at two different spatial scales for each meadow: (1) over the entire meadow and (2) separately within each cluster. Hourly data were averaged over 24-h periods. Based on the average ordinal day of first hibernation emergence (older males) across all years (15 April ±2 days) and previous studies showing that immergence occurs close to the beginning of August

(Neuhaus, 2000; Young, 1990b), we further divided the year in two phases: the active season (15 April–1 August) and the inactive (hibernation) season for the remainder of the year. This allowed us to test for possible effects of climate conditions during the winter and the previous summer on individual EDs. Besides air temperature (in degrees Celsius), soil temperature at 1 m depth (in degrees Celsius), relative humidity (in %), wind speed (in meters per second), and snow depth (in centimeters), we considered two additional climate variables: first day of the calendar year without snow cover on the ground (over the entire meadow or within each given spatial cluster, in ordinal date), and number of days with snow falls during the active period for investigation of late snowstorms on ED.

Data analyses

Quantifying variance in ED

Emergence date variance partitioning
To identify how much variance in ground squirrel ED (ordinal days) was explained by endogenous (sex, age category, and individual ID), spatial (meadow and emergence cluster within the meadow), and temporal (year) factors, we used a LMM with all variables specified as random terms (with 1|variable):

$$\text{ED} \sim (1|\text{sex}) + \left(1|\text{age}_{\text{category}}\right) + (1|\text{ID}) + (1|\text{meadow}/\text{cluster}) + (1|\text{year}) \qquad (1)$$

This model allowed us to partition variance components between the different random terms, (1|meadow/cluster) representing both the effect of the meadow and the effect of the cluster nested within the meadow.

Effects of sex and age on ED
Because sex and different age (especially sexually mature vs. immature individuals) classes face different reproductive constraints, we tested the effects of individual endogenous characteristics (sex and age specified as independent variables) on ED, while controlling for spatial and temporal effects (set as random terms):

$$\text{ED} \sim \text{sex} + \text{age}_{\text{category}} + \text{sex} \times \text{age}_{\text{category}} + (1|\text{ID}) + (1|\text{meadow}/\text{cluster}) + (1|\text{year}) \qquad (2)$$

Spatiotemporal variation in ED
Spatial variation in ED. Because of differences in slope and exposure at different meadows, we expected ED to vary spatially. To test for spatial variation in ED, we

assessed among and within meadow differences using separate LMMs. Differences were tested by specifying ED as the dependent variable, meadow (or cluster) as an independent variable, and year and the sex–age category (determined based on sex and age results) as random terms:

$$ED \sim meadow_{[MAvs.MBvs.MCvs.DOT]} + (1|year) \\ + \left(1|sex - age_{category}\right) + (1|ID) \tag{3}$$

$$ED \sim cluster + (1|year) + \left(1|sex - age_{category}\right) + (1|ID) \tag{4}$$

(one LMM per meadow).

Temporal variation in ED. Individuals might be phenotypically plastic, and time their ED to interannual variations, including directional changes in climate variables. We differentiated between interannual variation in ED and long-term directional changes in ED. Because emergence locations were not always known (especially in the early years, see above), we did not include spatial clusters in the following Models (5) and (6), enabling us to study potential changes in time over a larger data set (starting in 1992 instead of 1999).

To explore interannual variation in hibernation EDs, we built generalized additive mixed models (GAMMs) with ED as the response variable, and year as the independent variable. This facilitated identification of changes between years, and detection of nonlinear temporal variation. Because temporal trends could differ among meadows or according to the individual sex–age category, we considered interactions (specified with "by =") between the continuous variable (year) and these factors by constructing separate GAMMs, keeping individual ID as a random variable:

$$ED \sim s(year, by = meadow) \\ + s\left(year, by = sex - age_{category}\right) + sex - age_{category} \\ + meadow + (1|ID) \tag{5}$$

In a context of climate change, many phenological studies have shown advanced spring seasons (Cleland et al., 2007; Dingemanse & Kalkman, 2008; Walther et al., 2002). Yet, in Columbian ground squirrels, females older than 3 displayed a delay in spring emergence over a 20-year period (Lane et al., 2012). To test whether this long-term directional pattern was consistent over the four populations and over other sex/age categories, we ran

Model 5 as a LMM and assessed interactions between continuous (year) and categorical (meadow or sex–age$_{category}$) variables:

$$ED \sim year + sex - age_{category} + meadow + year \times meadow \\ + year \times sex - age_{category} + (1|ID) \tag{6}$$

Spatiotemporal variation in climate

Spatial variation in climate variables

To investigate microclimates, we assessed correlations among the 11 previously defined climate variables (air temperature during the active and inactive period, soil temperature at 1 m depth during the active and inactive period, relative humidity during the active and inactive period, wind speed during the active and inactive period, snow depth during inactive period, first day of calendar year without snow, and number of days with snow during the active period), using a principal component analysis (PCA) on data averaged by year and by cluster on each meadow. The objective was to identify principal variations related to spatial variables (clusters and meadows) given the large amount of climate data at a microscale within the meadows. Spatial differences in climate were analyzed from resulting components (PCs), through LMs at two different scales:

$$PCs \sim meadow \tag{7}$$

$$PCs \sim cluster \tag{8}$$

Based on results (see below), only climate variables expected to affect ED were kept for subsequent analyses. These included (1) snow depth (depth$_{snow}$) and soil temperature (temp$_{soil}$) at a 1-m depth during hibernation (inactive phase), and (2) air temperature (temp$_{air}$), relative humidity, and wind speed during the previous summer (active phase), in addition to the ordinal date of spring snowmelt (day$_{snowmelt}$) and the number of days with snow during the active period (days$_{snow}$).

Temporal variation in climate variables

Because interannual variability in climate often results from different processes such as directional trends in climate due to climate change, cyclic effects (e.g., El-Niño), and random year-to-year variation, we used a two-step approach. First, we focused on short-term variation using GAMs. Then, we tested for directional trends in ED as an expected result of climate change using LMs.

Climate variation. To explore how climate varied, we ran GAMs for each climate variable as a function of year. This allowed identifying changes between years and detecting nonlinear temporal variation. Because the interannual variability of climate could differ among meadows or among clusters, we also considered interactions of years with these factors in the following GAMs:

$$\text{Climate variable} \sim s(\text{year}, \text{by} = \text{meadow}) + \text{meadow} \quad (9)$$

$$\text{Climate variable} \sim s(\text{year}, \text{by} = \text{cluster}) + \text{cluster} \quad (10)$$

(one Generalized Additive Model per meadow).

Climate change. To test for long-term directional climate changes over 28 years, we ran the previous GAMs (9) and (10) as LMs (11) and (12), with each climate variable specified as a dependent variable and the year, meadow (or cluster), and their interaction as independent variables:

$$\text{Climate variable} \sim \text{year} \times \text{meadow} + \text{meadow} \quad (11)$$

$$\text{Climate variable} \sim \text{year} \times \text{cluster} + \text{cluster} \quad (12)$$

(one Linear Model per meadow).

Climate–ED relationships

We tested how climate might affect ED through two processes: energy expenditure and carryover effects of energy stored before hibernation. Because Columbian ground squirrels start breeding at 2 years old, the ED of $\geq$2-year-old individuals may vary with climate differently between males and females. Thus, we considered five sex–age categories for these analyses: yearlings, 2-year-old females, 2-year-old males, $\geq$3-year-old females, and $\geq$3-year-old males.

Mean relationships between climate and ED
To test for overall relationships between microclimates and hibernation EDs, EDs were averaged by year, meadow, and sex–age category. We built separate LMMs for the different age–sex categories, with ED as the dependent variable and climate variables (averaged by meadow and year) as independent variables:

$$\begin{aligned} \text{ED} \sim {}& \text{depth}_{\text{snow\_winter}} + \text{temp}_{\text{soil\_winter}} + \text{temp}_{\text{air\_activen-1}} \\ & + \text{humidity}_{\text{activen-1}} + \text{wind}_{\text{activen-1}} + \text{day}_{\text{snowmelt}} \\ & + \text{days}_{\text{snow\_active}} + (1|\text{year}) + (1|\text{meadow}) \end{aligned}$$
$$(13)$$

(one LMM per age–sex category).

Individual responses in ED might differ due to both spatial (related to spatial living locations) and temporal (plasticity that matches interannual variation) heterogeneity. To distinguish between temporal versus spatial effects of climate on hibernation ED, we ran two further analyses, building separate models for different sex–age categories.

Year-centered approach: Are spatial differences in ED related to spatial variation in climate?
To investigate spatial effects of climate variables on ED, we removed all temporal variation by centering ED and climate variables by year and sex–age category (mean of the years and category subtracted to each observation). During the active season, ground squirrels might visit most locations on the meadow in a single day. Because spatial clusters were defined from hibernation emergence locations and not the total active range of individuals, we only included in the model climate variables measured during hibernation (inactive phase). For each individual ED, we associated the climatic conditions of the given winter averaged over the spatial cluster in which the individual emerged. Thus, the LMM was:

$$\begin{aligned} \text{ED} \sim {}& \text{depth}_{\text{snow\_winter}} + \text{temp}_{\text{soil\_winter}} + \text{day}_{\text{snowmelt}} \\ & + \text{days}_{\text{snow\_active}} + (1|\text{cluster}) + (1|\text{ID}) \end{aligned} \quad (14)$$

Spatial-centered approach: Are interannual differences in ED related to interannual variation in climate?
To investigate temporal effects of climate variables on ED, we centered ED and all climate variables (including those considered during the active phase) by cluster and sex–age category. This way, spatial variations in climate were entirely removed from the data, and we tested whether yearly differences in climate could explain differences in ED among years.

$$\begin{aligned} \text{ED} \sim {}& \text{depth}_{\text{snow\_winter}} + \text{temp}_{\text{soil\_winter}} + \text{temp}_{\text{air\_activen-1}} \\ & + \text{humidity}_{\text{activen-1}} + \text{wind}_{\text{activen-1}} + \text{day}_{\text{snowmelt}} \\ & + \text{days}_{\text{snow\_active}} + (1|\text{year}) + (1|\text{ID}) \end{aligned}$$
$$(15)$$

Statistics

Statistical analyses were done in R version 4.0.3 (R Core Team, 2019). All tests were conducted with a probability error threshold of 5%. Results presented are means $\pm$ SE, along with the number of observations (n) and the number of individuals (N). Where appropriate (for LMMs and LMs), we ensured model residuals were normally

distributed by visual inspection of density distributions, Q–Q plots, cumulative distribution functions, and P–P plots using the "fitdistrplus" package in R (Delignette-Muller & Dutang, 2015). When the assumptions of a normal distribution of residuals were not met, we applied a Box-Cox transformation (MASS R package; Box & Cox, 1964) to the data (monotonous transformation), or removed extreme values from the data (i.e., EDs later than the 22nd of May for which we likely missed the actual ED, representing 2.7% [116/4351] of observations). Results with and without transformation or extreme values yielded similar results, and we present results obtained from complete and untransformed data sets for clarity (exceptions are specified in the results). Post hoc multiple comparisons were run to compare all factor levels of categorical variables, using the least square means (LSM) test, to account for multiple testing (Lenth, 2016). GAM(M)s were run using the "gam" and "gamm" functions in R ("mgcv" package; Wood, 2017). Principal component analyses were run using the "PCA" function, and components accounting for a meaningful amount of variance (i.e., from 75%; O'Rourke & Hatcher, 2013) were then considered in Models (7) and (8) ("FactoMineR" package; Lê et al., 2008). Whenever interactions between independent variables were included in LMs and LMMs, we compared the models with and without the interactions, and chose the final model according to Akaike's information criterion (AIC) (lowest AIC and for ΔAIC < 2, we chose the most parsimonious model; Burnham & Anderson, 2004). However, we also analyzed meadows separately to assess difference in trends between populations. The results on the link between climate and ED are presented from the full models, with all tested variables included. Multicollinearity was checked, and when variables were collinear, the one with the highest variance inflation factor (VIF) was removed, meaning that only variables with VIFs below three remained in the final models (Zuur et al., 2010). Finally, to allow comparisons of effect sizes in Models (13), (14), and (15), we standardized (by subtracting the mean and dividing by the SD) all explanatory climate factors.

RESULTS

Quantifying variance in ED

Emergence date variance partitioning

Across all individuals, meadows, and years, mean ED from hibernation was the 2nd of May $\pm$ 4 days (ordinal date 122 $\pm$ 4) and ranged from the 6th of April to the 30th of May (ordinal date 96–150). Model (1) with age, sex, meadow, cluster within meadow, year, and individual as random effects explained 65.7% of the total variance in ED (LMM, n = 4351 data points). Variables contributing most were age (26.3%), year (16.1%), and individual identity (14.6%). Within-meadow cluster, sex, and meadow explained fairly trivial amounts of variation, 3.9%, 3.1%, and 1.7% of the variance in ED, respectively.

Effects of sex and age on ED

Age, sex, and their interaction were all retained in the best model explaining ED (LMM 2, n = 4351, N = 1950 individuals, 26 years). We found differences in ED between males and females only in individuals ≥3 years old, with males emerging around 7.3 $\pm$ 0.4 days earlier than females (post hoc LSM, z = −18.3, p < 0.001). Post hoc comparisons revealed significant differences in EDs between four categories: yearlings, 2-year-old individuals, ≥3-year-old females, and ≥3-year-old males (LSM, all p < 0.001). On average, older males (≥3-year-old) emerged first around the 21st of April (111.2 $\pm$ 0.2 days), followed by older females (≥3-year-old) around the 28th of April (118.5 $\pm$ 0.2 days), 2-year-old individuals around the 2nd of May (121.8 $\pm$ 0.3 days), and finally 1-year-old individuals around the 6th of May (125.5 $\pm$ 0.2 days).

Spatiotemporal variation in ED

Spatial variation in ED

Analyses on spatial differences in hibernation EDs showed that individuals on Meadow DOT emerged 2.2 $\pm$ 0.5 days and 1.8 $\pm$ 0.4 days earlier than individuals on MC and MB, respectively. Meadow C and Meadow B individuals emerged 3.3 $\pm$ 0.4 days and 3.6 $\pm$ 0.3 days earlier than individuals on MA (LMM 3, post hoc LSM: all p < 0.001, n = 5873, N = 2436 individuals, 28 years). Similarly, within-meadow differences in EDs were found between different clusters (see cluster colors on Figure 1b). As an example, on MB, individuals in "bottom-west" cluster emerged between 1.9 $\pm$ 0.5 and 8.8 $\pm$ 2.5 days earlier than individuals from other clusters (LMM 4, post hoc LSM: p < 0.001, n = 1315, N = 579 individuals, 21 years). By contrast, individuals from the "top" cluster emerged between 4.6 $\pm$ 0.9 and 8.1 $\pm$ 0.8 days later than individuals from other clusters (post hoc LSM: p < 0.001, n = 1315, N = 579 individuals, 21 years) (see Figure 1b, Appendix S1: Table S2).

Temporal variation in ED

Interannual variability in ED. Emergence date exhibited marked interannual variations over the course of the study on all meadows and for each age–sex category (GAMM 5; 2.09 < edf < 8.73, 3.43 < F < 31.61, p < 0.001;

Figure 2), except for older males (≥3-year-old) on MB and MC ($p = 0.158$ and $p = 0.652$, respectively). Cyclic patterns over time were observed with a period varying from 6 to 10 years, depending on the period and the meadow considered. Older males (≥3-year-old) showed less variation in ED over time on MA than on Meadow DOT. Emergence date of yearlings and older females on MA was especially delayed between 1995 and 1997 as compared to 1999, as well as in 2011 compared to 2014–2017. On MB, the ED of yearlings and ≥3-year-old

females exhibited shorter fluctuations at the start of the monitoring period (1992–2002) than in recent years (2005–2019). Emergence date appeared to be delayed from 2005 to 2009, then advanced from 2009 to 2016, and delayed again from 2016 to 2019. On Meadow DOT, the ED for yearlings and older individuals showed lower variation than on other meadows, with fluctuations of smaller amplitude. Meadow C individuals exhibited the greatest variation during the most recent years, EDs being advanced between 2013 and 2015 and delayed
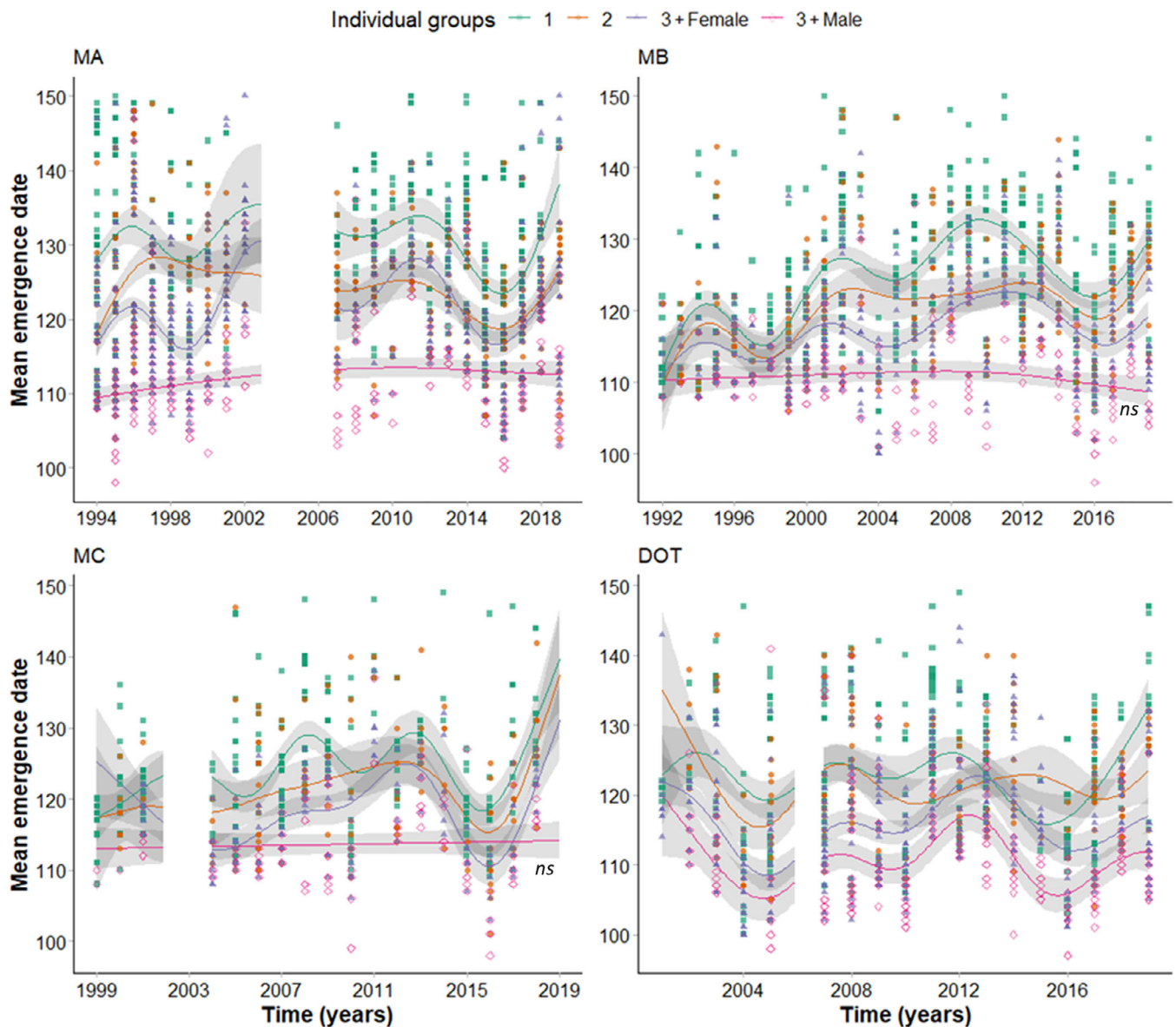
FIGURE 2 Interannual variability in emergence date. Temporal patterns of emergence dates (in ordinal days) on each meadow (Meadow A [MA], Meadow B [MB], Meadow C [MC], and Meadow DOT [DOT]) and for different individual categories. Yearlings (green squares, 1), 2-year-old individuals (orange circles, 2), older females (blue triangles, 3+ females), and older males (pink diamonds, 3+ males) are represented. Plotted lines correspond to significant temporal trends and their 95% confidence interval according to GAMs (5), excepting the temporal pattern of older males on MB and MC, which is nonsignificant (ns)

between 2016 and 2018. In general, the ED of 2-year-old individuals showed slightly lower fluctuations and a more stable pattern. On all meadows, individual EDs appeared to be earlier in 2015 and 2016 when compared with other years. Whereas the ED of MA and MB individuals was later in 2010 than other years, it was earlier on MC and Meadow DOT.

Long-term directional changes in ED. When testing for long-term directional linear changes in EDs, the interaction between year and meadow was retained in the best model (LMM 6, $\Delta AIC = 35$, $n = 5873$, $N = 2436$ individuals). On Meadow DOT, EDs of individuals did not significantly change in a directional manner through time for any of the sex–age categories (LMM, interaction year × sex–age not retained, $\Delta AIC = 5$, $t = 1.094$, $p = 0.274$, $n = 1303$ observations, $N = 503$ individuals) (see Appendix S1: Figure S4). On MC, regardless of sex and age (interaction year × sex–age not retained, $\Delta AIC = 2$), emergence from hibernation was significantly delayed over time, averaging a 4-day later emergence over an 18-year period (LMM, $+0.22 \pm 0.06$ day/year, $t = 3.769$, $p = 0.001$, $n = 704$ observations, $N = 385$ individuals). On other meadows, temporal trends differed according to the sex–age category ($\Delta AIC = 17$ and 22 for MA and MB, respectively). On MA, over a 22-year period, emergence was advanced by 2 days for 2-year-olds (LM, -0.11 ± 0.05 day/year, $t = -2.290$, $p = 0.023$, $n = 399$ observations, $N = 399$ individuals), delayed by 3 days for ≥3-year-old individuals (LMMs, ≥3-year-old females: $+0.14 \pm 0.04$ day/year, $t = 3.254$, $p = 0.001$, $n = 767$ observations, $N = 290$ individuals; ≥3-year-old males: $+0.13 \pm 0.04$ day/year, $t = 3.058$, $p = 0.003$, $n = 368$ observations, $N = 155$ individuals) and stable in yearlings (LM: $p = 0.053$, $t = -1.936$, $n = 625$ observations, $N = 625$ individuals). On MB, the hibernation emergence of yearlings, 2-year-old individuals, and ≥3-year-old females was delayed by 11, 7, and 5 days, respectively, over 28 years (LMs; yearlings: $+0.40 \pm 0.04$ day/year, $t = 9.110$, $p < 0.001$, $n = 631$ observations, $N = 631$ individuals; 2-year-olds: $+0.26 \pm 0.06$ day/year, $t = 4.678$, $p < 0.001$, $n = 318$ observations, $N = 318$ individuals; LMM: ≥3-year-old females: $+0.17 \pm 0.05$ day/year, $t = 3.455$, $p < 0.001$, $n = 531$ observations, $N = 164$ individuals), whereas the ED of ≥3-year-old males did not significantly change through time (LMM; $p = 0.379$, $n = 227$, $N = 83$).

Spatiotemporal variation in climate

Spatial variation in climate variables

The three most influential components of the PCA explained 78.3% of the variance in climate variables and each generated an eigenvalue higher than 1. The first component (PC1), explaining 39.4% of the variance, primarily reflecting air and soil temperature during the summer (active period), soil temperature during the winter (inactive period), and being negatively correlated with wind speed and humidity during the summer (see Figure 3, Appendix S1: Table S3). Winter air temperature and humidity were positively correlated with the second component (PC2, explaining 24.5% of the variance), whereas snow depth during winter loaded negatively on PC2. The third component (PC3, explaining 14.4% of the variance) was mainly related to wind speed during the winter. The three principal components varied depending on the meadow (LM 7, $p < 0.001$) and the cluster (LM 8, $p < 0.001$, see Appendix S1: Figure S5).

As presented on Figure 3b,d, clusters on MA were between 9.9% and 29.2% windier during the inactive period, between 16.3% and 26.4% windier during active periods, and between 0.6% and 2.7% more humid during the active period than clusters from other meadows. Conversely, soil temperatures of clusters on B were higher, during both winter (between 1.7% and 4.5%) and summer (between 2.4% and 6.6%), and the air during summer was between 1.4% and 4.3% warmer than on other meadows. Despite those general patterns, within-meadow variability was also quite high among clusters, especially on MB, which displayed both very positive and negative PCs clusters (Figure 3b,d, Appendix S1: Figure S5).

Temporal variation in climate variables

Climate variation

As predicted, all climate variables exhibited temporal variability (GAMs 9 and 10; $6.51 < edf < 8.78$, $2.79 < F < 15.33$, all $p < 0.01$; Figure 4). Interannual variation in these variables was similar among meadows (no year × meadow interactions retained, $N = 28$ years), although the absolute values in wind speed and relative humidity varied across meadows. This confirmed previous results that MA was the windiest and most humid meadow, while MB was the least humid and windy, MC and Meadow DOT being intermediate. Summer air temperature exhibited particularly high interannual variation, increasing and decreasing from 1 to 4°C from 1 year to the next (e.g., between 1997 and 1998), fluctuating on average between 7 and 13°C. During 2006–2007, air temperature was particularly high and much warmer than during the next 4 years. Conversely, the relative humidity during summer was particularly low in 2006–2007 compared to the next 4 years, staying relatively stable over
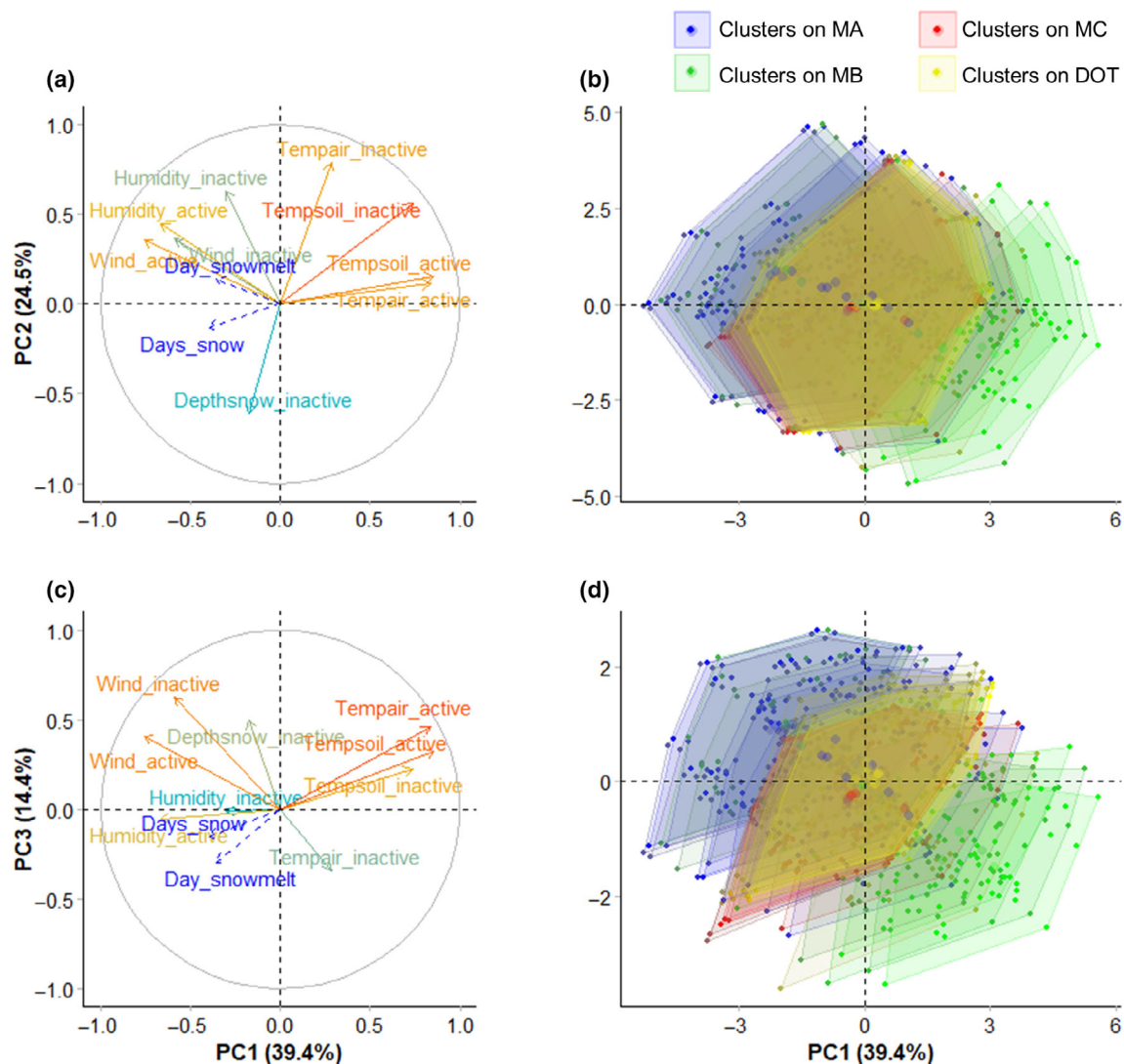
FIGURE 3 Spatial variation of climate conditions. Left side: Climate variables, considered either during the active or inactive period, included in the principal component analysis (PCA) along Dimensions 1 and 2 (a) and Dimensions 1 and 3 (c). The number of days with snowfalls during the active period (Days_snow) and the ordinal day of snowmelt (Day_snowmelt) were not used to estimate the PCA but projected on it. Right side: Annual mean values of climate conditions for each cluster of the four meadows. Clusters are represented by minimum convex polygons colored by meadows (Meadow A in shades of blue, Meadow B in shades of green, Meadow C in shades of red, and Meadow DOT in shades of yellow), with their center of gravity represented by larger dots

the rest of the study period. Wind speed during the active period showed regular cycles oscillating between 0.8 and 1.2 m/s every 5 years. During the inactive period, soil temperature varied between 2 and 5°C within approximately 5-year periods. Winter snow depth showed inter-annual variation as well, with especially low values in 2018 and 2019. Similarly, the ordinal day of snowmelt varied between mid-February and the 10th of April, depending on the year. The number of days with snow during the active period contrasted between years of no late snow falls (1992–1995, 1997–1998, 2004–2006, 2012, and 2015–2016) and years of late snow falls (between 2000 and 2003, and between 2008 and 2013).

Climate change

Temporal trends in climate did not differ between meadows (LMs: no year × meadow interactions retained, $N = 28$ years, see Appendix S1: Figure S6). Over 28 years, air temperature increased by 1.40°C during the active season (LM 11, active: 0.05 ± 0.01°C/year, $t = 3.510$, $p < 0.001$). Winter (inactive period) soil temperature at a 1-m depth increased at a slower rate of 0.03 ± 0.01°C/year (i.e., 0.84°C over 28 years, LM, $t = 5.642$, $p < 0.001$). Conversely, the snow depth during the inactive period (winter) decreased by -0.13 ± 0.06 cm/year, or 3.64 cm over the 28 years of study. During the active period, relative humidity increased by 0.08 ± 0.03% points/year (LM, $t = 2.818$, $p = 0.006$).
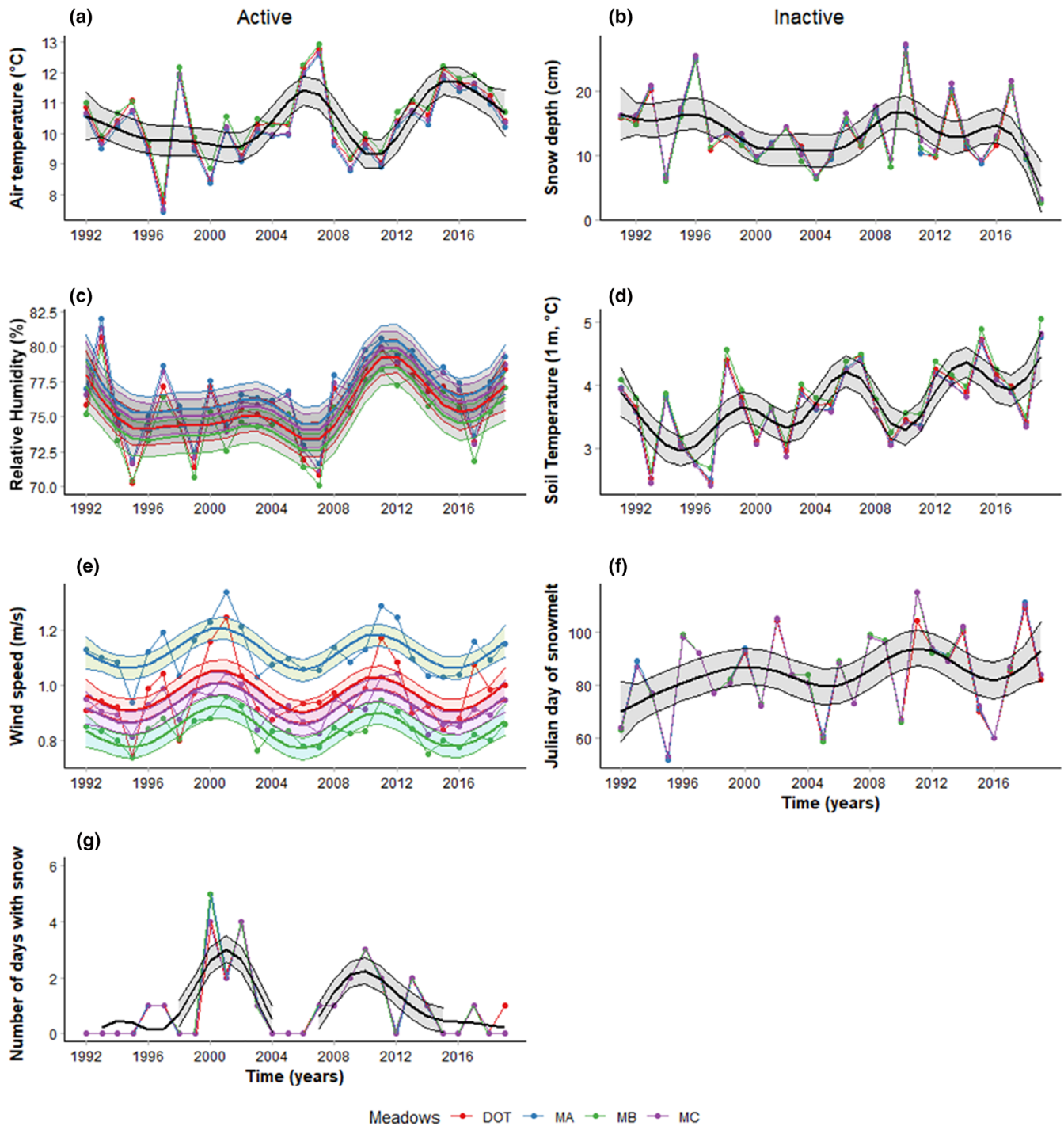
FIGURE 4 Climate interannual variability. Annual mean values of climate variables averaged by meadow. The lines correspond to temporal patterns of climate variables estimated by the GAM (9) on the four meadows (Meadow A [MA] in blue, Meadow B [MB] in green, Meadow C [MC] in purple, and Meadow DOT [DOT] in red) between 1992 and 2019. Climate time series were divided into two periods: inactive from the 1st of August to the 15th of April (right column) and then active the rest of the year (left column) and averaged by year. Where no difference was found between meadows (all variables except wind and humidity), a single prediction line was plotted for all locations (in black) with its 95% confidence interval (shaded area)

Moreover, the first ordinal day of complete snowmelt increased through time (delay of 13 days within 28 years, i.e., 0.45 ± 0.18 day/year, LM, $t = 2.509$, $p = 0.014$). The only climatic variables that appeared to remain relatively invariant over the study period were wind speed and the number of snow days during the active period (LMs, wind:

$t = 0.070$, $p = 0.944$, number of snow days: $t = 0.207$, $p = 0.836$). In summary, the climate tended to be warmer, more humid, and with a smaller snow cover during winter. Yet, this snow cover disappeared later in the spring.

Climate–ED relationships

Mean relationships between climate and ED

Among the different climate variables considered during winter (inactive phase) or the previous summer (active phase), only air temperature during previous summer had a VIF greater than three (between 5.244 and 5.460 according to the sex–age category considered) and was removed from the model (probably due to its high correlation with soil temperature; see Appendix S1: Figure S7). The ordinal day of snowmelt and wind during summer were positively related to annual mean ED (Figure 5). Emergence dates were delayed with a delay in the first day of snowmelt for all individual categories, apart from 2-year-old individuals (LMM 13, yearlings: $t = 2.211$, $p = 0.036$, $n = 84$ observations; 2-year-old females: $t = 1.713$, $p = 0.099$, $n = 82$ observations; 2-year-old males: $t = 0.424$, $p = 0.676$, $n = 77$ observations; $\geq$3-year-old females: $t = 2.994$, $p = 0.007$, $n = 83$ observations; $\geq$3-year-old males: $t = 3.958$, $p < 0.001$, $n = 83$ observations). Ground squirrels therefore emerged earlier when (and/or where) snow melted earlier; ED being delayed by approximately 0.25 day for a day of delayed snowmelt. Similarly, the summers with higher wind speed correlated with later emergences, but only for older females ($\geq$3-year-old, LMM, $t = 2.230$, $p = 0.037$, $n = 83$ observations). Indeed, older females emerged around 13 days later per 1 m/s increase in wind speed.

Year-centered approach: Are spatial differences in ED related to spatial variation in climate?

Once centered per year, no strong correlations were highlighted between climate variables, and we included all four of them in the model (VIFs <1.308; see Appendix S1: Figure S8). Day of snowmelt was positively related to ED, but only in yearlings and older ($\geq$3-year-old) females; individuals emerged later in locations where snow melted later (Figure 6; ED around 0.2 day later for a day of delayed snowmelt, ED and climate variables centered by year, LMM 14, yearlings: $t = 2.253$, $p = 0.024$, $n = 1450$ observations, $N = 1450$ individuals; $\geq$3-year-old females: $t = 2.389$, $p = 0.017$, $n = 1392$

observations, $N = 559$ individuals). Males of 2-year-old and $\geq$3-year-old seemed to emerge around 2 days later in locations where the snow depth was 1 cm higher during hibernation (LMMs, 2-year-old males: $t = 2.303$, $p = 0.023$, $n = 280$ observations, $N = 280$ individuals; $\geq$3-year-old males: $t = 2.085$, $p = 0.039$, $n = 693$ observations, $N = 300$ individuals, effect only marginally significant after transforming the data, Box–Cox transformation, $p = 0.058$). Soil temperature during winter tended to have an effect on the ED of yearlings and older males, with individuals emerging earlier from warmer hibernacula (Figure 6; LMMs, yearlings: $t = -1.625$, $p = 0.105$, $n = 1450$ observations, $N = 1450$ individuals; $\geq$3-year-old males: $t = -1.498$, $p = 0.137$, $n = 693$ observations, $N = 300$ individuals).

### Spatial-centered approach: Are interannual differences in ED related to interannual variation in climate?

When conducting the analysis, air temperature during the previous summer had a VIF greater than three (between 4.154 and 5.249) and was removed from the model (probably due to its high positive correlation with soil temperature, see Appendix S1: Figure S9). Regarding temporal effects of climate on ED, the ordinal day of snowmelt was positively correlated with ED for all individuals excepting 2-year-old males (ED and climate variables centered by cluster, LMM 15, yearlings: $t = 3.015$, $p = 0.003$, $n = 1450$ observations, $N = 1450$ individuals; 2-year-old females: $t = 2.821$, $p = 0.006$, $n = 525$ observations, $N = 525$ individuals; 2-year-old males: $t = 1.275$, $p = 0.211$, $n = 280$ observations, $N = 280$ individuals; $\geq$3-year-old females: $t = 3.246$, $p = 0.002$, $n = 1392$ observations, $N = 559$ individuals; $\geq$3-year-old males: $t = 3.610$, $p < 0.001$, $n = 693$ observations, $N = 300$ individuals). Thus, individuals emerged later in years when snow melted later (around 0.1 day later for a day of delayed of snowmelt, see Figure 7). Similarly, active periods with high wind speed positively correlated with delayed EDs of older individuals the next year (between 13 and 17 days delay per meter-per-second increase, LMMs, $\geq$3-year-old females: $t = 3.357$, $p = 0.001$, $n = 1392$ observations, $N = 559$ individuals; $\geq$3-year-old males: $t = 2.803$, $p = 0.006$, $n = 693$ observations, $N = 300$ individuals). Earlier ED of 2-year-old males correlated with higher summer humidity (LMMs, 2-year-old males: $t = -2.197$, $p = 0.036$, $n = 280$ observations, $N = 280$ individuals), although this effect was only marginally significant after transforming the data (Box–Cox
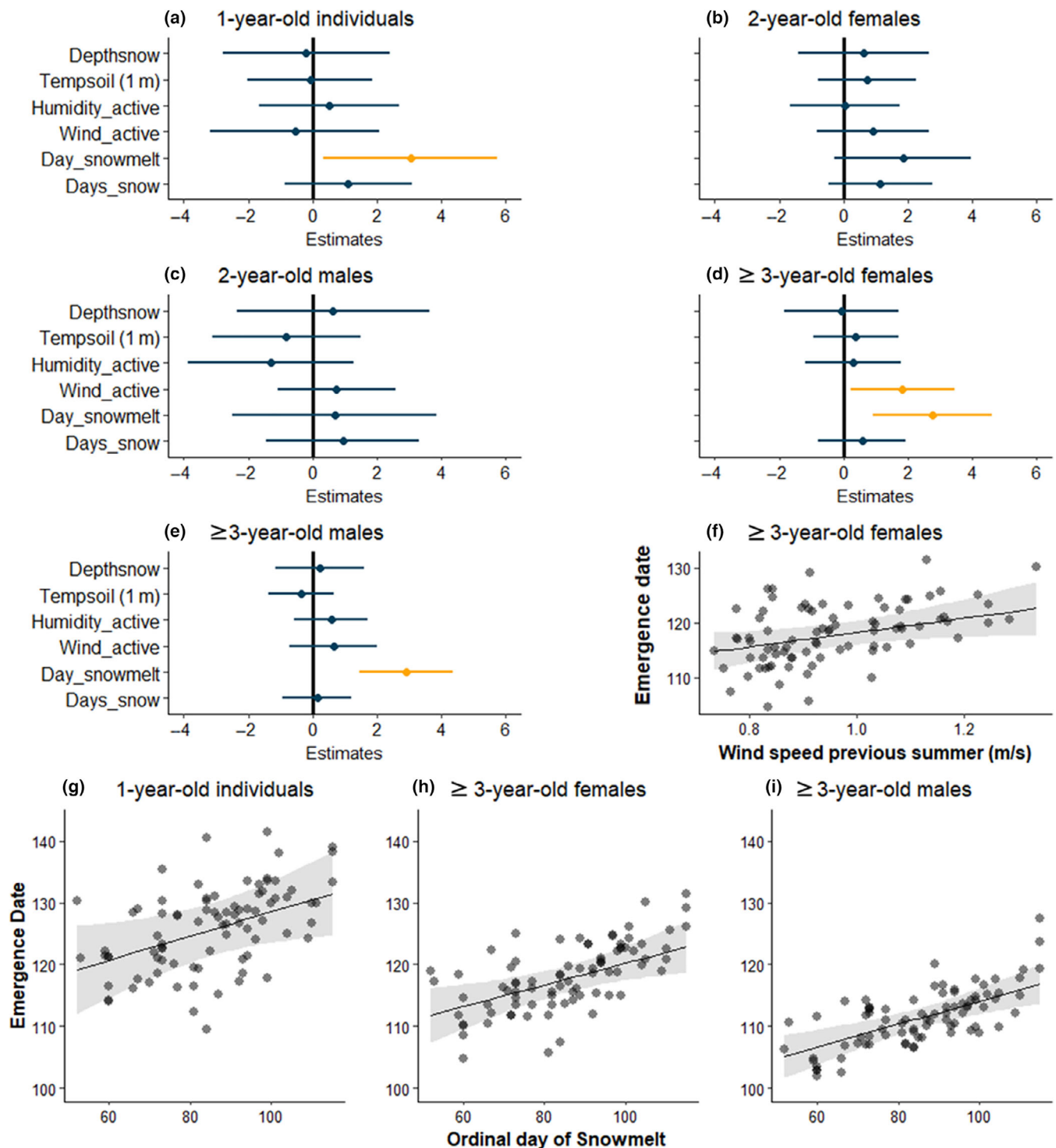
FIGURE 5 Climate effects on hibernation emergence date of different individual categories. From (a) to (e): Estimates and 95% confidence intervals (CIs) from the full linear mixed-effects model (13) explaining annual mean emergence dates per meadow are presented. Significant effects are presented in orange, while nonsignificant ones are blue. (f) Annual mean emergence date as a function of wind speed during the previous active period for ≥3-year-old females and model predictions (predicted line and 95% CI around). From (g) to (i): Annual mean emergence date as a function of the ordinal day of snowmelt and model predictions for 1-year-old individuals (g), ≥3-year-old females (h), and ≥3-year-old males (i)

transformation, $p = 0.054$). Depth of snow during winter may have a positive effect on the ED of older individuals, and the ED of 2-year-old males seems to be negatively associated with the soil temperature during hibernation (ED around 3 days earlier per degree increase of soil temperature at 1-m depth).
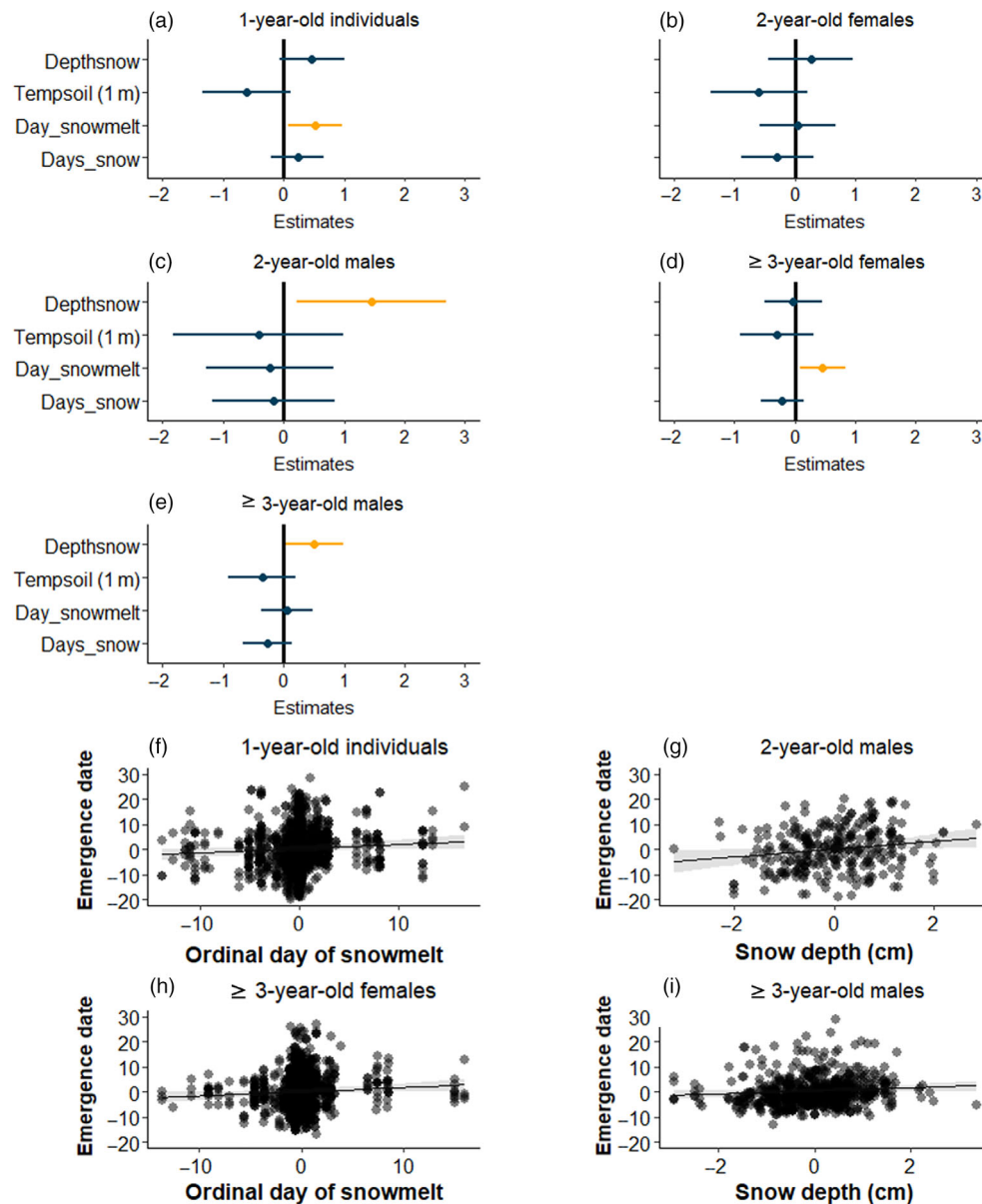
FIGURE 6 Spatial climate effects on centered emergence dates of different individual categories. From (a) to (e): Estimates and 95% confidence intervals from the full linear mixed-effects model (14) are presented with significant effects in orange. From (f) to (i): Spatial effect of climate on emergence date (year-centered observations to remove temporal variance). Model predictions are indicated along with their 95% confidence intervals (shaded area) on top of observations. Significant spatial effect of the ordinal day of snowmelt on emergence date of (f) yearlings and (h) older females (≥3-year-old and more). Significant spatial effect of the winter snow depth on the emergence date of (g) 2-year-old males and (i) ≥3-year-old males

DISCUSSION

Consistent with previous studies (Dobson et al., 1992; Murie & Harris, 1982), ground squirrel age and sex accounted for a substantial 29.4% of variation in ED. Older males emerged first from hibernation, followed by older females, 2-year-old individuals, and finally yearlings. Individual identity had a significant effect in the overall pattern of ED. This is consistent with previous knowledge on the heritability of ED of Columbian

ground squirrels ($h^2 = 0.22$ in females and 0.34 in males, Lane et al., 2011). The magnitude of the individual effect (14.6% of variance) was similar to the temporal variance in ED (16.1% of variance), in spite of strong individual plasticity in ED from year to year (Lane et al., 2012). These results confirm the importance of including among-individual heterogeneity in understanding population dynamics (Hamel et al., 2018).

ED varied over space and time (21.7% of variance), suggesting that this trait is plastic and capable of
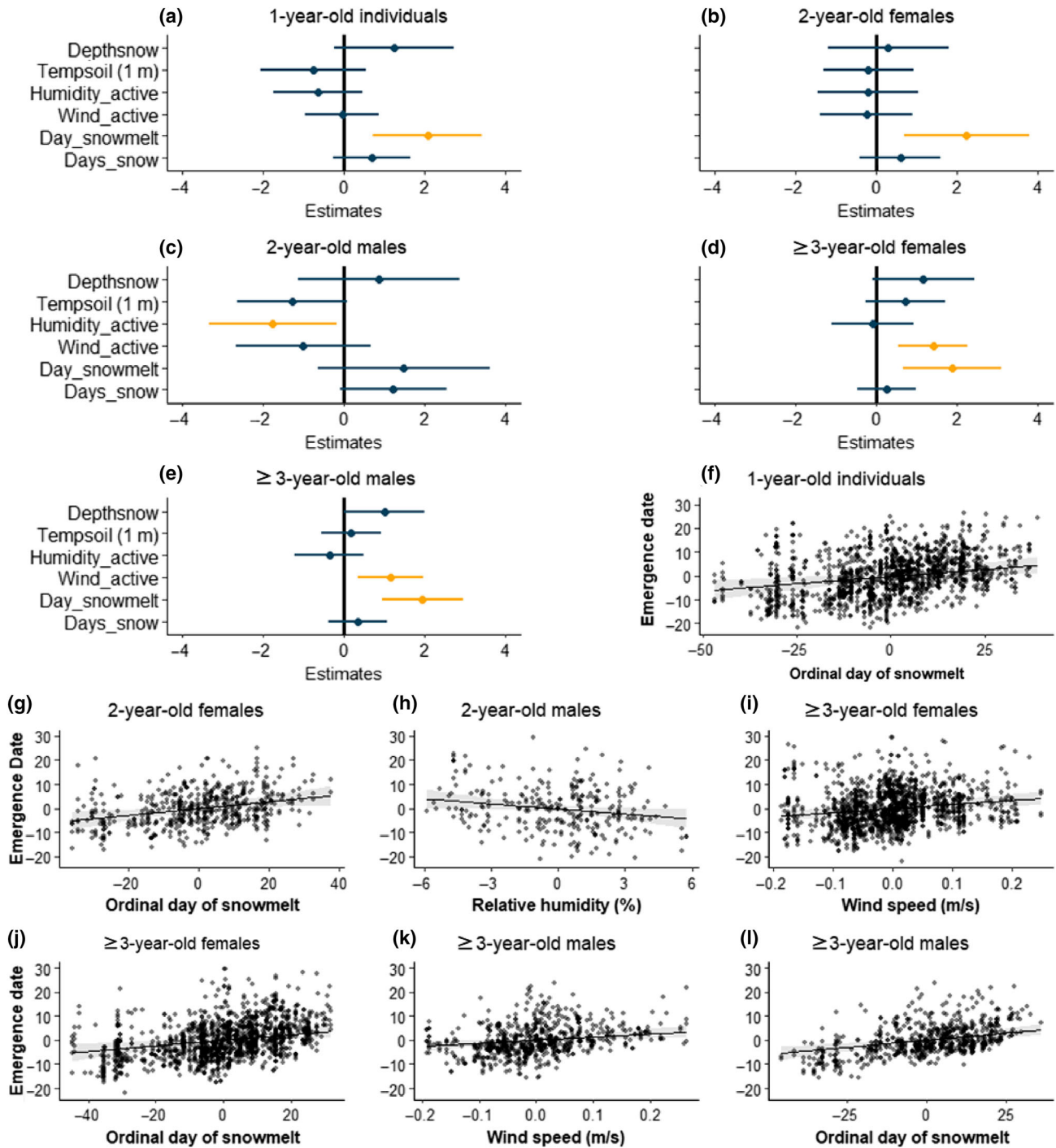
FIGURE 7 Temporal climate effects on centered emergence dates of different individual categories. From (a) to (e): Estimates and 95% confidence intervals from the full linear mixed-effects models (15) are presented with significant effects in orange. From (f) to (l): Temporal effect of climate on emergence date (all cluster-centered to remove the spatial variance). Model predictions are indicated along with their 95% confidence intervals (shaded area) on top of observations. Significant temporal effects of the ordinal day of snowmelt on the emergence dates (ED) of (f) yearlings, (g) 2-year-old females, (j) ≥3-year-old females, and (l) ≥3-year-old males. Significant temporal effects of (h) relative humidity during preceding summer on the ED of 2-year-old males and of wind speed on the ED of ≥3-year-old (i) females and (k) males

responding to climate variation (see also Dobson, 1988; Dobson & Kjelgaard, 1985; Lane et al., 2019). Separating the temporal and spatial effects of climate on ED by centering by cluster or by year enabled us to compare different mechanisms. Philopatric animals such as adult Columbian ground squirrels have adapted to the

environmental conditions in which they live. Oppositely, interannual variations in climate are more stochastic and might trigger plastic responses of animals. Whereas the years effects (16.1% of variance) are consistent with previous observations that ED was delayed through time in some populations (Lane et al., 2012; Neuhaus et al., 1999), our results importantly show that part of the variance (5.6%) in ED was also explained by spatial variation both within and among meadows. Such spatial heterogeneities were unlikely explained by variations in altitude (Dobson et al., 1992), since the four study populations are less than 70 m apart in terms of elevation. Interestingly, the variation in ED among individuals from different locations was even higher within than among meadows, ground squirrels from some parts of the meadows emerging earlier than others. This suggests that local heterogeneities occur at a microscale (∼40 m; see "Results") rather than mesoscale (1–10 km). These results add to the growing literature, showing that several animal and plant species are more sensitive to microscale than wider environmental variations (Lampei et al., 2019; Lundblad & Conway, 2021; Wang & Hou, 2021). Concurrently, spatial microclimate differences were found between clusters, suggesting a potential link between ED and local habitat conditions.

Emergence date relationship to climate

Our analyses of microclimate effects on ED focused on two distinct temporal phases: the climate conditions during the previous summer (active period) and those during hibernation (inactive period). First, our results showed the importance of carryover effects of the period preceding hibernation on ground squirrel EDs the subsequent year. In particular, we found that delayed emergence occurred in older individuals when the preceding summer was windier and associated with lower humidity (see Appendix S1: Figure S9 for temporal correlations between climate variables). Carryover climatic effects on animal phenology have mainly been documented in birds (Finch et al., 2014; but see Ockendon et al., 2013), fish (Wilson et al., 2021), and insects (Dingemanse & Kalkman, 2008; McCauley et al., 2018). Yet, carryover effects on phenology are likely widespread, including in mammals. For instance, carryover effects of food availability on the relationship between temperature and hibernation emergence were shown in edible dormice (Fietz et al., 2020). Such effects are thought to be primarily mediated through macronutrient supply (reviewed by Harrison et al., 2011). Climate may directly affect food availability/quality and/or foraging patterns (Levy

et al., 2016), with direct consequences on individual mass gain before hibernation. In particular, windy conditions may have decreased the time spent foraging for ground squirrels (Fairbanks & Dobson, 2007), while low humidity associated with decreased precipitation may have resulted in reduced primary productivity and inadequate forage quantity/quality, also affecting the accumulation of fat stores (Dobson et al., 2016; Dobson & Kjelgaard, 1985; Neuhaus et al., 1999). In turn, lower fat stores might have resulted in longer hibernation to avoid emerging when resources were scarce, explaining tardier EDs.

Similarly, climate conditions during hibernation had marked effects on the timing of emergence of ground squirrels, by either affecting the quality of hibernation and animal energy expenditure, or acting as cues indicating the end of the winter period. Years with later snow-melt resulted in later emergences for 1-year-old individuals, 2-year-old females, and ≥3-year-old individuals. Similarly, spatial clusters where snow melted later resulted in yearlings and ≥3-year-old females emerging later than in other areas. This was true both at the spatial and temporal scales, and for almost all individual categories, suggesting the necessity for snow to melt and uncover growing vegetation before ground squirrels emerge. In addition, a melting and wet snow pack makes it hard for the animals to easily move around the meadow (V. A. Viblanc, F. S. Dobson, and P. Neuhaus, personal observations) and likely increases the costs of thermoregulation, increasing overall energy expenditure at a time where their remaining fat stores are largely depleted. Local climate may thus act as a strong cue on the timing of ground squirrel emergence, though the immediate mechanism that stimulates emergence remains to be determined.

We found a positive spatial correlation between snow depth and emergence of 2-year-old and ≥3-year-old males, suggesting that males 2-year-old and older emerged later in locations where snow depth was higher during the inactive period. Higher snowpack or delayed snowmelt during the inactive period may also insulate and stabilize soil temperatures and hibernation conditions, decreasing fat reserve consumption, and thus allowing a longer hibernation or emergence in better condition (the latter being important for reproduction; Rubach et al., 2016). Snowpack thickness is an important variable influencing hibernating species, such as alpine marmots (Canale et al., 2016), hoary marmots (Patil et al., 2013), or northern Idaho ground squirrels (Goldberg & Conway, 2021). A negative correlation between the soil temperature during inactive period (at 1-m depth) and the ED of yearlings and ≥3-year-old males also seemed to apply. As for northern Idaho

ground squirrels (Goldberg & Conway, 2021), this result possibly indicates that unfavorable hibernating conditions lead to earlier emergence. For example, elevated soil temperatures could prevent animals from lowering their body temperature sufficiently for efficient energy saving during hibernation. In short, fat-storing and hibernating species might be sensitive to local environmental conditions and especially elevated temperatures that directly influence energy expenditure during this period of prolonged fasting.

Climatic variables correlating with ED differed between sex and age categories. Explanations for such diverging responses may be both ecological and physiological. Young (1990a) reported the existence of long posthibernation euthermic phases only in adult males, remaining several days underground before emerging despite favorable aboveground conditions, possibly to allow for gonadal maturation (Williams et al., 2017). Physiological and phenological differences in sex and age categories might therefore reflect distinct constraints between reproductively mature and nonmature individuals. Yearlings and 2-year-olds that emerge later in the spring likely do so when resources become more abundant and perhaps to avoid predator exposure or the social aggression related to reproduction (Constant et al., 2020; Murie & Harris, 1982). By contrast, mature individuals may optimize their ED according to the trade-off between energy resources (remaining fat stores and food availability) and the advantages of an early reproduction (Neuhaus, 2000). Furthermore, reproductive strategies might differ between males and females, with males taking advantage of earlier hibernation emergence to seek more breeding opportunities (Richardson's ground squirrels; Michener, 1983) and establish their territories (Manno & Dobson, 2008). Thus, environmental influences on a population might differ importantly between individuals with different life history constraints (e.g., age classes; Bonamour et al., 2020; Pardo et al., 2013).

Long-term changes in climate in relationship to ED

Previous studies have reported shifts in animal phenology linked to changes in climate, with species especially responding to ambient temperature (more so at high latitudes) and precipitations (Cohen et al., 2018). In the context of climate change, advancements in spring phenology have been found in the vast majority of cases (Parmesan & Yohe, 2003; but see Radchuk et al., 2019), however, mammals are poorly represented (Parmesan &

Yohe, 2003; but see Radchuk et al., 2019). Among those studied, *Marmotini* species respond differently to directional changes in climate. The phenology of Uinta ground squirrels did not change over time, despite a locally changing climate (Falvo et al., 2019). Yellow-bellied marmot have been found to emerge earlier in response to warming air temperatures (Inouye et al., 2000), while Columbian ground squirrels had been shown to display a trend toward later emergence, related to late spring snow fall (Lane et al., 2012).

Interestingly, our results are only partially consistent with previous findings on Columbian ground squirrels. We found evidence for delayed snowmelt (13 days) over the 28 years of study despite a general warming trend (air temperature increased by 1.40°C during the active season) and a positive effect of the first day without snow on ED (except for 2-year-old individuals). Despite such a climatic trend, different phenological responses were observed in Columbian ground squirrels of different age categories and meadows. As an example, on MC and MB, all individuals (except older males on MB) delayed emergences by 4 to 11 days over the 18- to 28-year period. Yet, no changes in emergences were observed on Meadow DOT for any age category, and long-term temporal trends in ED differed substantially depending on individual age and sex on MA. Two-year-old individuals advanced their emergence by 2 days over 22 years, whereas older individuals delayed their emergence by 3 days over the same period, and no change in ED was found for yearlings. Differences in ED trends between closely located meadows may be related to spatial heterogeneity of field, slope, or sun and wind exposure, with different effects of microclimates. Similar results were found in a recent study on the North American deer mouse (*Peromyscus maniculatus*), where temperature and photoperiod were positive cues of breeding phenology, the relationship varying among regions (McLean & Guralnick, 2021). Whether variation in ground squirrel phenology is linked to behavioral plasticity versus long-term adaptation remains to be seen. The small spatial scales tested here, and the diverging responses among nearby populations might suggest phenological plasticity (see Lane et al., 2019).

Many species responses to climate are likely to occur at microscale, rather than meso- or macro-scale (e.g., sockeye salmon; *Onchorhynchus nerka*; Martins et al., 2012). As highlighted here, the relationships between phenology and climate variables are likely to differ between neighboring populations of the same species, in response to contrasting microclimate conditions, even over small spatial scales. Thus, studies focusing on climate–phenology relationships in

animals would benefit by integrating fine local scale information on habitat.

CONCLUSION AND FURTHER PERSPECTIVES

Taken together, our results point to important differences in microclimate effects on animal phenology in neighboring populations. Of course, phenology may be linked to individual fitness and thereby the dynamics of the populations. Thus, we might also expect variation in these variables over small spatial scales. Integrating microclimatic variation in the study of climate change is likely to provide more accurate predictions of a variety of animal responses to a changing world.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Anouch Tamian, Claire Saraux, Vincent A. Viblanc, Peter Neuhaus, and F. Stephen Dobson involved in conception and design; F. Stephen Dobson, Peter Neuhaus, David Broussard, Tracey L. Hammer, Theodore G. Manno, Anna P. Nesterova, Shirley Raveh, Amy L. Skibiel, Nandini Rajamani, Vincent A. Viblanc, and Claire Saraux performed data acquisition; Anouch Tamian analyzed the data and prepared the manuscript; all authors read and commented on the final manuscript.

DATA AVAILABILITY STATEMENT
Data (Tamian, 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.19152923.

ORCID
Anouch Tamian https://orcid.org/0000-0003-1175-3326
Vincent A. Viblanc https://orcid.org/0000-0002-4953-659X
F. Stephen Dobson https://orcid.org/0000-0001-5562-6316
Peter Neuhaus https://orcid.org/0000-0002-6543-5561
Tracey L. Hammer https://orcid.org/0000-0003-3185-4909
Shirley Raveh https://orcid.org/0000-0003-0406-4928
Amy L. Skibiel https://orcid.org/0000-0002-2729-0402
Nandini Rajamani https://orcid.org/0000-0003-1356-8562
Claire Saraux https://orcid.org/0000-0001-5061-4009

REFERENCES
Alberta Parks. 2008. "Sheep River Provincial Park and Bluerock Wildland Provincial Park Management Plan—Open Government." https://open.alberta.ca/dataset/9780778574156.

Arnaud, C. M., F. S. Dobson, and J. O. Murie. 2012. "Philopatry and within-colony Movements in Columbian Ground Squirrels." *Molecular Ecology* 21: 493–504.

Barry, R. G. 1992. *Mountain Weather and Climate*. 2nd edn. London: Routledge.

Bonamour, S., L.-M. Chevin, D. Réale, C. Teplitsky, and A. Charmantier. 2020. "Age-Dependent Phenological Plasticity in a Wild Bird." *Journal of Animal Ecology* 89: 2733–41.

Box, G. E. P., and D. R. Cox. 1964. "An Analysis of Transformations." *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 26: 211–43.

Burnham, K. P., and D. R. Anderson. 2004. "Multimodel Inference: Understanding AIC and BIC in Model Selection." *Sociological Methods & Research* 33: 261–304.

Canale, C. I., A. Ozgul, D. Allainé, and A. Cohas. 2016. "Differential Plasticity of Size and Mass to Environmental Change in a Hibernating Mammal." *Global Change Biology* 22: 3286–303.

　　　　　　　　　　　　　　　　　　　　　　　　　　　　　　TAMIAN ᴇᴛ ᴀʟ.

Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. "Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild Bird Population." *Science* 320: 800–3.

Chmura, H. E., H. M. Kharouba, J. Ashander, S. M. Ehlman, E. B. Rivest, and L. H. Yang. 2019. "The Mechanisms of Phenology: The Patterns and Processes of Phenological Shifts." *Ecological Monographs* 89: e01337.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. "Shifting Plant Phenology in Response to Global Change." *Trends in Ecology & Evolution* 22: 357–65.

Cohen, J. M., M. J. Lajeunesse, and J. R. Rohr. 2018. "A Global Synthesis of Animal Phenological Responses to Climate Change." *Nature Climate Change* 8: 224–8.

Constant, T., S. Giroud, V. A. Viblanc, M. L. Tissier, P. Bergeron, F. S. Dobson, and C. Habold. 2020. "Integrating Mortality Risk and the Adaptiveness of Hibernation." *Frontiers in Physiology* 11: 706.

Davis, D. E. 1976. "Hibernation and Circannual Rhythms of Food Consumption in Marmots and Ground Squirrels." *The Quarterly Review of Biology* 51: 477–514.

Delignette-Muller, M. L., and C. Dutang. 2015. "fitdistrplus: An R Package for Fitting Distributions." *Journal of Statistical Software* 64: 1–34.

Dingemanse, N. J., and V. J. Kalkman. 2008. "Changing Temperature Regimes Have Advanced the Phenology of Odonata in the Netherlands." *Ecological Entomology* 33: 394–402.

Dobson, F. S. 1988. "The Limits of Phenotypic Plasticity in Life Histories of Columbian Ground Squirrels." In *Evolution of Life Histories of Mammals*, edited by M. S. Boyce, 193–210. New Haven, CT: Yale University Press.

Dobson, F. S., M. J. Badry, and C. Geddes. 1992. "Seasonal Activity and Body Mass of Columbian Ground Squirrels." *Canadian Journal of Zoology* 70: 1364–8.

Dobson, F. S., and J. D. Kjelgaard. 1985. "The Influence of Food Resources on Life History in Columbian Ground Squirrels." *Canadian Journal of Zoology* 63: 2105–9.

Dobson, F. S., J. E. Lane, M. Low, and J. O. Murie. 2016. "Fitness Implications of Seasonal Climate Variation in Columbian Ground Squirrels." *Ecology and Evolution* 6: 5614–22.

Durant, J. M., D. Ø. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. "Climate and the Match or Mismatch between Predator Requirements and Resource Availability." *Climate Research* 33: 271–83.

Fairbanks, B., and F. S. Dobson. 2007. "Mechanisms of the Group-Size Effect on Vigilance in Columbian Ground Squirrels: Dilution Versus Detection." *Animal Behaviour* 73: 115–23.

Falvo, C. A., D. N. Koons, and L. M. Aubry. 2019. "Seasonal Climate Effects on the Survival of a Hibernating Mammal." *Ecology and Evolution* 9: 3756–69.

Festa-Bianchet, M., and D. A. Boag. 1982. "Territoriality in Adult Female Columbian Ground Squirrels." *Canadian Journal of Zoology* 60: 1060–6.

Fietz, J., F. Langer, and W. Schlund. 2020. "They Like It Cold, but Only in Winter: Climate-Mediated Effects on a Hibernator." *Functional Ecology* 34: 2098–109.

Finch, T., J. W. Pearce-Higgins, D. I. Leech, and K. L. Evans. 2014. "Carry-over Effects from Passage Regions Are More Important Than Breeding Climate in Determining the Breeding Phenology and Performance of Three Avian Migrants of Conservation Concern." *Biodiversity and Conservation* 23: 2427–44.

Geiser, F. 2013. "Hibernation." *Current Biology* 23: R188–93.

Goldberg, A. R., and C. J. Conway. 2021. "Hibernation Behavior of a Federally Threatened Ground Squirrel: Climate Change and Habitat Selection Implications." *Journal of Mammalogy* 102: 574–87.

Graae, B. J., P. D. Frenne, A. Kolb, J. Brunet, O. Chabrerie, K. Verheyen, N. Pepin, et al. 2012. "On the Use of Weather Data in Ecological Studies along Altitudinal and Latitudinal Gradients." *Oikos* 121: 3–19.

Gultepe, I. 2015. Mountain weather: observation and modeling. *Advances in Geophysics*, 56: 229–312. https://doi.org/10.1016/bs.agph.2015.01.001

Hamel, S., J.-M. Gaillard, N. G. Yoccoz, R. D. Bassar, S. Bouwhuis, H. Caswell, M. Douhard, et al. 2018. "General Conclusion to the Special Issue Moving Forward on Individual Heterogeneity." *Oikos* 127: 750–6.

Harris, M. A., and J. O. Murie. 1984. "Inheritance of Nest Sites in Female Columbian Ground Squirrels on JSTOR." *Behavioral Ecology and Sociobiology* 15: 97–102.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. "Carry-over Effects as Drivers of Fitness Differences in Animals." *Journal of Animal Ecology* 80: 4–18.

Hengl, T., J. M. de Jesus, G. B. M. Heuvelink, M. R. Gonzalez, M. Kilibarda, A. Blagotić, W. Shangguan, et al. 2017. "SoilGrids250m: Global Gridded Soil Information Based on Machine Learning." *PLoS One* 12: e0169748.

Hollister, J., T. Shah, A. Robitaille, M. Beck, and M. Johnson. 2020. "elevatr: Access Elevation Data from Various APIs." R Package Version 0.3.1.

Huggett, R. J. 1995. *Geoecology: An Evolutionary Approach*. London: Routledge.

Humphries, M. M., D. W. Thomas, and D. L. Kramer. 2003. "The Role of Energy Availability in Mammalian Hibernation: A Cost-Benefit Approach." *Physiological and Biochemical Zoology* 76: 165–79.

Humphries, M. M., D. W. Thomas, and J. R. Speakman. 2002. "Climate-Mediated Energetic Constraints on the Distribution of Hibernating Mammals." *Nature* 418: 313–6.

Humphries, M. M., J. Umbanhowar, and K. S. McCann. 2004. "Bioenergetic Prediction of Climate Change Impacts on Northern Mammals." *Integrative and Comparative Biology* 44: 152–62.

Inouye, D. W., B. Barr, K. B. Armitage, and B. D. Inouye. 2000. "Climate Change Is Affecting Altitudinal Migrants and Hibernating Species." *Proceedings of the National Academy of Sciences* 97: 1630–3.

James, F. C., R. F. Johnston, N. O. Wamer, G. J. Niemi, and W. J. Boecklen. 1984. "The Grinnellian Niche of the Wood Thrush." *The American Naturalist* 124: 17–47.

Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, et al. 1996. "The NCEP/NCAR 40-Year Reanalysis Project." *Bulletin of the American Meteorological Society* 77: 437–72.

Kearney, M. R. 2020. "How Will Snow Alter Exposure of Organisms to Cold Stress under Climate Warming?" *Global Ecology and Biogeography* 29: 1246–56.

Kearney, M. R., P. K. Gillingham, I. Bramer, J. P. Duffy, and I. M. D. Maclean. 2020. "A Method for Computing Hourly,

Historical, Terrain-Corrected Microclimate Anywhere on Earth." *Methods in Ecology and Evolution* 11: 38–43.

Kreyling, J., and H. A. L. Henry. 2011. "Vanishing Winters in Germany: Soil Frost Dynamics and Snow Cover Trends, and Ecological Implications." *Climate Research* 46: 269–76.

Kunkel, K. E., D. R. Easterling, K. Hubbard, and K. Redmond. 2004. "Temporal Variations in Frost-Free Season in the United States: 1895–2000." *Geophysical Research Letters* 31.

Lampei, C., J. Wunder, T. Wilhalm, and K. J. Schmid. 2019. "Microclimate Predicts Frost Hardiness of Alpine *Arabidopsis thaliana* Populations Better than Elevation." *Ecology and Evolution* 9: 13017–29.

Lane, J. E., Z. J. Czenze, R. Findlay-Robinson, and E. Bayne. 2019. "Phenotypic Plasticity and Local Adaptation in a Wild Hibernator Evaluated through Reciprocal Translocation." *The American Naturalist* 197: 516–28.

Lane, J. E., L. E. B. Kruuk, A. Charmantier, J. O. Murie, D. W. Coltman, M. Buoro, S. Raveh, and F. S. Dobson. 2011. "A Quantitative Genetic Analysis of Hibernation Emergence Date in a Wild Population of Columbian Ground Squirrels." *Journal of Evolutionary Biology* 24: 1949–59.

Lane, J. E., L. E. B. Kruuk, A. Charmantier, J. O. Murie, and F. S. Dobson. 2012. "Delayed Phenology and Reduced Fitness Associated with Climate Change in a Wild Hibernator." *Nature* 489: 554–7.

Lê, S., J. Josse, and F. Husson. 2008. "FactoMineR: An R Package for Multivariate Analysis." *Journal of Statistical Software* 25: 1–18.

Lembrechts, J. J., and J. Lenoir. 2020. "Microclimatic Conditions Anywhere at Any Time!" *Global Change Biology* 26: 337–9.

Lenth, R. V. 2016. "Least-Squares Means: The R Package lsmeans." *Journal of Statistical Software* 69: 1–33.

Levy, O., T. Dayan, W. P. Porter, and N. Kronfeld-Schor. 2016. "Foraging Activity Pattern Is Shaped by Water Loss Rates in a Diurnal Desert Rodent." *The American Naturalist* 188: 205–18.

Lundblad, C. G., and C. J. Conway. 2021. "Nest Microclimate and Limits to Egg Viability Explain Avian Life-History Variation across Latitudinal Gradients." *Ecology* 102: e03338.

Maclean, I. M. D. 2020. "Predicting Future Climate at High Spatial and Temporal Resolution." *Global Change Biology* 26: 1003–11.

Maclean, I. M. D., A. J. Suggitt, R. J. Wilson, J. P. Duffy, and J. J. Bennie. 2017. "Fine-Scale Climate Change: Modelling Spatial Variation in Biologically Meaningful Rates of Warming." *Global Change Biology* 23: 256–68.

Manno, T. G., and F. S. Dobson. 2008. "Why Are Male Columbian Ground Squirrels Territorial?" *Ethology* 114: 1049–60.

Martay, B., M. J. Brewer, D. A. Elston, J. R. Bell, R. Harrington, T. M. Brereton, K. E. Barlow, M. S. Botham, and J. W. Pearce-Higgins. 2017. "Impacts of Climate Change on National Biodiversity Population Trends." *Ecography* 40: 1139–51.

Martins, E. G., S. G. Hinch, S. J. Cooke, and D. A. Patterson. 2012. "Climate Effects on Growth, Phenology, and Survival of Sockeye Salmon (*Oncorhynchus nerka*): A Synthesis of the Current State of Knowledge and Future Research Directions." *Reviews in Fish Biology and Fisheries* 22: 887–914.

Matheron, G. 1963. "Principles of Geostatistics." *Economic Geology* 58: 1246–66.

McCafferty, D. J., G. Pandraud, J. Gilles, M. Fabra-Puchol, and P.-Y. Henry. 2017. "Animal Thermoregulation: A Review of Insulation, Physiology and Behaviour Relevant to Temperature Control in Buildings." *Bioinspiration & Biomimetics* 13: 011001.

McCauley, S. J., J. I. Hammond, and K. E. Mabry. 2018. "Simulated Climate Change Increases Larval Mortality, Alters Phenology, and Affects Flight Morphology of a Dragonfly." *Ecosphere* 9: e02151.

McGuire, L. P., E. M. Johnson, W. F. Frick, and J. G. Boyles. 2021. "Temperature Alone Is Insufficient to Understand Hibernation Energetics." *Journal of Experimental Biology* 224(14): jeb239772.

McLean, B. S., and R. P. Guralnick. 2021. "Digital Biodiversity Data Sets Reveal Breeding Phenology and Its Drivers in a Widespread North American Mammal." *Ecology* 102: e03258.

Menzel, A. 2002. "Phenology: Its Importance to the Global Change Community." *Climatic Change* 54: 379–85.

Menzel, A., and P. Fabian. 1999. "Growing Season Extended in Europe." *Nature* 397: 659–9.

Michener, G. R. 1983. "Spring Emergence Schedules and Vernal Behavior of Richardson's Ground Squirrels: Why Do Males Emerge from Hibernation before Females?" *Behavioral Ecology and Sociobiology* 14: 29–38.

Moore, M. P., and R. A. Martin. 2019. "On the Evolution of Carry-over Effects." *Journal of Animal Ecology* 88: 1832–44.

Murie, J. O., and D. A. Boag. 1984. "The Relationship of Body Weight to Overwinter Survival in Columbian Ground Squirrels." *Journal of Mammalogy* 65: 688–90.

Murie, J. O., and M. A. Harris. 1978. "Territoriality and Dominance in Male Columbian Ground Squirrels (*Spermophilus columbianus*)." *Canadian Journal of Zoology* 56: 2402–12.

Murie, J. O., and M. A. Harris. 1982. "Annual Variation of Spring Emergence and Breeding in Columbian Ground Squirrels (*Spermophilus columbianus*)." *Journal of Mammalogy* 63: 431–9.

Murie, J. O., and M. A. Harris. 2011. "Social Interactions and Dominance Relationships between Female and Male Columbian Ground Squirrels." *Canadian Journal of Zoology* 66: 1414–20.

Nagy, L., and G. Grabherr. 2009. *The Biology of Alpine Habitats*. Oxford: OUP.

Neuhaus, P. 2000. "Timing of Hibernation and Molt in Female Columbian Ground Squirrels." *Journal of Mammalogy* 81: 571–7.

Neuhaus, P., R. Bennett, and A. Hubbs. 1999. "Effects of a Late Snowstorm and Rain on Survival and Reproductive Success in Columbian Ground Squirrels (*Spermophilus columbianus*)." *Canadian Journal of Zoology* 77: 879–84.

Norquay, K. J. O., and C. K. R. Willis. 2014. "Hibernation Phenology of *Myotis lucifugus*." *Journal of Zoology* 294: 85–92.

Norris, D. R. 2005. "Carry-over Effects and Habitat Quality in Migratory Populations." *Oikos* 109: 178–86.

Ockendon, N., D. Leech, and J. W. Pearce-Higgins. 2013. "Climatic Effects on Breeding Grounds Are More Important Drivers of Breeding Phenology in Migrant Birds Than Carry-over Effects from Wintering Grounds." *Biology Letters* 9: 20130669.

O'Rourke, N., and L. Hatcher. 2013. *A Step-by-Step Approach to Using SAS for Factor Analysis and Structural Equation Modeling*, Second ed. Cary, NC: SAS Institute.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. "Coupled Dynamics of Body Mass and Population Growth in Response to Environmental Change." *Nature* 466: 482–5.

Pachauri, R. K., M. R. Allen, V. R. Barros, J. Broome, W. Cramer, R. Christ, J. A. Church, et al. 2014. In *Climate Change 2014: Synthesis Report*. Contribution of Working Groups I, II and III to the Fifth

Assessment Report of the Intergovernmental Panel on Climate Change, edited by R. K. Pachauri and L. Meyer. Geneva: IPCC.

Pardo, D., C. Barbraud, M. Authier, and H. Weimerskirch. 2013. "Evidence for an Age-Dependent Influence of Environmental Variations on a Long-Lived Seabird's Life-History Traits." *Ecology* 94: 208–20.

Parmesan, C., and G. Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems." *Nature* 421: 37–42.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, 13: 1860–72. https://doi.org/10.1111/j.1365-2486.2007.01404.x

Paruchuri, S., A. T. Smith, Z. Fan, and F. S. Dobson. 2019. "Microhabitat Use by Plateau Pikas: Living on the Edge." *Journal of Mammalogy* 100: 1221–8.

Patil, V. P., S. F. Morrison, T. J. Karels, and D. S. Hik. 2013. "Winter Weather Versus Group Thermoregulation: What Determines Survival in Hibernating Mammals?" *Oecologia* 173: 139–49.

Pires, A. P. F., D. S. Srivastava, N. A. C. Marino, A. A. M. MacDonald, M. P. Figueiredo-Barros, and V. F. Farjalla. 2018. "Interactive Effects of Climate Change and Biodiversity Loss on Ecosystem Functioning." *Ecology* 99: 1203–13.

Potter, K. A., H. A. Woods, and S. Pincebourde. 2013. "Microclimatic Challenges in Global Change Biology." *Global Change Biology* 19: 2932–9.

Pretzlaff, I., and K. H. Dausmann. 2012. "Impact of Climatic Variation on the Hibernation Physiology of *Muscardinus avellanarius*." In *Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations*, edited by T. Ruf, C. Bieber, W. Arnold, and E. Millesi, 85–97. Berlin, Heidelberg: Springer.

QGIS Development Team. 2021. QGIS Geographic information system. *Open Source Geospatial Foundation Project*. http://qgis.osgeo.org

Radchuk, V., T. Reed, C. Teplitsky, M. van de Pol, A. Charmantier, C. Hassall, P. Adamík, et al. 2019. "Adaptive Responses of Animals to Climate Change Are Most Likely Insufficient." *Nature Communications* 10: 1–14.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing, https://www.R-project.org/

Rivoirard, J., J. Simmonds, K. G. Foote, P. Fernandes, and N. Bez. 2008. *Geostatistics for Estimating Fish Abundance*. Oxford: Blackwell Science.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. "Fingerprints of Global Warming on Wild Animals and Plants." *Nature* 421: 57–60.

Rubach, K., M. Wu, A. Abebe, F. S. Dobson, J. O. Murie, and V. A. Viblanc. 2016. "Testing the Reproductive and Somatic Trade-off in Female Columbian Ground Squirrels." *Ecology and Evolution* 6: 7586–95.

Saino, N., R. Ambrosini, M. Caprioli, A. Romano, M. Romano, D. Rubolini, C. Scandolara, and F. Liechti. 2017. "Sex-Dependent Carry-over Effects on Timing of Reproduction and Fecundity of a Migratory Bird." *Journal of Animal Ecology* 86: 239–49.

Saleeba, K., B. L. Phillips, M. O'Shea, and M. R. Kearney. 2020. "Using Biophysical Models to Improve Survey Efficiency for Cryptic Ectotherms." *The Journal of Wildlife Management* 84: 1185–95.

Saraux, C., J.-M. Fromentin, J.-L. Bigot, J.-H. Bourdeix, M. Morfin, D. Roos, E. V. Beveren, and N. Bez. 2014. "Spatial Structure and Distribution of Small Pelagic Fish in the Northwestern Mediterranean Sea." *PLoS One* 9: e111211.

Shaw, W. T. 1926. "The Storing Habit of the Columbian Ground Squirrel." *The American Naturalist* 60: 367–73.

Sparks, T. H., and T. J. Yates. 1997. "The Effect of Spring Temperature on the Appearance Dates of British Butterflies 1883–1993." *Ecography* 20: 368–74.

Strode, P. K. 2003. "Implications of Climate Change for North American Wood Warblers (Parulidae)." *Global Change Biology* 9: 1137–44.

Suggitt, A. J., P. K. Gillingham, J. K. Hill, B. Huntley, W. E. Kunin, D. B. Roy, and C. D. Thomas. 2011. "Habitat Microclimates Drive Fine-Scale Variation in Extreme Temperatures." *Oikos* 120: 1–8.

Tamian, A. 2022. "Tamianetal2022_data.csv." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.19152923.v1.

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., et al, 2016. Phenological Sensitivity to Climate Across Taxa and Trophic Levels. *Nature*, 535: 241–5. https://doi.org/10.1038/nature18608

Varner, J., and M. D. Dearing. 2014. "The Importance of Biologically Relevant Microclimates in Habitat Suitability Assessments." *PLoS One* 9: e104648.

Visser, M. E., and C. Both. 2005. "Shifts in Phenology Due to Global Climate Change: The Need for a Yardstick." *Proceedings of the Royal Society B: Biological Sciences* 272: 2561–9.

Visser, M. E., and L. J. M. Holleman. 2001. "Warmer Springs Disrupt the Synchrony of Oak and Winter Moth Phenology." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 268: 289–94.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. "Ecological Responses to Recent Climate Change." *Nature* 416: 389–95.

Wang, S., and F. Hou. 2021. "Burrow Characteristics and Ecological Significance of Marmota Himalayana in the Northeastern Qinghai-Tibetan Plateau." *Ecology and Evolution* 11: 9100–9.

Wiggett, D. R., D. A. Boag, and A. D. R. Wiggett. 1989. "Movements of Intercolony Natal Dispersers in the Columbian Ground Squirrel." *Canadian Journal of Zoology* 67: 1447–52.

Williams, C. T., B. M. Barnes, G. J. Kenagy, and C. L. Buck. 2014. "Phenology of Hibernation and Reproduction in Ground Squirrels: Integration of Environmental Cues with Endogenous Programming." *Journal of Zoology* 292: 112–24.

Williams, C. T., C. L. Buck, M. J. Sheriff, M. M. Richter, J. S. Krause, and B. M. Barnes. 2017. "Sex-Dependent Phenological Plasticity in an Arctic Hibernator." *American Naturalist* 190: 854–9.

Wilson, S. M., T. W. Buehrens, J. L. Fisher, K. L. Wilson, and J. W. Moore. 2021. "Phenological Mismatch, Carryover Effects, and Marine Survival in a Wild Steelhead Trout Oncorhynchus Mykiss Population." *Progress in Oceanography* 193: 102533.

Winder, M., and D. E. Schindler. 2004. "Climate Change Uncouples Trophic Interactions in an Aquatic Ecosystem." *Ecology* 85: 2100–6.

Woillez, M., J.-C. Poulard, J. Rivoirard, P. Petitgas, and N. Bez. 2007. "Indices for Capturing Spatial Patterns and Their Evolution in Time, with Application to European Hake (*Merluccius merluccius*) in the Bay of Biscay." *ICES Journal of Marine Science* 64: 537–50.

Wood, S. 2017. *Generalized Additive Models: An Introduction with R*. New York: Chapman and Hall/CRC.

World Meteorological Organization. 2015, November 26. "Climate." https://public.wmo.int/en/our-mandate/climate.

Young, P. J. 1990a. "Structure, Location and Availability of Hibernacula of Columbian Ground Squirrels (*Spermophilus columbianus*)." *The American Midland Naturalist* 123: 357–64.

Young, P. J. 1990b. "Hibernating Patterns of Free-Ranging Columbian Ground Squirrels." *Oecologia* 83: 504–11.

Zellweger, F., P. De Frenne, J. Lenoir, D. Rocchini, and D. Coomes. 2019. "Advances in Microclimate Ecology Arising from Remote Sensing." *Trends in Ecology & Evolution* 34: 327–41.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. "A Protocol for Data Exploration to Avoid Common Statistical Problems." *Methods in Ecology and Evolution* 1: 3–14.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.