

Delayed phenology and reduced fitness associated with climate change in a wild hibernator

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The most commonly reported ecological effects of climate change are shifts in phenologies, in particular of warmer spring temperatures leading to earlier timing of key events^{1,2}. Among animals, however, these reports have been heavily biased towards avian phenologies, whereas we still know comparatively little about other seasonal adaptations, such as mammalian hibernation. Here we show a significant delay (0.47 days per year, over a 20-year period) in the hibernation emergence date of adult females in a wild population of Columbian ground squirrels in Alberta, Canada. This finding was related to the climatic conditions at our study location: owing to within-individual phenotypic plasticity, females emerged later during years of lower spring temperature and delayed snowmelt. Although there has not been a significant annual trend in spring temperature, the date of snowmelt has become progressively later owing to an increasing prevalence of late-season snowstorms. Importantly, years of later emergence were also associated with decreased individual fitness. There has consequently been a decline in mean fitness (that is, population growth rate) across the past two decades. Our results show that plastic responses to climate change may be driven by climatic trends other than increasing temperature, and may be associated with declines in individual fitness and, hence, population viability.

The timings of key periodic events, or phenologies, in wild animal populations are assumed to have evolved to synchronize life cycles with seasonal availabilities of resources³. As temporal resource distributions are shifting rapidly owing to climate change⁴, the extent to which phenologies respond should therefore have important consequences for both the fitness of individuals and the viability of populations^{5,6}. Phenological shifts are indeed the most often cited ecological responses to climate change^{1,2}, with estimates of the mean responses across groups of species ranging from advances of 0.23 days (ref. 7) to 0.55 days (ref. 8) per year. Moreover, there is evidence that populations that have either not shown a phenological advance⁹, or have exhibited insufficient advances to remain synchronized with their primary food sources^{10,11}, are more likely to be in decline.

Unlike many bird species that undertake extensive migrations to cope with seasonal variation in resource availability, most mammals are sedentary and must therefore rely on adaptations to cope *in situ*. Hibernation is one such adaptation that is widespread across mammalian orders¹² and is assumed to have evolved in response to environmental resource shortages¹³. However, the environment in which hibernation has most often been studied, is the laboratory. Our understanding of the causes and consequences of natural variation in hibernation expression thus lags considerably behind that of its underlying physiological and biochemical mechanisms. The phenology of hibernation, particularly the date of emergence, is considered to have important consequences for individual fitness¹⁴, but the relative lack of data from wild populations currently limits our ability to adequately test this hypothesis and, by extension, make predictions as to how hibernating species will be affected by climate change. We

report here an analysis of hibernation phenology in a wild population of Columbian ground squirrels (*Urocitellus columbianus*).

Columbian ground squirrels are small (less than 1 kg), obligate hibernators resident in the Rocky Mountains of North America. The short growing seasons of plants in the alpine and subalpine regions that they inhabit require that they spend the majority of the year (8–9 months) hibernating¹⁵. Over the past 20 years, the mean date of emergence from hibernation of adult females in our study population in Alberta, Canada, has become later by 0.47 ± 0.15 days (\pm s.e.m.) per year ($F_{1,18} = 9.68$, $r^2 = 0.35$, $P = 0.006$; general linear model; Fig. 1a). To investigate the environmental factors contributing to this delay, we quantified the phenotypic responses of individuals to variation in two weather variables (date of snowmelt and spring temperature; see Methods for definitions) previously shown to influence emergence date in hibernating mammals^{6,16}, as well as the annual trends in these predictors.

Individuals responded plastically to both weather variables. Female ground squirrels emerged 0.07 ± 0.03 days (\pm s.e.m.) later with each 1-day delay in snowmelt, and 1.51 ± 0.47 days (\pm s.e.m.) later with each 1-°C decrease in temperature (Table 1, Fig. 1b and Supplementary Fig. 1). There was also significant variation between individuals in their average emergence date (partly because emergence date is heritable in this population¹⁷), but not in individual plasticity in response to either climatic variable (that is, a significant difference in intercept, but not slopes of individual reaction norms¹⁸; Table 1).

Date of snowmelt has been delayed by 2.83 ± 0.88 days (\pm s.e.m.) per year over the course of the study ($F_{1,18} = 10.38$, $r^2 = 0.37$, $P = 0.005$; general linear model; Fig. 1c), but there has not been a significant trend in spring temperature (-0.10 ± 0.05 °C (\pm s.e.m.) per year; $F_{1,18} = 3.00$, $r^2 = 0.10$, $P = 0.101$; general linear model; Fig. 1c). The delay in snowmelt has been caused by an increasing likelihood of late-season snowstorms ($\chi^2_1 = 8.97$, $P = 0.003$; generalized linear model). During the first decade of the study, there was only 1 year that experienced a substantial snowfall event (that is, ≥ 5 cm of snow deposited over > 1 day) after the middle of April, whereas in the most recent decade 7 years experienced such late snowstorms. This result follows consensus projections from current climate models of elevated atmospheric moisture flux and, over most of North America, increased precipitation. Specifically, an overall increase in both total winter precipitation and the frequency of heavy precipitation events is projected¹⁹.

Adult females are engaged in reproduction for approximately half of the 3–4-month active season (that is, 51 days: 24 days of gestation and 27 days of lactation²⁰), after which females and offspring must accumulate sufficient fat resources to endure the ensuing hibernation period. Therefore, we predicted that delayed emergence dates would have fitness costs for adult females. We calculated an annual contribution to individual fitness (hereafter referred to as ‘annual fitness’) from both individual over-winter survival (S) and reproductive success (R) as $S + 0.5 \times R$ (ref. 21) (analyses of S and R separately are provided in Supplementary Tables 1 and 2, and Supplementary Fig. 2). S was

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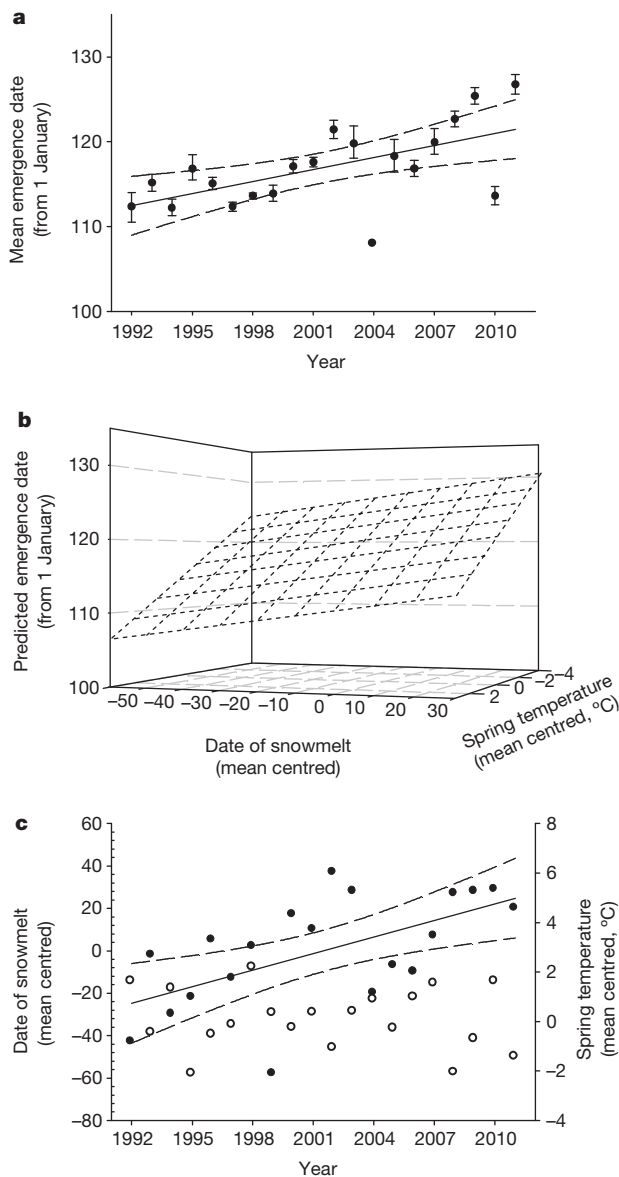


Figure 1 | Variation in emergence date from hibernation and two environmental predictors of emergence (spring temperature and date of snowmelt) for adult female Columbian ground squirrels during the past 20 years. **a**, Annual trend in mean emergence date ($b_{\text{year}} = 0.47, P = 0.006$). **b**, The influence of date of snowmelt (b_{W} (the within-subject effect) = 0.07, $P = 0.031$ (from within-subject mean centred analysis)) and spring temperature ($b_{\text{W}} = -1.51, P = 0.003$ (from within-subject mean centred analysis)) on emergence date. **c**, annual variation in the date of snowmelt (black circles; mean centred; $b_{\text{year}} = 2.83, P = 0.005$) and spring temperature (open circles; mean centred; $b_{\text{year}} = -0.10\text{ }^{\circ}\text{C}, P = 0.101$). Regression lines (with 95% confidence intervals) are indicated for all significant relationships in **a** and **c**. Data are shown as mean \pm s.e.m.

approximately 3 (ref. 23) and the average over-winter survival rate of juveniles is 30–35%²⁴; average R across all females and years was therefore 0.91 ± 0.05 (\pm s.e.m.) surviving offspring. Individuals of neither sex disperse as juveniles²⁵, and all animals surviving their first winter were therefore captured as yearlings the following spring.

We considered effects of variation both between and within years when investigating the relationship between annual fitness and emergence date. Years with late average emergence dates were associated with lower annual fitness of females (Table 2 and Fig. 2a), but there was no evidence of further effects of variation within years (Table 2; that is, within a given year, there was not a significant difference in the fitness of early versus late emergers). As average emergence date has become later over the past 2 decades, there has been an associated decrease in mean annual fitness within the population ($b_{\text{year}} = -32.63, F_{1,16} = 7.58, P = 0.014$; general linear model (where b_{year} is the linear coefficient term for year)). Although the decrease has slowed down recently ($b_{\text{year}}^2 = 8.00 \times 10^{-3}, F_{1,16} = 6.71, P = 0.020$; general linear model, where b_{year}^2 is the quadratic coefficient term for year), partly owing to two recent years in which emergence was relatively early (2004 and 2010; Fig. 1a), mean fitness has also become more volatile (Fig. 2b). During the first decade of the study, only 1 of the 10 years (10%) exhibited a mean fitness value of less than 1 (that is, population decrease), whereas 4 out of 9 years (44%) exhibited such values in the most recent decade.

Declines in population viability resulting from insufficient phenological advances can theoretically be mitigated by adaptive phenotypic plasticity²⁶ or microevolution⁵ serving to resynchronize populations with their food resources. However, the phenological shift in Columbian ground squirrels is in the very direction that seems to be detrimental to fitness (Fig. 2a). Heavy snow cover prevents access to the squirrels' vegetative food sources. Therefore, squirrels are unable to resume above-ground activity earlier. However, delayed emergence presumably challenges their ability to subsequently accumulate the necessary fat resources to survive ensuing hibernation. This challenge could be from a shortening of the active season and/or from the squirrels attempting to fatten during a less energetically favourable period (for example, after vegetative senescence). Regardless of the mechanism, the documented association between emergence date and individual fitness suggests that, should the projections of increased winter

scored as 0 or 1 depending on whether a female with a known emergence date in year_{*t*} survived to the spring of year_{*t*+1} (average across all years: $77.1 \pm 3.3\%$ (\pm s.e.m.)). Adult females are philopatric²² and the study population is fully censused; we were thus confident that all females surviving the winter were captured the following spring. R was calculated as the number of offspring that a female produced in a given year that survived over the winter. Average litter size is

Table 1 | Effect of date of snowmelt and spring temperature on hibernation emergence date of female Columbian ground squirrels.

Effects	Model terms	Coefficient (s.e.m.)	χ^2 (d.f.)	<i>P</i> value
Fixed effects	Intercept	118.46 (0.77)		
	Between-subject effect (snowmelt)	0.06 (0.04)	2.71 (1)	0.100
	Within-subject effect (snowmelt)	0.07 (0.03)	4.65 (1)	0.031
	Between-subject effect (spring temperature)	-2.77 (0.76)	12.40 (1)	<0.001
	Within-subject effect (spring temperature)	-1.51 (0.47)	8.66 (1)	0.003
Random effects	Age	Range: -4.93 (1.81; age = 9) to 0.95 (5.04; age = 11)	24.56 (9)	0.004
	Year	6.38	59.45 (1)	<0.001
	Random intercept	8.28	34.62 (3)	<0.001
	Random slope (snowmelt)	1.12×10^{-3}	0.77 (3)	0.856
	Random slope (spring temperature)	0.05	0.35 (3)	0.950
	Residual error	21.08		

Model outputs are from a random regression model with within-subject mean centring ($n = 512$ records from 150 females, across 20 years). The influences of date of snowmelt and spring temperature are partitioned into between- and within-subject effects. Age, in years (as a 10-level categorical factor), is included as a fixed effect to control for age-related influences on emergence date and we report the maximum and minimum of the 10 age coefficients. The random effect structure estimates the variance in both the intercept and slopes of individuals in response to the two environmental variables (see Methods for details). *P* values are based on likelihood ratio tests. d.f., degrees of freedom.

Table 2 | Influence of variation in hibernation emergence date on annual fitness of female Columbian ground squirrels.

Effects	Model term	Coefficient	95% Highest posterior density intervals
Fixed effects	Intercept	1.23	0.88 to 1.52
	Between-year gradient	-0.14	-0.27 to -0.03
	Within-year gradient	-0.03	-0.08 to 0.02
	Density	-9.68×10^{-3}	-2.04×10^{-2} to 1.90×10^{-3}
	Age	Range: -0.76 (age = 10) to 0.20 (age = 4)	-1.01 to -0.15 (age = 10); 0.09 to 0.43 (age = 4)
Random effects	Identity	0.06	
	Year	0.09	

Standardized linear (between-years and within-years) gradients, based on annual fitness, for hibernation emergence date of adult female Columbian ground squirrels. Age in years (as a 10-level categorical factor) is included as a fixed effect to control for age-related influences on fitness and we report the maximum and minimum of the 10 age coefficients. Density (number of adult females in the population) is included as a continuous fixed effect to control for density-dependent influences. Analyses are based on a sample size of $n = 459$ records, collected from 145 females for which we had both an emergence date phenotype and fitness estimate. The 95% highest posterior density intervals (from 1,000 Markov chain Monte Carlo samples) are indicated. Individuals are represented in the data set multiple times, and multiple records were produced each year, therefore the variances associated with the random effects of identity and year are also included. Complete definitions for all terms are provided in the Methods.

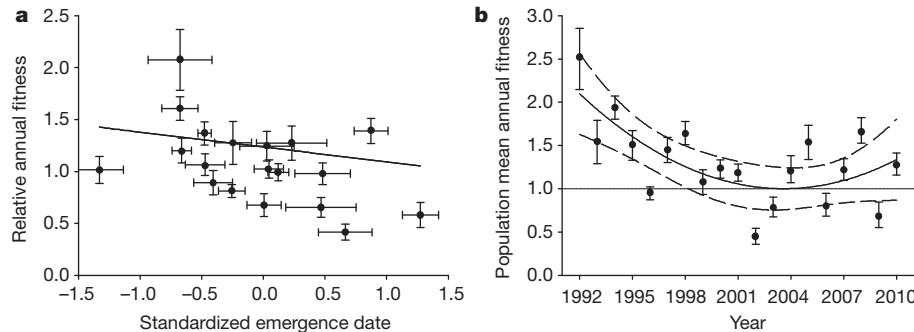


Figure 2 | Influence of mean emergence date from hibernation on, and the annual trend in, mean annual fitness of adult female Columbian ground squirrels over the past 20 years. **a**, The influence of standardized emergence date (standardized to a mean of zero and unit variance) on mean relative annual fitness (individual values divided by the population mean) (from mean-centred selection analysis, β_B (between-individual selection gradient) = -0.14; highest

posterior density interval, -0.27 - -0.03). **b**, The annual trend ($b_{\text{year}} = -32.63$, $P = 0.014$; $b_{\text{year}^2} = 8.00 \times 10^{-3}$, $P = 0.020$) in mean annual fitness. Regression lines (with 95% confidence intervals) are indicated for both significant relationships and the threshold between population growth and decline (mean annual fitness = 1.0) is indicated in **b**. Data are shown as mean \pm s.e.m.

precipitation hold true, continued phenological delays will lead to diminished and more volatile population dynamics.

A recent study has shown that earlier snowmelts led to advances in emergence date from hibernation and concordant increases in overwinter survival of yellow-bellied marmots (*Marmota flaviventris*)⁶. Thus, although the direction of the trend is directly opposite to what we observed in Columbian ground squirrels, the links between the environmental predictor, emergence phenology and fitness are consistent. This is important because the overwhelming majority of research to date on the effects of climate change in natural systems has focused on increasing temperatures (for example, a previous study² summarized over 25,000 climate-change-induced phenological shifts and all of these were in response to temperature). Spring temperature is certainly the most ecologically relevant cue for many species, but over many areas of the globe its influence will be moderated by the date of snowmelt. Historically, these two cues should have been correlated as warmer springs led to earlier melting of the snow pack. However, over the past 20 years, this correlation has been weak at our study site ($t_{18} = -1.85$, $r = -0.40$, $P = 0.081$; Pearson correlation) as the date of snowmelt is now heavily influenced by an increasing prevalence of late-season snowstorms. The results presented here highlight the extent to which aspects of climate change other than increasing temperature may affect natural populations.

METHODS SUMMARY

We documented dates of emergence from hibernation and annual fitness of all adult females ($n = 512$ records from 150 females) within a fully censused population of Columbian ground squirrels in Alberta, Canada (50° N, 114° W and 1,500 m above sea level) from 1992 to 2011. Unique alphanumeric eartags enabled individuals to be identified, and maternity assignment protocols are as described previously¹⁷. The date of snowmelt and spring temperature were recorded at a nearby weather station and a complete explanation of the treatment of climatic data are provided in the Methods. We used general linear models to quantify

annual trends in mean emergence date, the two environmental variables and mean fitness ($n = 20$ years, except for analyses involving fitness as 2011 data are not yet available). We also fit a generalized linear model with a binomial error structure to examine whether late-season snowstorms have become more likely in recent years. Plasticity of individuals was quantified using a random regression model with within-subject mean centering^{18,27}. We used a mean-centred mixed-effects model, implemented in a traditional linear selection analysis^{27,28}, to examine the influence of hibernation phenology on annual fitness both within, and across, years. Nonlinear and correlational selection gradients are presented in Supplementary Table 3.

Full Methods and any associated references are available in the online version of the paper.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions J.E.L., L.E.B.K., A.C. and F.S.D. developed the concept of the paper, and F.S.D. and J.O.M. collected the field data. J.E.L. performed all analyses and wrote the paper, and all other authors provided intellectual insight and detailed comments. All authors obtained funding.

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METHODS

Study system. We used previously established protocols¹⁷ to document dates of hibernation emergence of adult female Columbian ground squirrels (≥ 2 years of age). In brief, we began conducting daily surveys from observation towers before the emergence of the first individuals. As they emerged, squirrels were caught in live traps and identified with alphanumeric eartags. Almost all individuals ($n = 136$) were originally handled as juveniles and their ages were known with certainty. Adults in the first year of the study (1992; $n = 4$) and any immigrating animals ($n = 10$) received eartags on first capture and their ages were estimated either as yearlings or 2 years and older, based on body size and reproductive condition.

Weather variables. The date of snowmelt for each year was determined from data collected at a nearby weather station in Okotoks, Alberta (Environment Canada, <http://climate.weatheroffice.ec.gc.ca>; 50° N, 114° W, and 1,081 m above sea level; approximately 40 km from the study site). Patterns of snowmelt in this area can be extremely variable owing to adiabatic warming of winds from the Pacific Ocean²⁹ and frequent late-season snowstorms. We therefore chose the first day of the year with 0 cm of snow on the ground after continuous snow cover. However, if a substantial snowfall event (that is, ≥ 5 cm deposited over >1 day) occurred after this date, we selected the first day with 0 cm of snow after this event. The restriction to >1 day was chosen so that only snowfall events providing relatively consistent ground cover (as opposed to short-duration snow flurries) were included. A relatively moderate definition of ≥ 5 cm was chosen because the weather station, although relatively close in distance to the field site, is >400 m lower in elevation. Snowfall at the field site is therefore expected to be more severe. In 2 separate years (2002 and 2004) a substantial snowfall event occurred following the emergence of all females. The dates of snowmelt after these events were considered in the analyses of annual trends in weather variables. However, as they could not influence ground squirrel phenology, the dates of snowmelt before these events were used in the plasticity analyses.

Mean spring ambient temperatures (T_a) were calculated based on daily temperature recordings taken at the Okotoks station and a sliding window approach was used to determine the relevant period over which to calculate average temperature. We varied the window from 2 to 30 days and considered all possible windows from 1 January to 15 June. We selected the window (Julian days: 102–123 (12 April to 3 May in non-leap years)) that provided the highest r^2 with the mean annual emergence date ($r^2 = 0.54$). We used a Pearson's product-moment correlation test to estimate the correlation between the two weather variables.

Plasticity analyses. We used a random regression model to evaluate the influence of the two weather variables on the emergence dates of females¹⁷. Because we wished to quantify the extent of within-individual plastic responses to environmental variation, we used a within-subject mean centring approach that decomposes the environmental effects into those associated with the average environment experienced by an individual over its lifetime (a 'between-individual' effect), versus deviations of the environment in a given year from the individual's lifetime average (the 'within-individual' plastic effect)²⁷.

Emergence date (y_{ij}) for each individual i in year j was modelled as a continuous response to variation in the two weather variables, T_a and snow:

$$y_{ij} = b_0 + b_B \bar{T}_{a_i} + b_W (T_{a_{ij}} - \bar{T}_{a_i}) + b_B \bar{\text{snow}}_{i.} + b_W (\text{snow}_{ij} - \bar{\text{snow}}_{i.}) + \text{age} + [\text{year}] + [\text{ID}_i] + [\text{ID}_i \cdot (\text{snow}_{ij} - \bar{\text{snow}}_{i.})] + [\text{ID}_i \cdot (T_{a_{ij}} - \bar{T}_{a_i})] + e_{ij}$$

where b_0 represents the intercept and, as the weather variables were standardized to zero mean, is equivalent to the expected emergence date in the average environment. The between-subject effect (b_B) is estimated as the slope of y_{ij} on the mean value of each weather variable for each individual, i . The within-subject (b_W) effect is estimated as the slope of y_{ij} on the annual deviation of the weather variable from the subject mean. The random effects are shown in square brackets: $[\text{ID}_i]$ quantifies the variation in within-subject intercepts, and $[\text{ID}_i \cdot (T_{a_{ij}} - \bar{T}_{a_i})]$ and $[\text{ID}_i \cdot (\text{snow}_{ij} - \bar{\text{snow}}_{i.})]$ quantify the variation in the within-subject slopes for

the effects of the two weather variables (that is, the reaction norms¹⁸). Year [year] was included in order to model variation across years that is not explained by the weather variables and to account for multiple measures per year. Age in years was included as a 10-level fixed effect and e_{ij} represents the residual error. Significance of model terms was assessed with likelihood ratio tests ($-2 \times$ difference in log-likelihood between hierarchical models, tested against a chi-square distribution with the number of degrees of freedom that corresponded to the difference in the number of terms estimated).

Annual trends. We used general linear models implemented in R (ver. 2.10.0; R Core Development Team) to determine whether there was a significant annual trend (year fitted as a continuous fixed effect) in mean emergence date or in either of the weather variables. We also fit a generalized linear model with a binomial error structure to examine whether late-season snowstorms have become more likely in recent years. The female that emerged the earliest over the 20 years did so on 9 April. Therefore, whether a snowstorm, which deposited at least 5 cm of snow, was observed following 9 April (scored as 0 or 1) was entered as the dependent variable, with year fitted as a continuous fixed effect.

Fitness implications of variation in emergence date. We calculated annual contributions to lifetime fitness (which, for simplicity, we refer to as a measure of 'annual fitness') for individuals as $S + 0.5 \times R$, following a previous study²¹. S represents over-winter survival and R represents annual reproductive success (defined in the main text). Prior to the analysis, emergence dates were standardized to a mean of zero and unit variance, and relative fitness was calculated by dividing by the overall mean²⁸. Because we wished to test whether any association between annual fitness and emergence date was driven by between- versus within-year variation, for each individual we considered effects of the annual mean emergence date (\bar{y}_j) and the deviation of that individual from the annual mean ($y_{ij} - \bar{y}_j$).

$$\omega_{ij} = \beta_0 + \beta_B \bar{y}_j + \beta_W (y_{ij} - \bar{y}_j) + \text{age} + \text{density} + [\text{year}] + [\text{ID}_i] + e_{ij}$$

In this model, ω_{ij} represents relative annual fitness (divided by the overall population mean) of individual i at time j . β_0 is the intercept, β_B represents the influence of the annual mean emergence date that year and β_W represents the within-year variation. Age in years was included as a 10-level fixed effect. Population density (estimated as the number of adult females) varied substantially across the study period (range: 4–56) and was therefore included as a fixed effect to control for potential density-dependent effects on fitness. Explanations and results of quadratic and correlational analyses are included in Supplementary Table 3. Highest posterior density intervals were generated from 1,000 Markov chain Monte Carlo samples and are reported instead of standard errors and P values, as we cannot assume normality^{28,30}. The random effects of identity $[\text{ID}_i]$ and [year] were fitted to account for multiple records per individual and per year, respectively.

We used a general linear model to determine whether there has been a significant trend across years in the average annual fitness within the population and whether this trend has changed over time (by fitting both the linear and quadratic coefficients for year, respectively). Female survival rate (\bar{S}) was calculated as the percentage of females surviving over the winter and annual reproductive success (\bar{R}) was calculated as the mean number of pups surviving over the winter per female. Mean annual fitness across the population was then calculated as $\bar{S} + 0.5 \times \bar{R}$. Note that this also provides an approximation of population growth rate³¹.

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