# Phenotypic Plasticity and Local Adaptation in a Wild Hibernator Evaluated through Reciprocal Translocation*

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ABSTRACT: Phenological shifts are the most commonly reported ecological responses to climate change and can be produced rapidly by phenotypic plasticity. However, both the limits of plasticity and whether it will be sufficient to maintain local adaptation (or even lead to maladaptation) are less clear. Increased winter precipitation has been shown to lead to phenological delays and corresponding annual decreases in fitness in Columbian ground squirrels (*Urocitellus columbianus*). We took advantage of natural phenological variation (across elevations) in this species to better assess the extent of phenotypic plasticity in emergence dates and the relationships between emergence dates and individual annual fitness. We coupled a reciprocal translocation experiment with natural monitoring across two populations separated by ~500 m in elevation. Individuals in both populations responded plastically to both spring temperature and winter precipitation. Translocated individuals adjusted their emergence dates to approach those of individuals in their adoptive populations but did differ significantly in their emergence dates from residents. There were no differences in annual fitness among treatment groups nor selection on emergence date within a year. Phenotypic plasticity is thus sufficient to allow individuals to respond to broad environmental gradients, but the influence of variation in emergence dates on annual fitness requires further investigation.

*Keywords:* climate change, hibernation, maladaptation, phenotypic plasticity.

## Introduction

Selection should favor phenotypes that optimally schedule energetically expensive life-history events, such as reproduction, in response to both intra- and interannual variation in resource availability (Levins 1968; Fretwell 1972). By definition, seasonality represents intra-annual variation: periods of energetic abundance (e.g., summers in northern temperate environments) are punctuated by extended periods of energetic shortfalls (e.g., winters). In response to seasonal variation, organisms have evolved coordinated suites of adaptations to capitalize on the periods of abundance while withstanding or escaping the shortfalls (Humphries et al. 2004). For example, many birds migrate to more energetically favorable climates during the winter (Alerstam et al. 2003), while many insects, plants, mammals, and other taxa enter states of dormancy in situ (e.g., Brown and Hodek 1983; Carey et al. 2003; Rohde and Bhalerao 2007; Lane 2010). The precise timing of these seasonal transitions varies due to interannual variation in prevailing weather conditions (e.g., Lamb 1950), and adjustments in phenologies (i.e., the timing of periodic life-history events) are necessary to maintain synchrony with the environment (e.g., Visser and Both 2005). However, climate change is altering the timing of seasonal transitions, and it is uncertain whether phenological shifts will be able to keep pace (e.g., Møller et al. 2008).

Theoretically, interannual variation should result in fluctuating selection on phenological traits, with two expected outcomes: the evolution of within-individual phenotypic plasticity in and the maintenance of between-individual genetic variation underlying these traits (Tufto 2015). Empirical data from wild populations have provided evidence in support of both of these expectations (summarized in Merilä and Hendry 2014). For example, among mammals, North American red squirrels (*Tamiasciurus hudsonicus*), red deer (*Cervus elaphus*), Soay sheep (*Ovis aries*), and Columbian ground squirrels (*Urocitellus columbianus*) exhibit both phenotypic plasticity and additive genetic variance in phenological traits (Kruuk and Hadfield 2007; Clements et al. 2010; Lane et al. 2011, 2012, 2018; Boutin and Lane 2014). However, there is concern as to whether current levels of

phenotypic plasticity and additive genetic variance will be sufficient to prevent local maladaptation or even extinction in response to climate change (Merilä and Hendry 2014; Boutin and Lane 2014).

Evaluating phenotypic expression across a broader environmental gradient than is typically afforded by contemporary local conditions provides a means to assess both the limits of plasticity and the extent of genetic determination. Weather conditions (e.g., ambient temperature and precipitation) vary along both latitudinal and elevation gradients. While challenging (and for many wild species even impossible), individuals of some species can be translocated among populations along these gradients. In addition to evaluating the extent of phenotypic plasticity and genetic determination, reciprocal translocation experiments also provide a powerful tool to assess local adaptation versus maladaptation (Leimu and Fischer 2008; Hereford 2009; Bolnick and Stutz 2017). By comparing the fitness of resident individuals to that of foreign individuals, inferences of local adaptation (i.e., resident fitness > foreigner fitness), a lack thereof (resident fitness = foreigner fitness), or even maladaptation (resident fitness < foreigner fitness) can be made (Leimu and Fischer 2008; Hereford 2009).

Among vertebrates, most empirical research into plasticity and (mal)adaptation in response to climate change has focused on income-breeding birds (e.g., Both et al. 2006; Charmantier et al. 2008; Møller et al. 2008; Charmantier and Gienapp 2014). In these systems, climate change is weakening and/or changing previous associations between phenological cues (e.g., photoperiod and temperature). As the birds rely to different degrees on these cues compared with their primary food sources, maladaptation arises due to temporal asynchrony between the two trophic levels (Visser et al. 1998; Both et al. 2006; but see Charmantier et al. 2008; Reed et al. 2013). The extent to which these results may be applicable to species employing some degree of capital breeding, such as many hibernating mammals, is not well known. Although hibernators have received comparatively little research interest in this area (Parmesan 2006; Boutin and Lane 2014), two recent studies have highlighted the interactions among climate change, hibernation phenology, and fitness. Yellow-bellied marmots (*Marmota flaviventris*) are an alpine-dwelling species that has exhibited a phenotypically plastic advance in emergence dates from hibernation over a period of more than 3 decades due to earlier dates of snowmelt (Ozgul et al. 2010). Columbian ground squirrels as well respond plastically to the timing of snowmelt; however, in the Rocky Mountains of southern Alberta, Canada, an increasing prevalence of late-season snowstorms over a period of nearly 2 decades resulted in delayed snowmelt dates and, consequently, emergence dates (Lane et al. 2012). In both species, there were negative correlations between emergence date and annual fitness. However, as the direction of the trend in emergence dates of yellow-bellied marmots was opposite that of Columbian ground squirrels, so too were the fitness consequences (a phenological advance and increased annual fitness in the former; a phenological delay and reduced annual fitness in the latter).

On the surface, the observed phenological delay of Columbian ground squirrels appears to be maladaptive. Such a conclusion, however, depends on both the mechanism giving rise to the fitness decrease and the reference point to which fitness is being compared. If the delay was ipso facto detrimental (e.g., if it hindered females from completing reproduction and subsequently preparing for hibernation during their already-short active season; Dobson et al. 1992) and/or the reference point was to a population that was not delayed (e.g., the population at a previous point in time), then a conclusion of maladaptation is justified. In contrast, if the decline in annual fitness resulted from the population becoming desynchronized with aspects of their environment (e.g., the phenologies of their plant food resources) and the reference point was to a population that did not respond plastically, then it could be argued that the response was, in fact, adaptive (albeit insufficient to prevent the decline).

Our aim was thus to explore the weather–phenology–annual fitness relationships in Columbian ground squirrels by taking advantage of natural variation in emergence dates and conducting a reciprocal translocation experiment. Columbian ground squirrels reside along an elevation gradient in the Rocky Mountains, and emergence dates correspond to local environmental conditions (being later in higher-elevation populations, with shorter growing seasons; Murie and Harris 1982). In addition to being phenotypically plastic in response to dates of snowmelt and spring temperature (Lane et al. 2012), emergence date in Columbian ground squirrels is heritable (Lane et al. 2011). Therefore, to test the extent to which phenotypic variation across populations is due to plasticity and/or genetic variation and whether populations are locally adapted, we coupled the translocation of individuals between two populations (separated in elevation by ~500 m) with natural monitoring of emergences and annual fitness at each of the sites. Our objective was to evaluate two hypotheses: if phenotypic variation is primarily due to phenotypic plasticity, we predicted that translocated individuals would adjust their phenologies to emerge from hibernation at the same time as their adoptive population. Under this scenario, we expected that translocated individuals would have similar annual fitness to residents. Alternatively, if phenotypic variation is primarily due to genetic differences, we predicted that the phenologies of translocated individuals would more closely resemble their natal population. The annual fitness of translocated individuals relative to residents would then depend on whether reductions in annual fitness result from asynchrony with the environment or are a simply a result of being delayed. If it is the former, we

expected that individuals would have lower annual fitness than residents, regardless of the population to which they were translocated. If it is the latter, we expected that individuals translocated from the high to low population (and thus emerging later than the low-elevation residents) would have reduced annual fitness. This would not be the case for individuals translocated from the low to high population, however, as these individuals would emerge earlier than the high-elevation residents and potentially experience an annual fitness benefit from doing so.

## Material and Methods

### Study Species and Populations

Columbian ground squirrels are obligate hibernators, resident to the northern Rocky Mountains of North America (Elliott and Flinders 1991). They are semifossorial and herbivorous and, due to the short growing seasons in the Rocky Mountains, spend ~65%–75% of the year in hibernation. As a consequence, reproduction and the accumulation of sufficient fat resources to survive the subsequent hibernation bout must be completed within a short 3–4-month active season (Dobson et al. 1992). From 2009 to 2013, we studied two wild populations in southern Alberta, Canada, separated by ~45 km and differing in elevation by ~500 m. The lower-elevation population inhabited a mixed-species grassy meadow (~28 ha) in Sheep River Provincial Park (lat. 50.6, long. 114.6; 1,500 m asl). The study grid (12.5 ha) was bordered on one side by the Sheep River and on another by a secondary highway. On two sides it was open to adjacent meadow habitat, and immigration/emigration was possible. The higher-elevation population inhabited an alpine meadow (~18 ha) ~45 km south of the low-elevation population (lat. 50.2, long. 114.4; 2,000 m asl). It was bisected by a secondary highway and bordered by either coniferous forest or mountain peaks on all sides.

Beginning in the early spring (prior to emergence of the first individual), we conducted daily surveys on both sites to search for emergent squirrels. On emergence from hibernation, we caught individuals in live traps (Tomahawk Live Trap, Tomahawk, WI) that we baited with peanut butter and placed in the immediate vicinity of the exit tunnel from the hibernaculum. Columbian ground squirrels hibernate individually (Young 1990) and are relatively sedentary until females enter estrus 3–4 days after emergence (Lane et al. 2011). This life-history pattern provided a measure of certainty that we captured the focal animal for which we observed the emergence date. Further evidence that a captured animal emerged recently was provided by the presence of exfoliated epidermal (skin) flakes in the fur (sensu Michener 1983) that are removed through grooming by the animal within a few days of emergence and, for females, the

appearance of the genitalia. Female emergence and estrous dates are strongly correlated (phenotypic correlation: 0.99 ± 0.01 [SE]; genetic correlation: 0.98 ± 0.01 [SE]; Lane et al. 2011), and prior to estrus the vulva swells and opens. The condition of the vulva at capture can thus be used as an indicator of days since emergence. We analyzed only data from squirrels for which we were confident of emergence date (through a combination of behavioral observations, presence of skin flakes, and, for females, condition of the vulva).

On capture, we weighed individuals to the nearest 5 g by means of a Pesola spring scale and uniquely marked their dorsal pelage with dye (Clairol commercial hair dye or Nyanzol fur dye) to facilitate subsequent observation from a distance. If the animal was captured for the first time (adults in the first year of the study or captured as immigrants as well as juveniles on emergence from their natural burrow), we tagged both of its ears with unique alphanumeric ear tags. We knew the age of individuals that were originally handled as juveniles or yearlings with certainty and assigned a minimum age estimate of 2 years to any animals caught as adults (if the animal had bred and/or body mass indicated that it was no longer a yearling). We subsequently followed animals until natural death, emigration from the study population, or conclusion of the study. Therefore, any resident animals surviving for 2 years or more had the potential to provide repeated measurements of traits.

We calculated annual contributions to lifetime fitness (hereafter referred to as a measure of "annual fitness," for simplicity) for females as $S + 0.5 \times R$, following Qvarnström et al. (2006), as has been done previously for Columbian ground squirrels (Lane et al. 2012). Overwinter survival (i.e., 1/0 whether the female survived/died in the year following emergence) and annual reproductive success (number of offspring surviving until the following year) are represented as $S$ and $R$, respectively. Prior to the analysis, we standardized emergence dates to a mean of zero and unit variance, and we calculated relative annual fitness for each individual by dividing their annual fitness by the overall mean (Lande and Arnold 1983).

### Weather Data

We accessed weather data from the Alberta Climate Information Service (ACIS; https://agriculture.alberta.ca/acis/). To identify local environmental (weather) cues for hibernation emergence for each of the populations, we used data collected from weather stations near and similar in elevation to each of the study locations. From 2010 to 2013, we used data from the Sheep River II station for the low-elevation population (lat. 50.65, long. 114.62; 1,525 m asl; ~2 km from the study site). There were no data from Sheep River II before March 21, 2009, so for November 1, 2008, to March 20, 2009,

we used the average of the values from the three closest sites: Burns Creek (lat. 50.62, long. 114.88; 1,899 m asl), Black Diamond (lat. 50.7, long. 114.15; 1,156 m asl), and Forget Me Not Mountain (lat. 50.74, long. 114.73; 1,739 m asl). We used data from the Mount Odlum III station for the high-elevation population for all years (lat. 50.5, long. 114.9; 2,000 m asl; ~40 km from the study site). The date of snow-melt has previously been identified as a cue for emergence in this species; however, snow-on-ground data are not reported for ACIS stations, so we used mean winter precipitation (mm day$^{-1}$) for each site.

We calculated daily mean ambient temperature ($T_a$) and mean precipitation based on daily recordings taken at the weather stations and used a sliding window approach to determine the relevant periods over which to represent annual values. The sliding window approach is a commonly used technique to identify relevant weather periods (van de Pol et al. 2016) and has previously been used in this context for Columbian ground squirrels in this area (Lane et al. 2012; Dobson et al. 2016). We varied the windows from 2 to 227 days and considered all possible windows from November 1 to June 15. We selected the windows that provided the highest $r^2$ with the site-specific mean annual emergence date. The two weather variables were significantly correlated (Pearson product-moment correlation $r_P = -0.92$, $t_8 = 6.89$, $P = .0001$). Therefore, we fit two separate sets of models below for each weather variable.

### Reciprocal Translocation

From 2008 to 2011, we reciprocally translocated adult females between the two study populations. In years prior to the translocation, these females were treated as controls. In each year, we captured pregnant females and relocated them either to the other population (translocation treatment) or to another location within the same population (treatment controls). We treated all unmanipulated individuals as natural controls. We released translocation treatment and treatment control individuals into soft release enclosures consisting of a 1.0 × 1.5 × 0.3-m (width × length × height) wire mesh enclosure equipped with a 0.3 × 0.3 × 0.3-m wooden nest box that was furnished with hay and shredded burlap for nesting material. We fed individuals twice daily with a combination of a protein-rich grain mixture (horse feed), lettuce, and apple (for hydration) and a selection of plants collected from the surrounding area. We held females in the enclosures until they weaned their litter (to protect the young, as conspecific females can be infanticidal; Waterman 1984). After weaning, we dug the start of a burrow system (by digging a ~10-cm-diameter hole with a fence posthole digger ~30–50 cm deep), cut a hole in the bottom of the enclosure, and allowed the females and their offspring to burrow their way out. We chose to translocate pregnant females for two

reasons. First, female Columbian ground squirrels benefit from the presence of kin (Viblanc et al. 2010). Moving a female with her litter thus created "kin clusters" in the adoptive population. Second, females should be less likely to disperse from the translocation site if they have young of the year offspring (Arnaud et al. 2011). Following release from the enclosure, we monitored all translocated and control individuals (females and their offspring) using identical protocols as for residents (i.e., emergence from hibernation and annual fitness were monitored the following year and each subsequent year while the individuals were alive and resident until the completion of the study).

In total, we had sufficient confidence to include 51 emergence observations from 31 translocation treatment individuals, 87 emergence observations from 49 treatment controls, and 908 emergence observations from 620 natural controls. For the translocation treatment individuals, we analyzed 33 observations from 22 individuals translocated from the low to the high elevation and 18 observations from 9 individuals translocated from the high to the low elevation. We analyzed 66 observations from 35 treatment controls in the low-elevation population and 21 observations from 14 treatment controls in the high-elevation population. Last, we analyzed 602 observations from 382 natural controls in the low-elevation population and 306 observations from 238 treatment controls in the high-elevation population.

### Statistical Analyses

*Plasticity Analysis.* We used two separate general linear mixed effects (LME) models (package lme4 in R ver. 3.5.0; R Core Team 2014) to evaluate the influence of each of the weather variables on the emergence dates of individuals. We wanted to quantify the extent of within-individual plastic responses to environmental variation. Therefore, we used a within-subject mean centering approach that decomposed 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; van de Pol and Wright 2009).

The saturated model included two three-way interactions: location × treatment × ($X_{ij} - \bar{X}_i$) and location × treatment × $\bar{X}_i$, where ($X_{ij} - \bar{X}_i$) and $\bar{X}_i$ represent, respectively, the within- and between-individual effects. We also fit the interaction between sex and age class (yearling or adult) on the basis of known variation in emergence dates between these sex-age groups (Lane et al. 2011) and year as a five-level categorical factor. We fit individual ID as a random effect and estimated repeatability in the rptR library in R (Nakagawa and Schielzeth 2010). We assessed significance of model terms with likelihood ratio tests ($-2\times$ difference in log like-

lihood between hierarchical models, tested against a $\chi^2$ distribution with the number of degrees of freedom that corresponded to the difference in the number of terms estimated). We assessed the significance of the random effect by comparing models fit with restricted maximum likelihood and the significance of the fixed effects by comparing models fit with maximum likelihood.

*Translocation Study.* We used LME models with a two-way interaction (location × treatment) to evaluate the effects of the translocation treatment on emergence date from hibernation. Location represented the two (high- and low-elevation) study sites in which the individuals were observed to emerge. Treatment type represented whether the animal was a control (i.e., born at that location to a resident dam) or treatment (i.e., translocated to that location or one of the offspring born to the female during the year of the translocation). We found no difference between the emergence times of treatment control individuals and natural control individuals (statistics not shown), so they were combined for all analysis. We fitted individual ID as a random effect and estimated repeatability as well as the significance of model terms as described above.

*Selection.* We used LME models to evaluate the influences of standardized hibernation emergence date on relative annual fitness at both study locations and for both translocated and control individuals. For each individual, we decomposed the influence of standardized emergence date on relative annual fitness into the effects of the annual mean emergence date ($y_i$) as well as the deviation of that individual from the annual mean ($y_{ij} - y_i$). The within-year gradient approximates the standardized selection gradient (sensu Lande and Arnold 1983) if selection were standardized and annual fitness were relativized within each year. We also fitted treatment group (a two-level factor) and year (a five-level factor) as fixed effects and individual ID as a random effect. We generated 95% confidence intervals from 1,000 bootstrapped samples and report these instead of standard errors and $P$ values because we cannot assume normality.

## Results

### Natural Variation in Temperature and Precipitation

From November 1 to June 15, the Sheep River II weather station (used for the low-elevation study population) received between 235.6 mm (2010) and 423 mm (2011) of total precipitation. During that same time period, the average temperature ranged from −4.1°C (2011) to −1.2°C (2012), the coldest daily average ranged from −32.6°C (2012) to −23.3°C (2013), and the warmest daily average ranged from 15.2°C (2013) to 11.8°C (2011).

From November 1 to June 15, the Mount Odlum III weather station (used for the high-elevation study population) received over double the amount of total precipitation as Sheep River II, ranging from 510.6 mm (2010) to 945.5 mm (2012). During that same time period, the average temperature ranged from −4.5°C (2013) to −6.2°C (2011), the coldest daily average ranged from −33.0°C (2012) to −18.0°C (2013), and the warmest daily average ranged from 11.8°C (2009) to 7.4°C (2011).

For the low-elevation population, the periods of May 15 to May 29 (mean $T_a$) and January 17 to May 31 (mean precipitation) were the most predictive windows for explaining variation in emergence date (mean $T_a$, $r^2 = 0.99$; mean precipitation, $r^2 = 0.99$). The equivalent periods were March 21 to June 15 (mean $T_a$) and April 15 to May 4 (mean precipitation) for the high-elevation population (mean $T_a$, $r^2 = 0.99$; mean precipitation, $r^2 = 0.98$; fig. 1). During the selected windows, the mean $T_a$ for the low-elevation population ranged from 5.7° to 6.9°C, and the mean $T_a$ for the high-elevation population ranged from −1.2° to 0.3°C. Mean precipitation for the low-elevation population ranged from 1.4 to 2.4 mm day$^{-1}$, and mean precipitation for the high-elevation population ranged from 2.6 to 4.5 mm day$^{-1}$ (fig. 1). From 2009 to 2013, the earliest emergence date in the low-elevation population was April 9, and the latest was June 11. In the high-elevation population, the earliest emergence date was April 20, and the latest was June 24.

### Response in Translocated Individuals

There was a significant difference in emergence dates between the two populations, with control adults at the low elevation emerging 10.9 days earlier than control adults at the high elevation. There was also a significant effect of treatment (table 1). Individuals transplanted from low to high elevation emerged an average of 14.0 days later than control adults remaining in the low-elevation population and 3.1 days later than control adults in the high-elevation population. Adults transplanted from the high- to the low-elevation population emerged an average of 5.2 days earlier than control individuals remaining in the high-elevation population but 5.7 later than residents in the high-elevation population (fig. 2).

We also found that there was a significant interaction between sex and age on emergence date (table 1). Adults, on average, emerged 11.1 days before yearlings and, although average yearling emergence differed between the sexes by only 0.7 days, adult males emerged on average 7.7 days earlier than adult females (table 1). Year also influenced emergence date, with individuals emerging latest in 2011 and earliest in 2012. Individuals differed significantly in their emergence dates ($V_{ID} = 8.24$), yielding a repeatability of $r = 0.15 \pm 0.05$ ($P < .01$).
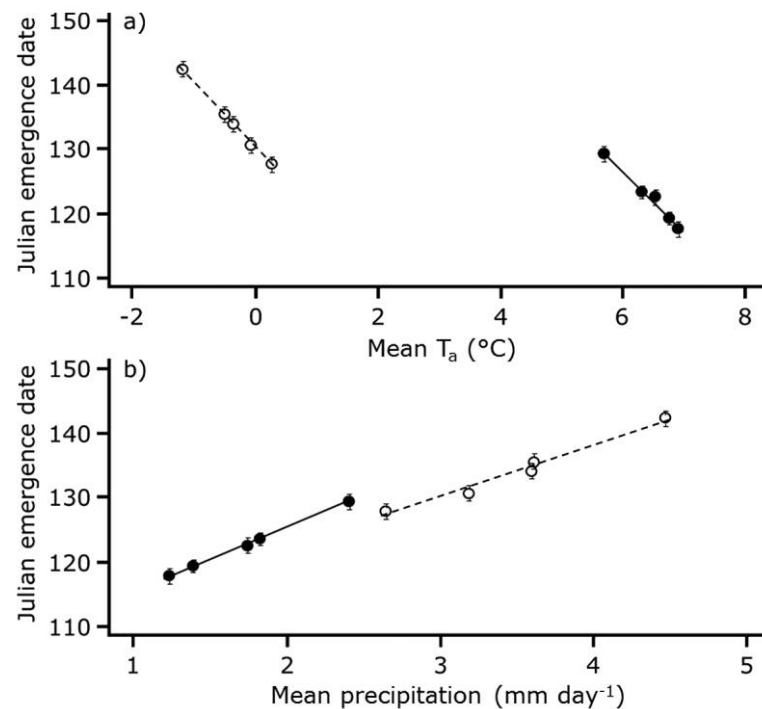
**Figure 1:** Average (±SE) emergence date from hibernation (Julian days after December 31) of Columbian ground squirrels from two study populations of varying elevation in the Rocky Mountains of southern Alberta from 2009 to 2013 in relation to prevailing weather variables. We used a sliding window approach (see "Methods") to determine the relevant periods over which to calculate mean ambient temperature ($T_a$; *a*) and mean precipitation (*b*) for each population. For the low-elevation population, the periods May 15 to May 29 (mean $T_a$) and January 17 to May 31 (mean precipitation) were the best predictors for emergence date ($T_a$, $r^2 = 0.99$; precipitation, $r^2 = 0.99$; solid lines). The equivalent periods for the high-elevation population were March 21 to June 15 for mean $T_a$ and April 15 to May 4 for mean precipitation ($T_a$, $r^2 = 0.99$; precipitation, $r^2 = 0.98$; dashed lines).

### Plasticity of Control and Treatment Individuals at Each Study Location

Individuals that were translocated had higher levels of within-individual plasticity to mean $T_a$ than controls (indicated by the significant within-individual plasticity × treatment interaction; table 2). The sex × age interaction was also significant. The model also indicated that emergence date was influenced by location, with high-elevation individuals emerging later than their low-elevation counterparts (table 2). The between-subject effect was also retained as significant in the final model; however, its coefficient ($-2.48 \pm 0.43$) mirrored the within-individual effect ($-3.32 \pm 0.51$), indicating that the overall response is adequately described by within-individual phenotypic plasticity (van de Pol and Wright 2009; Porlier et al. 2012; Lane et al. 2018). Here, too, individuals differed significantly in their emergence dates ($V_{ID} = 9.13$), yielding a repeatability of $r = 0.19 \pm 0.05$ ($P < .001$).

The model that best described variation in emergence date in response to mean precipitation was similar to the model describing variation in response to mean $T_a$, which is unsurprising given the strong correlation between these two weather variables. The final mean precipitation model similarly included the interactions between level of within-individual plasticity and treatment and between sex and age (table 3). The between-subject effect was also retained as significant in the final precipitation model, and as for the mean $T_a$ model, its coefficient ($5.82 \pm 0.27$) was similar to that for the within-individual effect ($7.28 \pm 0.74$). The two models differed, however, in the retention of location as significant in the precipitation model. This indicates that whereas the variation in emergence date across the two populations is adequately explained by their plastic response to temperature, plasticity in response to precipitation does not fully capture the between-population variation (table 4; fig. 2). Individuals differed significantly in their emergence dates in this model ($V_{ID} = 9.12$), yielding a repeatability of $r = 0.19 \pm 0.05$ ($P = .001$).

### Annual Fitness of Control and Treatment Individuals at Each Study Location

We obtained a total of 17 relative annual fitness measures from 12 females translocated from the low- to high-elevation

**Table 1:** Full and reduced linear mixed effects models to evaluate the influence of reciprocal translocation on emergence dates from hibernation in Columbian ground squirrels

| | Emergence | |
|---|---|---|
| Model | Full | Reduced |
| Fixed effects: | | |
|   Intercept | 133.39 ± .67 | 133.41 ± .66 |
|   Sex × age | 6.78 ± 1.09 | 6.78 ± 1.09 |
|   Treatment × location | −.61 ± 2.29 | n.f. |
|   Year (2010) | −4.24 ± .68 | −4.24 ± .68 |
|   Year (2011) | 7.62 ± .77 | 7.61 ± .77 |
|   Year (2012) | −5.23 ± .70 | −5.24 ± .70 |
|   Year (2013) | .74 ± .70 | .73 ± .70 |
|   Treatment (translocated) | 4.07 ± 1.37 | 3.86 ± 1.10 |
|   Location (low elevation) | −10.11 ± .50 | −10.14 ± .49 |
|   Sex (male) | −7.03 ± .54 | −7.03 ± .54 |
|   Age (yearling) | 9.11 ± .76 | 9.12 ± .76 |
| Random effects: | | |
|   ID | 7.56 | 7.46 |
|   Residual | 42.74 | 42.84 |

Note: Model coefficients (fixed effects ± SE) and estimated variances (random effects) are given for terms that were included in the model, with "n.f." indicating terms that were not included in the final model. The full model includes ID as a random effect (as well as residual variance), the interactions (×) between experimental treatment and emergence location, and the interaction between sex and age. Model terms were dropped sequentially from the full model based on log-likelihood ratio tests, using $P > .05$ as a cutoff.

population and 14 measures from six females translocated from the high- to low-elevation population. Control females in the low-elevation population ($N = 149$) provided 254 relative annual fitness measures, and control females in the high-elevation population ($N = 86$) provided 115 relative annual fitness measures. Relative annual fitness did not differ between the two treatment groups at either the low elevation (control: 1.05 ± 0.05; translocated: 1.18 ± 0.16) or the high elevation (control: 0.93 ± 0.05; translocated: 0.56 ± 0.05), and in both populations the relative annual fitness of translocated individuals did not differ significantly from that of residents (table 4).

We found no evidence of selection on emergence date within years (table 4). Years with late average emergence dates were associated with lower relative annual fitness of females, indicated by the significant between-year fixed effect (table 4), but there was no evidence of further effects of variation within years, indicated by the within-year fixed effect. Year did influence relative annual fitness.

## Discussion

A long-term trend in emergence dates from hibernation of Columbian ground squirrels previously provided one of the few empirical examples of an apparent maladaptive phe-

nological delay in response to climate change (Lane et al. 2012). In this study, we took advantage of natural between-population variation in prevailing weather conditions and resulting hibernation phenologies to investigate the causes and consequences of phenological variation with a reciprocal translocation experiment. We found that individuals were repeatable in their emergence dates and that translocated individuals had significantly different emergence dates than control individuals. However, there was also substantial within-individual phenotypic plasticity observed in both the control individuals and the translocated individuals. Moreover, the relative annual fitness of translocated individuals and residents did not differ in either population, and there was no within-year selection on variation in emergence dates.

Our aim was to test two (non-mutually-exclusive) hypotheses: that phenotypic variation in emergence dates from hibernation between the two populations is due to genetic variation and/or phenotypic plasticity. Repeatability of emergence date from hibernation provides support that phenotypes may be to some extent genetically determined. Although this result itself is not definitive because genetic variance is but one of many mechanisms that can produce individual repeatability (Kruuk and Hadfield 2007), it does align with previous results from a nearby population of ground squirrels in which variation in emergence date was shown to be heritable (Lane et al. 2011).

There was also a main effect of treatment, with translocated individuals emerging, on average, 3.4 days later than controls. This effect cannot be explained as an artifact due to the soft-release protocol, as emergence dates of treatment controls were indistinguishable from those of natural controls. Instead, it must indicate that translocated individuals, despite being phenotypically plastic to both weather variables, remained slightly out of synchrony with their adoptive environment during subsequent emergences from hibernation. Interestingly, this effect resulted in the individuals translocated from the low-elevation to the high-elevation population shifting their phenologies by almost three times the amount of those translocated in the other direction (14.0 days later vs. 5.2 days earlier). However, the treatment × location interaction was not retained as significant, potentially due to insufficient statistical power.

Our results also provide support for individual emergence dates being phenotypically plastic. Although levels of plasticity can vary both within and across populations (Porlier et al. 2012), we found that responses to both temperature and precipitation were remarkably consistent between our two populations. In addition, translocated individuals were able to respond plastically to the environmental conditions encountered in their new habitat. Individuals translocated in both directions displayed a plastic response in the expected direction and, on average, steeper reaction norms than control animals. The latter effect was primarily driven by the individ-
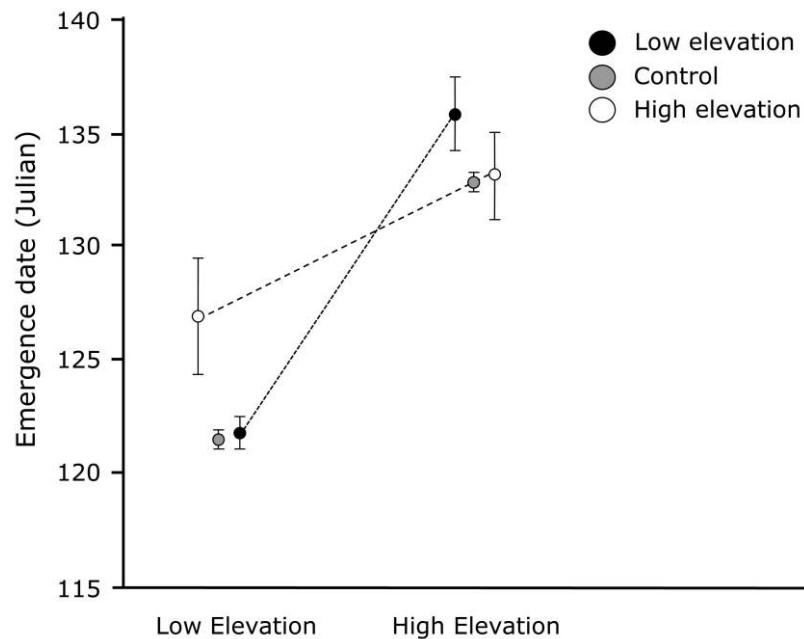
**Figure 2:** Average (±SE) emergence dates from hibernation of Columbian ground squirrels resident to and translocated between high- and low-elevation sites. Gray circles represent natural control individuals from the high-elevation population ($N = 336$ observations from 238 individuals) and the low-elevation population ($N = 602$ observations from 381 individuals). White circles represent average emergence dates of high-elevation treatment control individuals ($N = 21$ observations from 14 individuals) and individuals translocated to the low-elevation population ($N = 18$ observations from nine individuals). Black circles represent average emergence dates of low-elevation treatment control individuals ($N = 66$ observations from 35 individuals) and individuals translocated to the high-elevation population ($N = 33$ observations from 22 individuals).

uals translocated from the low-elevation to the high-elevation population overshooting (i.e., emerging even later than) the residents in the high-elevation population. Although the individuals translocated in the other direction undershot (i.e., did not advance to reach) the low-elevation residents, there were almost half the number of observations for these individuals than for those translocated to the high-elevation population. These results, in combination with those of Lane et al. (2012), provide a measure of confidence that phenotypic plasticity will be sufficient in the short term to allow individuals to adjust their hibernation phenologies to match climate change–induced shifts in weather, at least within the range of variation that we explored.

We expected that if translocated individuals were able to adjust their phenologies to approximate the emergence dates of resident individuals in their adoptive population, relative annual fitness between these two treatment groups would be similar. Although there was a significant treatment effect, the relative annual fitness of translocated individuals was statistically indistinguishable from residents in both populations. If this equivalency is real (and not due to a lack of statistical power), it would ostensibly suggest that phenotypic plasticity is sufficient to prevent declines in relative

annual fitness due to shifted environments. The absence of within-year selection on emergence dates for either population as well could indicate that both populations are locally adapted because directional selection is not expected to be observed in populations residing at their phenotypic optima (MacPherson et al. 2015).

At an extreme level, phenotypic optima must exist for these hibernators. A drastically advanced emergence date would potentially lead to increased predation pressure (Turbill et al. 2011; Turbill and Prior 2016) and, undoubtedly, to starvation, as plants would be buried under a deep snowpack. On the other hand, substantial delays in emergence date would challenge the ability of reproductive females to complete the necessary periods of gestation, lactation, and preparation for the subsequent hibernation bout (Williams et al. 2013). Currently, we are unable to distinguish between two potential interpretations. Each of our populations could have resided on separate phenotypic optima, and phenotypic plasticity allowed translocated individuals to transition to their new optimum (Ghalambor et al. 2007). Alternatively, there may be a global optimum that is sufficiently broad to encompass the entire range of emergence dates expressed at both locations (Van Tienderen 1991). We expect that these

**Table 2:** Full and reduced linear mixed effects models to evaluate levels of phenotypic plasticity in emergence date from hibernation to mean ambient temperature ($T_a$) in Columbian ground squirrels across two populations varying in elevation by ~500 m in the Rocky Mountains of southern Alberta, Canada

| | Mean $T_a$ | |
|---|---|---|
| Model | Full | Reduced |
| **Fixed effects:** | | |
| Intercept | 119.03 ± 4.02 | 124.71 ± 1.65 |
| Location × treatment × ($\bar{X}_{i\cdot}$) | −5.85 ± 4.71 | n.f. |
| Location × treatment × ($X_{ij} − \bar{X}_{i\cdot}$) | −4.22 ± 4.59 | n.f. |
| Treatment × ($\bar{X}_{i\cdot}$) | 2.87 ± 3.32 | n.f. |
| Location × ($\bar{X}_{i\cdot}$) | 1.66 ± 1.33 | n.f. |
| Treatment × ($X_{ij} − \bar{X}_{i\cdot}$) | 4.50 ± 3.07 | 1.91 ± .73 |
| Location × ($X_{ij} − \bar{X}_{i\cdot}$) | 1.66 ± 1.01 | n.f. |
| Sex × age | 6.88 ± 1.07 | 6.83 ± 1.07 |
| Treatment × location | −4.42 ± 16.04 | n.f. |
| ($\bar{X}_{i\cdot}$) | −4.07 ± 1.13 | −2.48 ± .43 |
| ($X_{ij} − \bar{X}_{i\cdot}$) | −4.82 ± 1.01 | −3.32 ± .51 |
| Year (2010) | −3.80 ± .67 | −3.83 ± .67 |
| Year (2011) | 4.46 ± .89 | 4.84 ± .84 |
| Year (2012) | −3.57 ± .74 | −3.97 ± .71 |
| Year (2013) | .80 ± .69 | .60 ± .68 |
| Treatment (translocated) | 14.43 ± 11.68 | 3.86 ± 1.09 |
| Location (low elevation) | 11.86 ± 4.46 | 6.50 ± 2.92 |
| Sex (male) | −6.81 ± .55 | −6.85 ± .54 |
| Age (yearling) | 8.94 ± .76 | 8.95 ± .76 |
| **Random effects:** | | |
| ID | 9.13 | 9.07 |
| Residual | 38.89 | 39.17 |

Note: Model coefficients (fixed effects ± SE) and estimated variances (random effects) are given for terms that were included in the model, with "n.f." indicating terms that were not included. The full model includes the random effect of ID, three-way interactions (×) among fixed effects terms (e.g., within-individual variation ($X_{ij} − \bar{X}_{i\cdot}$) or between-individual variation ($X_{ij}$) with experimental treatment and emergence location), and the two-way interaction between sex and age. Model terms were dropped sequentially from the full model based on log-likelihood ratio tests, using $P > .05$ as a cutoff.

challenges of interpretation will be general in reciprocal translocation studies: even for heritable traits (such as emergence date from hibernation), it is nearly impossible to either support or refute a conclusion of local (mal)adaptation when phenotypic plasticity leads to the foreigners resembling residents (Conover and Shultz 1995). Testing these two alternatives, in our case, would require evaluating the fitness consequences of a greater diversity of emergence phenotypes than are currently expressed. Such an approach could be possible, for example, by translocating individuals across even more extreme environmental gradients, such as has been reported by Murie and Harris (1982; if phenotypic plasticity is limited beyond the range over which we assessed it). Alternatively,

artificially adjusting emergence dates of individuals within a population may be possible, for example, by manipulating snow cover over individual hibernacula (as is commonly done in studies of plant phenology; Wipf and Rixen 2010).

Although there was evidence of neither within-year selection on emergence date nor a difference in the relative annual fitness of translocated individuals versus residents, there was a signal of later years, on average, producing lower mean relative annual fitness values (i.e., the between-year effect was retained as significant). This result was also shown by Lane et al. (2012), and, notably, in their long-term data set emergences had become progressively later, leading to a trend for

**Table 3:** Full and reduced linear mixed effects models to evaluate levels of phenotypic plasticity in emergence date from hibernation to mean amount of precipitation in Columbian ground squirrels ($N = 1,076$ observations of emergence dates from 672 individuals) across two populations varying in elevation by ~500 m in the Rocky Mountains of southern Alberta, Canada

| | Mean precipitation | |
|---|---|---|
| Model | Full | Reduced |
| **Fixed effects:** | | |
| Intercept | 135.32 ± 3.93 | 131.57 ± 1.95 |
| Location × treatment × ($\bar{X}_{i\cdot}$) | 4.18 ± 6.21 | n.f. |
| Location × treatment × ($X_{ij} − \bar{X}_{i\cdot}$) | 1.42 ± 4.42 | n.f. |
| Treatment × ($\bar{X}_{i\cdot}$) | 2.93 ± 4.08 | n.f. |
| Location × ($\bar{X}_{i\cdot}$) | 1.81 ± 1.49 | n.f. |
| Treatment × ($X_{ij} − \bar{X}_{i\cdot}$) | −3.79 ± 2.47 | −4.43 ± 1.69 |
| Location × ($X_{ij} − \bar{X}_{i\cdot}$) | 1.77 ± 1.08 | n.f. |
| Sex × age | 6.98 ± 1.07 | 6.90 ± 1.07 |
| Treatment × location | −.40 ± 16.85 | n.f. |
| ($\bar{X}_{i\cdot}$) | 4.05 ± 1.20 | 5.82 ± .27 |
| ($X_{ij} − \bar{X}_{i\cdot}$) | 6.34 ± .96 | 7.28 ± .74 |
| Year (2010) | −1.98 ± .73 | 2.28 ± .68 |
| Year (2011) | 2.37 ± .99 | 2.31 ± .86 |
| Year (2012) | −1.39 ± .84 | −1.12 ± .75 |
| Year (2013) | 1.01 ± .68 | 1.20 ± .68 |
| Treatment (translocated) | −16.69 ± 12.37 | −8.24 ± 4.61 |
| Location (low elevation) | −1.64 ± 4.79 | n.f. |
| Sex (male) | −6.85 ± .54 | −6.83 ± .54 |
| Age (yearling) | 8.50 ± .75 | 8.57 ± .75 |
| **Random effects:** | | |
| ID | 9.87 | 9.12 |
| Residual | 37.79 | 38.71 |

Note: Model coefficients (fixed effects ± SE) and estimated variances (random effects) are given for terms that were included in the model, with "n.f." indicating terms that were not included. The full model includes the full complement of random effects terms, three-way interactions (×) among fixed effects terms (e.g., within-individual variation ($X_{ij} − \bar{X}_{i\cdot}$) or between individual variation ($X_{ij}$) with experimental treatment and emergence location), and the two-way interaction between sex and age. Model terms were dropped sequentially from the full model based on log-likelihood ratio tests, using $P > .05$ as a cutoff.

**Table 4:** Full and reduced linear mixed effects models assessing the influences on relative fitness in resident and translocated Columbian ground squirrels across two populations separated by ~500 m in elevation in the Rocky Mountains of southern Alberta, Canada

| | Fitness | |
| --- | --- | --- |
| Model | Full | Reduced |
| Fixed effects: | | |
|   Intercept | 6.97 (.32 to 12.95) | 4.17 (2.26 to 6.12) |
|   ($\bar{y}_{i\cdot}$) | −.05 (−.09 to 2.93 × 10⁻³) | −.03 (−.04 to −.01) |
|   ($y_{ij} - \bar{y}_{i\cdot}$) | 1.28 × 10⁻³ (−.01 to .01) | n.f. |
|   Location (low elevation) | −.27 (−.80 to .29) | n.f. |
|   Treatment (translocated) | −.14 (−.42 to .18) | n.f. |
|   Year (2011) | .80 (.30 to 1.30) | .61 (.34 to .87) |
|   Year (2012) | .03 (−.21 to .27) | .11 (−.06 to .30) |
|   Year (2013) | .03 (−.28 to .35) | −.07 (−.26 to .13) |
| Random effects: | | |
|   ID | .09 (.11 to .45) | .08 (.05 to .41) |
|   Residual | .44 (.59 to .73) | .44 (.59 to .73) |

Note: Model coefficients (fixed effects with 95% confidence intervals [CIs]) and estimated variances (random effects with 95% CIs) are given for terms that were included in the model, with "n.f." indicating terms that were not fitted. The full model includes the full complement of random effects terms, the fixed effects of experimental treatment and emergence location, and the within-year ($y_{ij} - \bar{y}_{i\cdot}$) and between-year ($\bar{y}_{i\cdot}$) effects of emergence date. Model terms were dropped sequentially from the full model based on CIs overlapping zero.

diminished mean relative annual fitness over nearly 2 decades. Can we justifiably define this result as maladaptation? The answer depends on the definition.

Broadly speaking, maladaptation refers to suboptimal fitness (S. Brady, D. Bolnick, R. Barrett, et al., unpublished manuscript); however, confusion arises when defining the reference point for the fitness comparison. For example, the reference point may be a population at another time or place or one that occupies a theoretically different region of phenotype space (Crespi 2000; S. Brady, D. Bolnick, R. Barrett, et al., unpublished manuscript). In reciprocal translocation experiments, the "theoretically" different regions of phenotype space are made real by relocating phenotypes (individuals) to environments in which they do not naturally occur. Although phenotypic plasticity in emergence dates rendered an interpretation of local (mal)adaptation equivocal in this context, if we change our comparison group to the population at a different point in time, then a conclusion of maladaptation is justified. In this case, maladaptation is most likely caused by a decaying fitness peak at the optimum (sensu Pleasants and Oberhauser 2013; S. Brady, D. Bolnick, R. Barrett, et al., unpublished manuscript). Such an effect could potentially be due to a shortened growing season resulting from the delay and is likely exacerbated by a separate trend for warmer and dryer conditions occurring later in the season (leading, presumably, to desiccation of the ground squirrels' plant food resources; Dobson et al. 2016).

The potential for widespread maladaptation in response to rapid anthropogenic environmental change (in addition to the potential for confusion in interpreting and defining maladaptation) calls for a unified framework with which to study it as well as substantially more empirical data from taxonomically diverse wild species. Fortunately, S. Brady, D. Bolnick, R. Barrett, et al. (unpublished manuscript) have recently articulated such a unified framework. Empirical limitations, however, remain. This is particularly true for mammals and other terrestrial vertebrates. For example, in Hereford's (2009) quantitative survey of local (mal)adaptation, only four of the 74 studies assessed were of vertebrates, and none were of mammals (one lizard and four anurans were represented). A lack of mammalian representation in the data set is not surprising considering the tremendous logistical difficulties in translocating wild mammals. We, too, experienced these challenges: despite completing a large-scale translocation endeavor over 3 years, our sample sizes of translocated animals were admittedly modest. Fortunately, our statistical power was improved by some individuals providing more than one subsequent emergence record, but such an experiment may be impossible for more dispersive species untied to a central location, such as a burrow system.

From a conservation standpoint, overcoming the logistical challenges of local (mal)adaptation studies in mammals is imperative. Sedentary mammals, as a group, are predicted to be vulnerable to climate change due to their more limited abilities to disperse to more favorable locations (compared with birds; Schloss et al. 2012). This limitation means that local adaptation is likely to play a more important role in preventing extinction of sedentary species. The direct consequences of a warming climate for hibernators have also recently been shown in a meta-analysis of hibernating and

winter-active mammals (Turbill and Prior 2016). With each 1°C increase in mean annual temperature, Turbill and Prior (2016) reported a 5.1% decrease in annual survival in mammalian hibernators. Such an effect was not seen in winter-active mammals, leading the authors to conclude that the response was due to a shortening of the hibernation season (and subsequent increased exposure to environmental threats, such as predation). A decrease in survival, if not compensated for by an increase in reproduction, represents an additional mechanism producing maladaptation, and one that is not contingent on species becoming desynchronized from their food resources. We were unable to detect a similar effect in our study. Mean temperature from March 20, 2009 (the first date of available data from the Sheep River II station), to March 19, 2013, was 2.96°C warmer for the low-elevation population (2.29°C) than for the high-elevation population (−0.67°C). Mean survival, however, was actually slightly higher within our low-elevation population (low elevation: 0.67 ± 0.03 [SE]; high elevation: 0.58 ± 0.05 [SE]). The relatively short duration of our study, however, does call for caution in drawing conclusions from these values, and, of note, earlier work on Columbian ground squirrels did suggest that individuals in higher-elevation populations experienced higher survival (Zammuto and Millar 1985).

An additional logistical limitation in assessing the role of plasticity in allowing populations to respond to environmental change is the range of environmental conditions over which plasticity can be measured. Climate change is predicted to push climates beyond historical levels of variation (IPCC 2014) and potentially beyond the limits of phenotypic plasticity (Lande and Shannon 1996). Applying estimates of phenotypic plasticity based on current levels of interannual variation to future scenarios thus necessitates extrapolation. We argue that it is imperative that we evaluate phenotypic plasticity (and fitness) across a broader environmental gradient than is typically afforded by contemporary local conditions. Gradients across species ranges may provide the raw material to do so. Natural variation in weather conditions along both latitudinal and elevation gradients may, in fact, be what prevents extinction from maladaptation (by providing more favorable conditions to dispersing individuals; Lomolino 2001; Roy and Goldberg 2007; Rolland et al. 2014). Here we have shown that if the logistical hurdles of reciprocal translocation experiments can be overcome, it is also an ingredient for potentially powerful investigations of phenotypic plasticity.

## Acknowledgments

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Special Feature Editor: Joseph Travis



"The family of Plagiaulacidæ is one of the most peculiar among those of the Mammalia, whether we consider its structure or its relations to geological time. Commencing in the Jurassic period, it persisted through the Cretaceous to the Eocene. It then disappeared from view to remind us once more of its existence by its probable descendant, the extraordinary pouched lion of the Pliocene period of Australia, *Thylacoleo carnifex* Owen." From "The Tertiary Marsupialia" by E. D. Cope (*The American Naturalist*, 1884, 18:686–697).