Variability in winter climate and winter extremes reduces population growth of an alpine butterfly

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Abstract. We examined the long-term, 15-year pattern of population change in a network of 21 Rocky Mountain populations of Parnassius smintheus butterflies in response to climatic variation. We found that winter values of the broadscale climate variable, the Pacific Decadal Oscillation (PDO) index, were a strong predictor of annual population growth, much more so than were endogenous biotic factors related to population density. The relationship between PDO and population growth was nonlinear. Populations declined in years with extreme winter PDO values, when there were either extremely warm or extremely cold sea surface temperatures in the eastern Pacific relative to that in the western Pacific. Results suggest that more variable winters, and more frequent extremely cold or warm winters, will result in more frequent decline of these populations, a pattern exacerbated by the trend for increasingly variable winters seen over the past century.

Key words: alpine habitat; climate change; climate extremes; climate variability; Jumpingpound and Lusk Ridges, Alberta, Canada; Pacific Decadal Oscillation, PDO; Parnassius smintheus; population dynamics; Rocky Mountain Apollo butterfly.

INTRODUCTION

The phenomenon of climate warming provides the basis for purported range shifts, either higher in latitude or in elevation, of a number of animal species (Parmesan et al. 2000, Hill et al. 2002, Parmesan and Yohe 2003). Such shifts are based on the reasonable expectation that a warmer climate facilitates population growth in areas where a colder climate had previously prevented it. However, predictions for climate change are not only for a monotonic pattern of warming, but also for increased variability in climate and weather (IPCC 2012), a concomitant increased likelihood of extreme weather events (Morss et al. 2011), and hence a greater impact of such events for ecological processes (Jentsch et al. 2007, Smith 2011). Increased climate variability may lead not only to more extreme warm events, but also to more extremes of precipitation and of cold (Morss et al. 2011). Recent weather extremes, both warm and cold (e.g., Le Page 2011) serve to reinforce the fact that climate change is not simply a gradual warming, but will be fraught with local and regional extremes in both temperature and precipitation (Morss et al. 2011, Smith 2011). Animal populations therefore will have to respond to both general warming and to greater climate variation (Drake 2005) and to more frequent extremes (Parmesan et al. 2000, Jentsch et al. 2007). It is not clear whether extremes at both ends of the climatic range will be equally deleterious to population growth.

Many studies of vertebrate populations have successfully related population growth to indices of climate based on ocean water temperature, e.g., El Niño Southern Oscillation, ENSO (Wilson and Arcese 2003), the North Atlantic Oscillation, NAO (Post et al. 1997, Post and Stenseth 1998, Sæther et al. 2000), the North Pacific Oscillation, NPO (Hebblewhite 2005), and the Pacific Decadal Oscillation, PDO (Ezard et al. 2009, Glenn et al. 2010, Hegel et al. 2010). These studies emphasize the value of using a broadscale climate variable that integrates both temperature and precipitation with which to relate population change. The resulting pattern of response provides a subsequent framework for detailed mechanistic studies on the effect of temperature and precipitation (and their interaction) in particular seasons. Virtually all such studies report a negative effect on population growth at one end of the range of climate variation, implying that climate change will have, for any given species, either a negative or positive linear effect on population growth.

Climate effects identified for populations of long-lived vertebrate species with overlapping generations may be buffered somewhat because they act primarily on only one age class or cohort (e.g., Song Sparrows [Wilson and Arcese 2003] and pikas [Morrison and Hik 2007]). Extreme weather and climate events would be expected to show similar population effects (Parmesan et al. 2000, Jentsch et al. 2007, Frederiksen et al. 2008, Smith 2011) but, by their nature, would do so over a short interval relative to the life span of these animals. Short-lived, univoltine ectotherms, on the other hand, would have little or no such buffering because survival and
reproduction of the entire population would be strongly affected even over a short time interval.

As a taxon, butterflies provide perhaps the best example of range shifts both poleward and in elevation due to a warming climate (Parmesan et al. 1999, Hill et al. 2002, Lewis and Bryant 2002, Kharouba et al. 2009, Forister et al. 2010). Despite this strong pattern for butterflies, there are few studies that relate climate change to population growth per se (but see Nowicki et al. 2009, Boggs and Inouye 2012). More typically, climate and weather variables have been related to the incidence of butterflies (Thorne et al. 2006, Forister et al. 2010), their abundance (Pollard and Moss 1995, Roy et al. 2001, Vandenbosch 2003), and their distribution (Hill 2010), their abundance (Pollard and Moss 1995, Roy et al. 2001, Vandenbosch 2003), and their distribution (Hill et al. 2002, Kharouba et al. 2009, Forister et al. 2010). Rates of population change for the well-studied Bay checkerspot butterfly Euphydryas editha bayensis over a 35-year period were successfully related to precipitation (McLaughlin et al. 2002); timing of snow melt was strongly related to nine years of growth data for alpine populations of the Mormon fritillary Speyeria mormonia (Boggs and Inouye 2012); and short-term (two-year) rates of change for the skipper Atalopedes campestris were related to winter temperatures (Crozier 2004). Climate and weather effects may be particularly strong for butterfly populations in montane and alpine environments, where the season is short and where butterflies have evolved many adaptations in response to cold (e.g., Roland 1982, Kingsolver and Watt 1983, Ashton et al. 2009).

Here we use long-term (15-year) estimates of population size for 21 subpopulations of alpine Parnassius smintheus Doubleday (Rocky Mountain Apollo butterfly) and identify a strong effect of regional climate on annual rates of population change. We do this using the Pacific Decadal Oscillation (PDO) index as a measure of relatively short-term but broadscale climate, and as a general measure of both regional temperature and precipitation (Mantua et al. 1997).

MATERIALS AND METHODS

Study species

Parnassius butterflies are a common component of the butterfly community in alpine regions of North America, Europe, and Asia. P. smintheus is common in alpine meadows of the Rocky Mountains of North America from New Mexico north through Alberta and northern British Columbia. P. smintheus overwinter as pharate larvae inside the egg. The aposomatic larvae hatch in May and they feed on the obligate perennial host plant, Sedum lanceolatum, from which they presumably sequester cyanide-based compounds (Nishida and Rothschild 1995; but see Bjarnholt et al. 2012), pupating in late June. Quality of the host plant is reduced slightly by previous herbivory (Roslin et al. 2008), and late snowmelt can render the defensive chemicals in this plant more adverse (Guppy and Shepard 2001). Adults emerge in late July, and females oviposit near, but not on, the host plant through August. Populations of this butterfly are particularly well studied in Alberta, Canada (Roland et al. 2000, Roland and Matter 2007, Matter and Roland 2010), and occur in relatively small subpopulations, have limited dispersal, and exhibit some characteristics of metapopulations. Despite our understanding of their population structure and dispersal, the drivers of their dynamics, including the effects of climate are largely not known.

Study sites

Parnassius smintheus butterflies were monitored yearly from 1995 to 2009 in 21 meadows along Jumpingpound (see Plate 1) and Lusk Ridges, Alberta, Canada (50°57′ N, 114°54′ W) in the front range of the Rocky Mountains (Keyghobadi et al. 2005, Roland and Matter 2007). Meadows occur above treeline (2100 m), range in area from 0.2 ha to 22.7 ha, and are variously disconnected from each other by intervening forest that limits butterfly dispersal (Roland et al. 2000) and gene flow (Keyghobadi et al. 1999), and that reduces synchrony of dynamics among the subpopulations (Roland and Matter 2007, Matter and Roland 2010). All 21 meadows are within 12 km of each other, and are affected by similar weather and have a range of aspects and slopes. Depictions of the study site are available elsewhere (Roland et al. 2000).

Population size and rate of population change

In most years, population size was estimated for each subpopulation using mark–recapture data in combination with “Craig’s method” (Craig 1953, Matter and Roland 2004). This method makes use of the statistical distribution of number of butterflies captured once, twice, thrice, and so on, and then, by assuming that butterflies are encountered randomly, estimates the zero term of the Poisson distribution (number of butterflies never captured) and adds that number to the number of butterflies actually captured. By using mark–recapture data to estimate population size, we reduce the potential effect of differing amounts of movement among years on the population estimates. Populations were sampled three to four times during the six-week adult flight period. Samples averaged 1852 captures of 951 individual butterflies per year (minimum 177 captures of 94 individuals in 2003; maximum 3338 captures of 1940 individuals in 2008). In 1997–2000, “Pollard” transects (Pollard 1977) were used to estimate abundance, which, combined with a conversion factor between the two methods (Matter and Roland 2004), provided a 15-year time series. Rate of population change \(R_t\) was estimated for each population in each year \(t\) as the difference between the \(log_{10}\) estimate of adult butterfly abundance in year \(t + 1\) and the \(log_{10}\) estimate for year \(t\). Some small populations had an abundance of zero (local extinction) in some years. For this reason, we added 0.5 to all population estimates prior to log-transformation
and calculation of $R_t$. These data provided up to 14 estimates of population change for each meadow.

Climate variable

We chose the Pacific Decadal Oscillation (PDO) index (Mantua et al. 1997) as a climate variable with which to relate population change. The PDO index contrasts the spatial distribution of sea temperatures between the northeastern and northwestern Pacific Ocean after correction for mean global temperature (JISAO 2012). Positive PDO values indicate that warmer water lies along the west coast of North America and negative values indicate that cooler water lies along that coast. The PDO index provides a single integrative measure of climate across western North America through its strong temporal correlation with both temperature and precipitation (Mantua et al. 1997). Positive values of the PDO are associated with generally warm, dry years inland, and negative values with cool, wet years. It is of notable coincidence that our study site in west-central Canada is in the region of North America that exhibits the strongest correlation between PDO and both weather variables, in particular between PDO and precipitation (Mantua et al. 1997: Fig. 3).

We chose to use the PDO index for this analysis because it has proved to be a useful quantification of general climatic conditions, for both aquatic vertebrates (Mantua et al. 1997, Glenn et al. 2010) and terrestrial vertebrates (Ezard et al. 2009, Hegel et al. 2010) and for risk of forest fires (Schoennagel et al. 2007); it was also used successfully for analysis of bighorn sheep population growth in nearby areas of the Rocky Mountains of Alberta (Ezard et al. 2009). Although PDO has been successfully related to abundance of the painted lady butterfly Vanessa cardui (Vandenbosch 2003), it has not, to our knowledge, been related to rates of population change of any butterfly species.

We chose not to use temperature and precipitation variables for the current analysis for three reasons. First, although interpolated temperature data could be obtained for our sites (e.g., Daly et al. 2002), there are no appropriate precipitation data available, in particular snow depth data. Second, our intent here is to identify broad patterns with respect to climate, in particular to determine the season in which climate has its greatest effect, rather than to identify any particular weather variable and season among the myriad possible affecting various butterfly life stages. When faced with many potential temperature/precipitation/season combinations, other studies have had to resort to subjectively selecting among them based on biological significance when statistical analysis fails to winnow the number of variables sufficiently (e.g., Roy et al. 2001), or have resorted to using a proxy of weather (such as adult longevity as a proxy for summer weather; Nowicki et al. 2009) in their final analysis. In the absence of a specific hypothesis regarding weather variables, the PDO index serves as a useful starting point. Third, there exist a number of studies that successfully use PDO or similar ocean-temperature-based climate indices, as a regional climate variable with which to relate animal population dynamics.

Monthly PDO values were obtained from the Joint Institute for the Study of the Atmosphere and Oceans (JISAO 2012). Rather than using the mean PDO index for the respective calendar years, we used the mean for the annual interval, PDO(annual), from September (after oviposition by adult female P. smintheus butterflies) through the following August, when the next generation of adult butterflies would be flying. In addition to this year-long estimate, we calculated mean PDO for several shorter sequences of months in order to identify parts of the year, and hence part of the Parnassius life cycle, that are particularly affected by climate. Spring PDO is the mean for April through June, PDO(Apr–Jun), the interval between egg hatch and the end of the larval stage and start of pupation. Summer PDO is the mean for July and August, PDO(Jul–Aug), the conditions experienced by adult butterflies, and probably related to successful mating and oviposition. Two values of summer PDO are included in the analysis: that for year $t$ when females are actively laying eggs for the next generation, and that for year $t + 1$ when weather might affect butterfly activity and our estimate of $R_t$ simply through increased (or decreased) detectability. Winter PDO is the average monthly PDO from November through March, PDO(Nov–Mar), and reflects the conditions that the eggs experience each year.

Statistical analyses

We fit a series of generalized linear (GLM), additive (GAM), and linear mixed-effects (lme) models to the data using R version 2.13.1 (R Development Core Team 2011) in an effort to identify variables affecting population change ($R_t$). We first fit a generalized linear model with Gaussian errors to data for all meadows combined to test for linear effects of butterfly abundance and climate on population growth (see Appendix). A generalized additive model (Wood 2006) with spline smoothers (Appendix) identified any additional nonlinear effects of each variable that should be accounted for. The ability to detect nonlinear effects became crucial as model development progressed. Any nonlinear effects detected using GAM (Appendix), were accounted for in subsequent mixed-effects models by the inclusion of appropriate polynomial terms for that variable.

We then fit a mixed-effects model (Pinheiro and Bates 2000) to the same data, including the individual meadows (subpopulations) as a random effect. In this way, we determined whether the same fixed-effects model is adequate for all of the 21 subpopulations by simply allowing for variability in the intercept among them. If we found a significant effect of annual PDO on $R_t$, we sequentially replaced it in a series of alternative mixed-effects models, each with a mean PDO estimate...
for the shorter seasonal segments as previously described. In this way, we could identify which seasonal climate interval is most closely related to population change ($R_t$), and hence which life stage affects annual population change the most. Competing mixed-effects models were compared based on the Akaike Information Criterion (AIC; Burnham and Anderson 2002) and on the significance of the estimated coefficients. Competing models with AIC that differed by $<$2 were considered equally well supported.

**RESULTS**

Butterfly population size ($N_t$), rate of population change ($R_t$), and the PDO(annual) varied strongly over the 15-year interval (Fig. 1). Preliminary analyses of the data using GLM and GAM (Appendix) indicated that $R_t$ was negatively and linearly related to the current year’s abundance, and weakly related to the previous year’s abundance, and that PDO(annual) was curvilinear, with positive growth at intermediate values of PDO(annual) and negative at both high and low values, a pattern that could be accounted for sufficiently with the inclusion of a quadratic term for PDO (see Appendix). These patterns suggest that biotic factors such as density-dependent dispersal or rapidly induced defense of the host plant (Roslin et al. 2008) may affect population growth, and that lagged effects of abundance, such as natural enemies and between-year induced defenses in the host plant, play a small role in *P. smintheus* dynamics.

Based on the initial analyses (Appendix), we included linear terms for butterfly abundance and both linear and quadratic terms for PDO in a series of alternative mixed effects models that included either the mean annual PDO or mean PDO estimates for each of the different seasonal segments. The strongest effect of PDO on $R_t$, and the best model fit, was provided by the model with PDO for the overwinter interval (Table 1). In fact, models that included PDO for the non-winter segments of the year provided poorer fits than did the model using annual PDO (Table 1). Again, the most important effect of overwinter PDO in the model was through the quadratic term (Table 2): positive growth rates in moderate winters and population decline both in years with warm, dry winters and with cold, snowy winters. The strong effect of overwinter climate suggests that egg and first-instar survival dominates the dynamics of this insect, but in a nonlinear manner. A model including a random effect on slopes for the effect of winter PDO was less well supported (AIC = 271) than was the model with only a fixed effect for slope (AIC = 267), indicating a similar effect of PDO(winter) on population growth among meadows. Inclusion of an interaction term between PDO(winter) and $N_t$ was also less well supported (AIC = 273 vs. 267), indicating that the effect of PDO(winter) on growth rate was similar regardless of abundance.

To determine the relative importance of PDO (abiotic effects) and density (biotic effects) on rate of population change, we alternatively dropped the term for PDO(winter) and for $N_t$ from the final model, and assessed the respective change in AIC for each. Change in AIC was 84.7 when PDO was dropped but only 37.3 when log $N_t$ was dropped, indicating that the abiotic effect of climate on alpine *P. smintheus* population growth is more important than are density-related biotic factors such as parasitism, competition, and interaction with its host plant *Sedum lanceolatum*.

**Table 1.** Mixed-effects model fits for effects of abundance, lagged abundance, and the Pacific Decadal Oscillation on rate of population change ($R_t$) of *Parnassius smintheus* butterflies in Alberta, Canada.

<table>
<thead>
<tr>
<th>Candidate model</th>
<th>Model terms</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Annual</td>
<td>$\log N_t + \log N_{t-1} + \text{PDO(annual)} + \text{PDO(annual)}^2</td>
<td>Meadow</td>
<td>271</td>
</tr>
<tr>
<td>2) Spring</td>
<td>$\log N_t + \log N_{t-1} + \text{PDO(Apr-Jun)} + \text{PDO(Apr-Jun)}^2</td>
<td>Meadow</td>
<td>267</td>
</tr>
<tr>
<td>3) Summer, $j$</td>
<td>$\log N_t + \log N_{t-1} + \text{PDO(Jul-Aug, j)} + \text{PDO(Jul-Aug, j)}^2</td>
<td>Meadow</td>
<td>267</td>
</tr>
<tr>
<td>4) Winter</td>
<td>$\log N_t + \log N_{t-1} + \text{PDO(Nov-Mar)} + \text{PDO(Nov-Mar)}^2</td>
<td>Meadow</td>
<td>267</td>
</tr>
<tr>
<td>5) Summer, $j+1$</td>
<td>$\log N_t + \log N_{t-1} + \text{PDO(Jul-Aug,j+1)} + \text{PDO(Jul-Aug,j+1)}^2</td>
<td>Meadow</td>
<td>267</td>
</tr>
</tbody>
</table>

**Notes:** Each model uses mean PDO of different segments of the year (see *Materials and methods*). Models include the random effect of the 21 meadows (subpopulations) on intercepts. The best-supported model is the one that uses mean PDO from November through March (model 4).
PDO over the past century

Not only does overwinter PDO predict population growth of *P. smintheus*, but also the curvilinear pattern of its effect implies that both components of climate change, warmer winters (upper end of the PDO range) and more variable winters (both ends of the PDO range), are associated with negative population growth. The number of years that overwinter PDO is in the range producing negative population growth can be determined from records of PDO dating back to 1900 (JISAO 2012). This allows the determination of any trend in the PDO(winter) index over the past century. We used results for the subpopulation in meadow M (Fig. 2) to help determine how often PDO is in the range producing negative population growth. Meadow M is the largest subpopulation at our study site (Roland et al. 2000) and is the most stable in terms of pattern of population growth (Fig. 2). Values of overwinter PDO less than $-1.0$ and greater than $0.7$ are associated with negative $R_t$ in this meadow (Fig. 2). We call these “extreme” years, regardless of whether they are extremely positive or negative. Interestingly, there is a pattern of increasing probability of winters being extreme in one direction or the other vs. a “normal” year, over the past century (Fig. 3a; logistic regression, $\beta = 0.016, P = 0.036$; coded “1” for both types of extreme PDO year and coded “0” for normal years). This pattern is consistent

### Table 2. Coefficients of the best mixed-effects model (Table 1: model 4) for the effect of abundance and PDO (Nov–Mar) on rate of population change for *P. smintheus* butterflies (Fig. 2).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Coefficient</th>
<th>$t$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.83</td>
<td>5.40***</td>
</tr>
<tr>
<td>$\log N_t$</td>
<td>-0.58</td>
<td>-9.45***</td>
</tr>
<tr>
<td>$\log N_t + PDO(Nov–Mar)$</td>
<td>-0.054</td>
<td>-1.57</td>
</tr>
<tr>
<td>PDO(Nov–Mar)$^2$</td>
<td>-0.350</td>
<td>-10.19***</td>
</tr>
</tbody>
</table>

*Notes: Meadow (subpopulation) is included as a random effect (variable intercept), and its contribution to variation in $R_t$ is indicated. Meadow SD = 0.46; residual SD = 0.39.

*** $P < 0.001$.

![Fig. 2](image-url)  
**Fig. 2.** Effect of mean monthly PDO during winter on the rate of population change of *P. smintheus* butterfly populations at Jumpingpound Ridge, Alberta, Canada. Each point is an estimate of adult population change between summers for each meadow (panel) and the PDO value for the intervening winter. The regression line was fit using a mixed-effects model with fixed effects for PDO and butterfly abundance and a random effect (intercepts) for the 21 meadows. Individual meadows are indicated by letters as identified elsewhere (Matter and Roland 2010).
with the increased variability in the shorter-frequency component of winter PDO over the past century (Gedalof et al. 2002). Several years of extreme warm winters oscillate with several years of extreme cold winters (Fig. 3b), and the tendency for extreme winters increases over time (Fig. 3b). Although this pattern is evident over the entire century (1900–2000), there was no such pattern within the shorter time interval over which we have population data (1995–2009). In fact, variability in PDO index has declined slightly over that interval (Fig. 3b), which, as would be expected, is associated with the slight trend for increasing *P. smintheus* abundance (Fig. 1).

**DISCUSSION**

The specter of increased climate variability and more frequent climate extremes poses important consequences for animal population growth affected by climate. Our results show a strong effect of overwinter climate, combined with a weaker effect of population size, on the population growth of alpine *Parnassius smintheus* butterflies. The greater importance of extrinsic effects of climate on alpine *P. smintheus* population growth is in contrast to similar analyses for lower elevation *Maculinea alcon* and *M. teleius* (Nowicki et al. 2009), *Euphydryas aurinia* (Schtickzelle et al. 2005), and the Karner blue *Lycaeides melissa samuelis* (Pickens 2007), for which unidentified density-related factors played a more important role than did weather and climate. The dynamics of another alpine butterfly, *Speyeria mormonia*, are similarly dominated by climate effects (Boggs and Inouye 2012), specifically by the date of snowmelt in spring. Not only does climate dominate population growth of *P. smintheus*, its effects are curvilinear, wherein both extremes of winter climate result in population decline. In contrast, population growth of alpine *Speyeria mormonia* is dramatically reduced by extreme winter weather, but only in warmer, drier winters with little snow (Boggs and Inouye 2012).

The biological significance of a quadratic term in the final model is of importance for a number of reasons. First, it suggests a greater importance of increased climate variability and of climate extremes on population dynamics (Drake 2005) compared to only the effect of climate warming. Second, it implies a more complex mechanism(s) by which climate affects population growth compared to that for a linear effect. Third, it suggests less opportunity for adaptation to a generally warming climate due to the concomitant occurrence of extreme cold events despite the warming trend. In addition, negative growth at both ends of the extreme implies complications on how range shifts might be brought about by climate change. The significance of each will be discussed further.

**Climate variability and extremes**

Virtually all other studies on the effect of broad climate variables (such as ENSO, NAO, NPO, or PDO) on animal population growth identify a linear effect on population growth. Warmer climate improves population growth of elk (Hebblewhite 2005), caribou (Hegel et al. 2010), Dippers (Sæther et al. 2000), and Spotted Owls (Glenn et al. 2010), whereas warmer climate can reduce population growth for others (e.g., moose and white-tailed deer; Post and Stenseth 1998). Similarly, the abundance of the butterfly *Vanessa cardui* was linearly related to PDO (Vandenbosch 2003). Nonlinear effects of climate on population growth have been considered
for at least two other butterfly studies. Population growth of Edith’s checkerspot butterfly (*Euphydryas editha bayensis*) is negative at both ends of the range of precipitation (McLaughlin et al. 2002); wet weather reduced larval growth and dry weather reduced host plant growth and produced a phenological mismatch with larvae. Analysis of the effect of temperature and precipitation on population growth rates of 31 species of butterfly in Britain (Roy et al. 2001) included quadratic terms, but found none to be significant in the final models. More general climate variables such as PDO integrate the effects of both temperature and precipitation, which may account for the more complex pattern of response by *Rt*.

**Mechanisms**

*Parnassius smintheus* butterflies, like many species in the genus, are alpine. As such, they are subject to a generally cold and unpredictable environment, for which they exhibit behavioral, morphological, and physiological adaptation. Population decline in both cold, snowy winters and warm, dry winters suggests that they are susceptible to multiple climate-related factors. We do not yet know what overwinter mechanisms are operating for *P. smintheus*, but suggest several that involve both temperature and precipitation, particularly snow cover and snow distribution, that may be associated with the respective ends of the range of PDO index.

A similar mechanism may be operating at both ends of the PDO range. At both extremes of PDO, pharate larvae in eggs could simply freeze. *Parnassius smintheus* eggs, at our sites, freeze at −30°C (Matter et al. 2011) an air temperature that occurs commonly there. Because eggs are laid at or near ground level, snow cover acts as an insulating barrier keeping temperature generally between 0°C and −5°C. In cold, snowy winters (negative PDO), temperature is much more likely to reach lethal levels. Although there is typically more snow in these years, it is still redistributed by wind to the extent that some parts of meadows remain snow-free and hence susceptible to the cold. In warm, dry winters (positive PDO), temperatures may reach lethal levels less frequently, but there is also less insulating snow. The combination of these factors could produce the quadratic relationship seen between growth and overwinter PDO.

Different mechanisms may operate at each end of the range of PDO values. For example, eggs may freeze in cold winters and suffer desiccation in warm, dry winters. It is of interest that insects deal with both freezing and desiccation tolerance by the same means: high concentrations of sugars such as sorbitol and glycerol (Duman et al. 2010). Therefore, adaptation to either freezing or desiccation (either tail of the range of PDO values) could convey benefits for the other.

Warm, dry winters could negatively impact populations in several additional ways. If larvae emerge prematurely during warm, dry winters (Matter et al. 2011), they may be subject to more variable and harsher spring conditions (see Plate 1). These conditions could either affect survival directly by freezing, or, because metabolic rates are higher after hatch than during diapause, could result in depletion of fat reserves (Irwin and Lee 2003). Premature emergence could also cause a phenological mismatch with host plants (e.g., Boggs and Inouye 2012), but because *S. lanceolatum* is a succulent perennial, any mismatch might be due less to the timing of leafing out or senescence (e.g., Singer and Parmesan 2010), and more to the fact that plants retain toxicity until the time of snowmelt (Guppy and Shepard 2001) and remain of lower quality for caterpillars emerging early in the season. Warm winters may facilitate early development of larval host plants, which are then susceptible to late spring frost (e.g., Inouye 2008). Loss of nectar plants due to late frost could lead to decreased reproductive output by female *P. smintheus* (Matter et al. 2009).

**Butterflies vs. vertebrates**

Most previous studies of the effect of sea temperature-based climate variables, such as PDO, on animal
population growth have been on vertebrates such as salmon (Mantua et al. 1997), ungulates (Post and Stenseth 1998, Ezard et al. 2009), and terrestrial (Wilson and Arcese 2003, Glenn et al. 2010) and aquatic birds (Frederiksen et al. 2008). For such species, the observed effects are likely to be buffered for these populations as a whole because they often act on vital rates of only part of the population. For short-lived univoltine insects such as \emph{P. smintheus}, the effects are probably much stronger. With only one generation per year, and no overlapping cohorts, there would be no such demographic buffering; climate effects in any one year would affect the survival and reproduction of the entire population (but see Boggs and Inouye 2012).

\textbf{Range shifts}

Climate warming should facilitate either a poleward or elevational shift in butterfly distribution (Hill et al. 2002, Thorne et al. 2006, Kharouba et al. 2009, Forister et al. 2011). Our data on alpine \emph{Parnassius smintheus} support this, in that warming of previously cold sites, where net population growth was previously negative, would sustain positive population growth. More importantly perhaps, our data also suggest that lower latitude and low-elevation range margins might be affected more, as warmer, drier winters also promote negative population growth. The lower limit of distribution would move up mountains, and, in the Northern Hemisphere, the southern range limit would move north. More variable climate and more extremes of climate (both extremes of PDO index) could have the effect of retracting both margins of an animal’s distribution. The details of such range shifts would depend, of course, on the details of the statistical distribution of the “new” range of climate variation and extremes (e.g., Smith 2011, IPCC 2012).

\textbf{Adaptation}

The curvilinear pattern of population growth in response to PDO index also has important consequences for adaptation to the new climate regime. If temperature minima were to shift upward (warmer) but concurrently become more variable, then long-term adaptation to these warmer minima, such as by the loss of cold tolerance (e.g., Crozier 2003), would render populations more vulnerable to any short-term regional extreme cold events. If the “cold” extremes shift lower, because of increased variation, there would clearly be population decline.

Female \emph{P. smintheus}, like other \emph{Parnassius}, oviposit off of the host plant, laying eggs on virtually any substrate other than the larval host plant. As a result, females may be selecting among microclimates that are more variable than are those in which the host plant grows. During cold extremes, some eggs will be in sufficiently warmer sites and during warm extremes some will be in sufficiently colder microsites. The net effect of this behavior is that a subset of eggs will be in a microclimate less variable than that caused by annual winter extremes, thus providing the same benefit that active selection of microclimates by caterpillars provides for \emph{Parnassius apollo} (Ashton et al. 2009), and that variation in topography provides for \emph{E. edita bayensis} caterpillars (Weiss et al. 1988) to buffer broad climate effects. Such behaviors act to stabilize populations (McLaughlin et al. 2002, Oliver et al. 2010) by compensating for broader effects of climate variability.

\textbf{Conservation}

The long-term pattern of increasing variability in winter PDO values (Fig. 3a, b) suggests three things. First, alpine \emph{Parnassius} populations are at increasing risk of shrinking in abundance (more years of negative growth). Second, it may be difficult for selection to counter climatic extremes because counter selection could act at both ends of the PDO index, in contrast to a linear effect of climate for which selection might be more directional. Third, increased winter variability, and the potential for more frequent extreme events at both ends of the range of PDO index, could act to “shrink” the geographic range of this insect, depending on how the specific “events” interact with the general climate trend (Drake 2005, Jentsch et al. 2007, Frederiksen et al. 2008). Short-term, but more frequent, extremes in weather could curtail gradual shifts, particularly for animals in capricious environments such as the alpine, and especially if such events occur over several years in sequence.

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\textbf{Literature Cited}


**Supplemental Material**

**Appendix**

Preliminary analysis of data using generalized linear models (GLM) and generalized additive models (GAM) to identify nonlinear effects (Ecological Archives E094-016-A1).