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ARTICLE

Animal Ecology

Life stage hypothesis modeling determines insect vulnerability during developmental life stages to climate extremes

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Funding information

Disney Conservation Fund; The Xerces Society for Invertebrate Conservation; Montana State University; Iowa State University Graduate Program in Ecology and Evolutionary Biology; Iowa State University Department of Ecology, Evolution, and Organismal Biology; University of Wyoming NPS Research Station; Decagon Devices; The Center for Global and Regional Environmental Research

Handling Editor: Robert R. Parmenter

Abstract

Butterflies are important bioindicators that can be used to monitor the effects of climate change, particularly in montane environments. Changes in butterfly population size over time, reflective of indicator life stages, can signal changes that have occurred or are occurring in their environment indicating ecosystem health. From the perspective of understanding butterflies as bioindicators in these systems, it is essential to identify influential environmental variables at each life stage that have the greatest effect on population dynamics. Life stage hypothesis modeling was used to assess the effects of multiple temperature and precipitation metrics on the population growth rate of a *Parnassius clodius* butterfly population from 2009 to 2018. Extreme maximum temperatures during the larval-pupal life stages were identified to have a significant negative effect on population growth rate. We speculate that higher temperatures during the spring ephemeral host plant's flowering, and *P. clodius*' larval stage, may lead to earlier plant senescence and lower *P. clodius* growth. Because *Parnassius* butterflies are well studied from a global perspective, results may aid in understanding the potential indicator life stages of other insect species in montane environments to climatic changes. Findings from this study demonstrate the value in assessing a butterfly species' response to short-term weather variation or long-term climatic changes *at each life stage* in order to protect and conserve insects and their interactions with other organisms.

KEYWORDS

butterfly, climate change, indicator life stages, influential weather variables, life stage hypothesis modeling, montane meadows, population dynamics

INTRODUCTION

Insects are responding to climate change globally (Diamond et al., 2011; Forister et al., 2021; Parmesan et al., 1999; Parmesan & Yohe, 2003)—sparking a need to

investigate how weather affects insect population dynamics. It is becoming increasingly crucial to identify specific influential weather variables that play a role in insect population change and distributional shifts (Roland & Matter, 2016). Once identified, these influential weather

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variables may help in predicting population changes that could result from either short-term weather variation or long-term climatic changes (Roland & Matter, 2016) and reflect greater changes occurring in the environment (Samways et al., 2010).

Butterflies in particular are important bioindicators that can be used to monitor the effects of climate change over time (Diamond et al., 2011; Kevan, 1999). As an easily surveyed, small ectothermic organism with a rapid generation time, butterflies are an ideal model organism to evaluate biodiversity and shifts in species distributions geographically in response to weather and climate variation (Kevan, 1999). Changes in butterfly population size over time can be a strong signal of changes that have occurred or are occurring in their environment (Horn, 2003; Kevan, 1999). Suitable butterfly habitat is decreasing globally due to human land use intensification, landscape-scale degradation due to pollution, and climate change, leading to declining butterfly population sizes and shifting range distributions in North America, the United Kingdom, and other locations (Forister et al., 2021; Thomas, 2016; White & Kerr, 2006, 2007). The abundances of butterfly species in North America and Europe have been declining during the last half century in response to habitat changes due to warming and drying (Forister et al., 2021), habitat changes from direct anthropogenic influences (Nakonieczny et al., 2007), and distributions have shifted northward and to higher elevations in response to declining suitable habitat (Hill et al., 2002; Parmesan et al., 1999). Butterflies that persist in small, isolated populations with specific habitat requirements are at greater risk of decline or extinction compared with other butterfly species (Szcodronski et al., 2018). For example, the critically imperiled Fender's blue butterfly (*Icaricia icarioides fenderi*) exists in small, isolated patches of Oregon prairie where <0.5% of its original habitat contains its larval host plant, Kincaid's lupine (*Lupinus sulphureus kincaidii*) (Schultz, 2001; Schultz & Crone, 2005). Further, butterfly ranges have been shifting upward in elevation and poleward in relation to shifting environmental conditions (Condamine & Sperling, 2018; Hill et al., 2002; Parmesan et al., 1999; Parmesan & Yohe, 2003), with butterfly phenological responses advancing three times stronger than their plant counterparts (Parmesan, 2007) in response to climate change.

Identification of influential weather variables at each butterfly life stage (i.e., life stage hypothesis modeling) is needed so that scientists and managers can prioritize butterfly conservation efforts during the most vulnerable life stage in the most threatened geographic locations. A study conducted over 17 years in two mountainous regions of the Czech Republic tested the effect of climatic conditions during two larval phases

(i.e., fall/spring activity and overwintering) on subsequent adult abundances of two *Erebia* butterflies (*Erebia epiphron* and *Erebia sudetica*) to evaluate which weather variables drive population dynamics of these montane insects (Konvicka et al., 2021). Decreased precipitation and warmer temperatures during overwintering were associated with decreased adult abundances, while increased adult abundances were observed with warmer temperatures in fall and warmer and drier springs during active larval phases (Konvicka et al., 2021). Additionally, higher minimum temperatures during the adult flight season were associated with decreased butterfly abundances (Konvicka et al., 2021). This research demonstrates that evaluating life stages may identify vulnerabilities of insect species life cycles to weather patterns. A meta-analysis uncovered a 1.6% annual reduction in the number of individual butterflies in the Western United States over the past 40 years in response to warmer fall temperatures, with single brood (univoltine) species declining more severely (Forister et al., 2021). Conversely, more butterflies were observed in response to warmer temperatures during summer months in some Western United States areas and in response to increased precipitation associated with positive effects on interacting plant species (Forister et al., 2021). These research projects detail the positive and negative effects that short-term weather variation or long-term climatic changes can have on butterfly species. Observational research conducted over 15 years in Alberta, Canada, investigated the direct and indirect effects of various weather variables on subpopulations of *Parnassius smintheus* to predict their response to a changing climate (Filazzola et al., 2020; Matter et al., 2011). Direct effects included increased overwintering mortality in response to extreme minimum temperatures reaching -27.9°C and frequent loss of snow cover, and premature larval development under elevated temperatures, associated with earlier emergence which negatively affected survival and population growth (Matter et al., 2011; Roland & Matter, 2016). Indirect effects included temperature and precipitation changes affecting growth and survival of host and nectar plant species limiting larval and adult resources, thus affecting butterfly distribution (Filazzola et al., 2020; Matter et al., 2011). Due to the increasing frequency of short-term extreme weather events, such as extreme temperature, precipitation, and natural disasters (van Aalst, 2006), and longer-term changes in variables such as minimum and maximum daytime and nighttime temperatures and annual snowpack (IPCC, 2021; Whitlock et al., 2017), understanding these relationships will become even more important in the future.

Parnassius butterflies serve as model species for insect conservation in montane ecosystems across the globe

(Nakonieczny et al., 2007; Todisco et al., 2010). *Parnassius* are nonmigratory butterflies, making them susceptible to short-term weather variation and the long-term effects of climate change. These butterflies live in local populations with limited fecundity, making their populations susceptible to change. *Parnassius* are restricted to high elevation montane meadows, environments predicted to be at greater risk and expected to undergo rapid change under a changing climate (Kim et al., 2002; Nakonieczny et al., 2007; Roland & Matter, 2013; Thuiller et al., 2005). Further, these butterflies' lifecycles are intricately dependent on the climatic patterns associated with seasonality in montane meadows. Changing climate patterns will likely lead to earlier larval emergence due to prolonged warm weather in fall and/or spring (Crees & Debinski, 2021). Altered butterfly life stage timing could induce a mismatch between the timing of larval emergence and host plant emergence and availability for senescing host plant species (Calabrese et al., 2008; Crees & Debinski, 2021). For instance, *Parnassius apollo* and *P. smintheus* population dynamics are directly influenced by changing climatic conditions due to phenological shifts in life stage responses. *P. apollo* and *P. smintheus* early larval emergence has been observed in response to warming temperatures in June (Kuhn et al., 2005) and November (Calabrese et al., 2008) leaving them susceptible to extreme weather events, limiting successful reproduction (Nakonieczny et al., 2007). Prolonged periods of cool temperatures and rain following unusual warm spring temperatures will likely result in reduced larvae activity and development leading to subsequent increased larvae mortality (Nakonieczny et al., 2007) and population declines.

Here, we analyzed the population dynamics of a *Parnassius clodius* population in Grand Teton National Park, WY, USA, from 2009 to 2018 in relation to weather data to assess how this species' life stages are responding to changing climate in a montane region. Populations of *P. clodius* are well distributed in the Teton region, with 78% of suitable surveyed meadows occupied in 2013 (Szcudronski et al., 2018). However, many of the monitored populations had low numbers of individuals. Like many insect species, *P. clodius* population dynamics have yet to be evaluated in determining their conservation status. *P. clodius* is currently not threatened or endangered in its native range of North America. However, it faces similar threats as its European sister species, *P. apollo*, which is listed on the IUCN red list of threatened species due to habitat loss from forest encroachment, climatic changes, heavy metal contamination, over collection, and genetic erosion (Nakonieczny et al., 2007). By studying how *P. clodius* population dynamics are correlated with interannual variation in weather variables at each life

stage, and comparing these results with responses of other species within the genus of *Parnassius* butterflies, we may be able to develop a more generalized understanding of montane insect responses to climatic extremes. The goal of this research was to evaluate how the interannual variation in population size of *P. clodius* was correlated with weather variables assumed to affect *Parnassius* butterflies within specific life stages. Weather conditions during the overwintering period (i.e., pharate first instars or egg life stage) were hypothesized to have the greatest effect on population size compared with the larval/pupal and adult life stages based on previous observations of *P. smintheus* (Roland & Matter, 2013, 2016).

MATERIALS AND METHODS

Species description

P. clodius (Lepidoptera: Papilionidae) is a medium-sized butterfly that is mostly white with a hairy yellow body and inhabits Western Canada and United States (Figure 1). They are often found in open montane woodlands and meadows but can extend to higher elevations



FIGURE 1 *Parnassius clodius* butterfly. Photo credit: J. Simone Durney.

and reside on mountaintops. Their host-plant is steer's head (*Dicentra uniflora*) (Scott, 1986), a small herbaceous perennial and a spring ephemeral (Crees & Debinski, 2021). The primary nectar source of *P. clodius* in this region is sulfur flower buckwheat (*Eriogonum umbellatum*) (Auckland et al., 2004) along with several other flowering plant species (Crees & Debinski, 2021; Szcodronski et al., 2018). Previous research revealed suspected positive associations between *P. clodius* occupancy and bare ground associated with low sagebrush (*Artemisia arbuscula*) and *D. uniflora* (i.e., *P. clodius*'s host plant), with the presence of big sagebrush (*Artemisia tridentata*) and lupine (*Lupinus* spp.) having a clear negative association with *P. clodius* occupancy (Szcodronski et al., 2018).

P. clodius is a univoltine species that overwinters as a pharate first instar larva (hereafter, egg) (Scott, 1986). Following spring snowmelt, the larvae emerge to feed and take 2–3 weeks to mature (Crees & Debinski, 2021). Larvae form a chrysalis on the ground typically among rocks and debris to pupate over a 1-to-2-week period. Typically, adults emerge from pupae in mid to late June with males emerging prior to females. Peak flight is usually late June to early July in Grand Teton National Park, although this can vary by several weeks, depending upon spring conditions (D. Debinski and S. Durney, personal observation, 2009–2022). *P. clodius* females oviposit on vegetation, such as sagebrush and the undersides of balsamroot leaves, near host plants for the remainder of the flight season, which often ends in mid-July (Crees & Debinski, 2021). Microclimatic conditions influence the timing of when each life stage takes place (i.e., the phenological progression) (Crees & Debinski, 2021).

Study area

The study area (Pilgrim Creek) was a relatively homogeneously vegetated sagebrush meadow with dry, gravelly soils surrounded by coniferous woodlands along the meadow edge in Grand Teton National Park at 43.9159° N, –110.5788° W and 1500 m × 300 m in size. The meadow is relatively flat, and at an elevation of 2120 m. The vegetation community of the meadow included mostly low sagebrush (*A. arbuscula*), some big sagebrush (*A. tridentata*), several known *P. clodius* nectar plant species listed in the *species description* section, and *P. clodius*' host plant—*D. uniflora*. Temperatures in this area range from –30 to 30°C (USDA Base Camp SNOTEL). Snow water equivalents vary from 0 to 69 cm, with snow depths of up to 236 cm (USDA Snake River Station SNOTEL). Date of snowmelt can vary by weeks with the earliest snowmelt date recorded on May 4 and

the latest on June 10 while conducting the research presented here.

Butterfly mark-recapture

Mark-recapture methods were used to study a population of *P. clodius* at Pilgrim Creek in Grand Teton National Park, Wyoming, USA, across annual flight seasons between 2009 and 2018 during June and July. Surveys were not carried out in 2012 and 2013. Six 50 m × 50 m plots a minimum of 100 m apart, were located using GPS units, flagged prior to the flight season of *P. clodius*, and surveyed each year. Survey plots were initially established in 2000 in an effort to balance increasing the area sampled, decreasing the number of recaptures, and maintaining independent sampling within a single meadow (Auckland et al., 2004). Mark-recapture surveys began a few days after the beginning of the flight season and continued until only one or two butterflies per plot were caught during a survey period. Plots were monitored daily if weather permitted throughout each flight season. Surveys were conducted when temperatures were above 21°C, wind was <16 km h^{–1}, and clouds were not obscuring the sun. If weather prevented all six plots from being sampled in 1 day, the rotation was completed the following day. The order in which plots were surveyed rotated throughout the flight season to vary the time of day surveys was conducted for each plot.

Two people surveyed each plot for 20 min between 10:00 and 17:00. All *P. clodius* butterflies in a plot were netted by hand and held in glassine envelopes until the survey ended. The time of capture and activity of the butterfly when captured (i.e., nectaring, chasing, and stationary) was noted on each envelope. Following each survey, captured butterflies were marked with a permanent marker on each hindwing with an identification number indicating the plot it was caught in and the butterfly's individual number (Figure 1). The number corresponded to the consecutive butterfly count throughout a season. The following metrics were recorded for each captured butterfly: date, plot number, identification number, time of capture, sex, and whether the butterfly was a recapture. After data were collected for each butterfly and butterfly markings were added, all butterflies were released in the center of each plot by placing butterflies on surrounding plants, rather than being placed on the ground where they could be stung by ants.

Weather variable selection

A list of meaningful weather variables expected to affect populations of *P. clodius* butterflies was formulated based

upon previous research that identified influential weather variables affecting the population dynamics of other *Parnassius* species (Matter et al., 2011; Matter & Roland, 2017; Roland & Matter, 2013, 2016) as well as our observations at Pilgrim Creek over time. The list of explanatory variables included date of snowmelt, maximum snow water equivalent (in centimeters), mean snow water equivalent (in centimeters), mean temperature (in degrees Celsius), mean maximum temperature (in degrees Celsius), extreme maximum temperature (in degrees Celsius), mean minimum temperature (in degrees Celsius), extreme minimum temperature (in degrees Celsius), accumulated rainfall (in centimeters) from 2008 to 2018 (Table 1). All temperature data were sourced from the USDA Base Camp SNOTEL site located at 43.93333° N, -110.45000° W at 2151 m in elevation and 10.7 km from Pilgrim Creek meadow. All snow water equivalent and precipitation data were sourced from the USDA Snake River Station SNOTEL site located at 44.13333° N, -110.66667° W at 2109 m in elevation and 25.1 km from Pilgrim Creek meadow.

Analysis

The goal of these analyses was to identify which weather variables, known to affect other butterfly species, explain variation in *P. clodius* population growth through each life stage. Estimates of population change were calculated for the Pilgrim Creek, WY, population of *P. clodius* for the duration of the study (i.e., 2009–2011, 2014–2018). Calculations of population change (R_t) were estimated as the ratio of the number of caught butterflies (N_t) for one flight season after accounting for effort, relative to the number of caught butterflies of the previous flight season

after accounting for effort. Effort was measured as the number of two-person 20-min plot surveys conducted during each flight season. R_t was calculated as $\log_{10}((N_{t+1}/\text{effort}_{t+1})/(N_t/\text{effort}_t))$ (Roland & Matter, 2016). This simplified approach to estimating population size used in previous research (Roland & Matter, 2016) uses information regarding known observed butterflies in combination with standardized sampling effort allowing researchers to produce tangible values. Our estimate of population size was included in each model to evaluate density dependence as an explanatory variable on population growth. Population size was estimated by taking the log of the number of caught butterflies divided by the number of surveys conducted for each flight season (i.e., $\log_{10}(N_t/\text{effort}_t)$).

A life stage hypothesis modeling approach was used to evaluate the effect of each chosen weather variable during each life stage on the population growth (i.e., R_t) of *P. clodius* butterflies. The observed values for each weather variable were partitioned by life stage to evaluate each variable's effect during each stage of the *P. clodius* lifecycle. Dates of each life stage were estimated from researcher observations (L. Crees, personal communication, October 2022) of *P. clodius* over time to capture the estimated beginning and end dates of each life stage. We categorized the egg stage as July 21–April 30, the larva-pupa stage as May 1–May 31, and the adult stage June 1–July 20. Each weather variable was tabulated for the egg stage, larva-pupa stage, and the adult butterfly stage (Table 1). The larva and pupa life stages were combined due to the uncertainty of the date of when one stage ended and the other began.

Correlation tests were conducted between all explanatory weather variables to prevent the inclusion of highly correlated variables in models, which could lead to multicollinearity and unreliable estimates. Uncorrelated precipitation and temperature explanatory variables and $\log N_t$ (i.e., density dependence) were included in each generalized linear model. Then, generalized linear models using the *glm* function in R were fit to evaluate which explanatory weather variables were the most descriptive in explaining population change (R_t). Additionally, generalized additive models using the *gam* function in R were fit to evaluate quadratic relationships between population change (R_t) and explanatory weather variables. Akaike information criterion (AIC) comparison between models was conducted to determine the most informative explanatory variables. Following generalized linear models that included $\log N_t$ and interactions between the most informative temperature and precipitation explanatory variables were used to evaluate potential interactive effects between weather variables on population change. Final

TABLE 1 The nine explanatory weather variables included in analyses tabulated by each *Parnassius clodius* life stage for each year of this study.

Weather variables evaluated	Weather variable units	Weather variable ranges
Day of year snowmelt	No units	124 to 161
Maximum snow water equivalent	cm	23 to 69
Mean snow water equivalent	cm	7 to 20
Mean temperature	°C	0 to 14
Mean maximum temperature	°C	8 to 23
Extreme maximum temperature	°C	20 to 31
Mean minimum temperature	°C	−6 to 3
Extreme minimum temperature	°C	−4 to −31
Accumulated rainfall	cm	64 to 110

AIC comparison was conducted to determine the best model to describe population change for each *P. clodius* life stage.

RESULTS

A *P. clodius* population was monitored from 2009 to 2018, excluding 2012 and 2013, producing eight interannual estimates of population change. During the study, 532 surveys were conducted and 3868 *P. clodius* individual butterflies were caught. Population size and change (R_t) varied over the study with population increases occurring in 2011, 2017, and 2018 and population declines occurring 2009, 2010, 2014, 2015, and 2016 (Figure 2).

Egg life stage

Correlation tests revealed that extreme maximum temperature during the egg stage was not highly correlated (i.e., $-0.5 < R < 0.5$) with the other explanatory weather

variables and thus was included in the full generalized linear model. Due to collinearity among the remaining weather variables, generalized linear models were constructed with population change (i.e., response variable) and each remaining explanatory weather variable (i.e., day of year snowmelt, maximum and mean snow water equivalent, mean temperature, mean maximum temperature, mean minimum temperature, extreme minimum temperature, and accumulated rainfall) (Table 2). AIC comparison between those models was conducted to determine which weather variables were the most descriptive in explaining population change (Table 2). Thus, mean snow water equivalent, mean minimum temperature (Table 2), and extreme maximum temperature were the best descriptors of population change during the *P. clodius* egg life stage. However, including those weather variables with and without interactions along with previous populations size in generalized linear models resulted in no explanation of significant independent variation of population change during the egg life stage and did not significantly differ from the null model ($F_{3,7} = 4.0271$; $p = 0.1059$) (Table 3). Further, including each descriptive weather variable in its own generalized

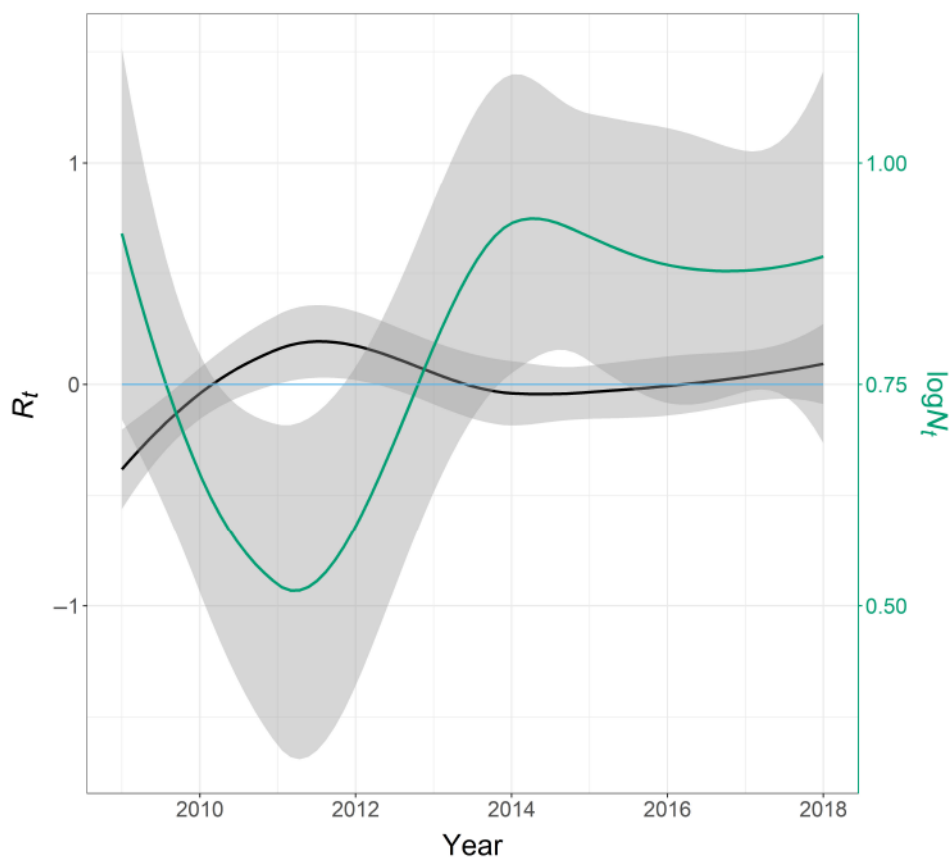


FIGURE 2 Years of study with associated population change (R_t) in black and density dependence ($\log N_t$) in green represented as lines. The shaded areas represent the 95% CI. The horizontal blue line represents no population change. Surveys were not carried out in 2012 and 2013.

TABLE 2 Akaike information criterion (AIC) comparison table for models testing for the best predictive weather explanatory variables among highly correlated (i.e., $R > 0.5$) variables to be included in full generalized linear models for each life stage (i.e., egg, larval-pupal, and adult).

Life stage	Weather variable type	Model	df	AIC
Egg	Precipitation	$R_t \sim$ Day of year snowmelt	3	−0.7088
		$R_t \sim$ Max snow water equivalent	3	−0.7237
		$R_t \sim$ Mean snow water equivalent	3	−1.3919
	Temperature	$R_t \sim$ Mean maximum temperature	3	−0.9940
		$R_t \sim$ Mean minimum temperature	3	−1.3306
		$R_t \sim$ Mean temperature	3	−0.6472
Larval-pupal	Precipitation	$R_t \sim$ Accumulated rainfall	3	−1.3621
		$R_t \sim$ Day of year snowmelt	3	−0.7088
		$R_t \sim$ Max snow water equivalent	3	−0.7500
		$R_t \sim$ Mean snow water equivalent	3	−0.8933
	Temperature	$R_t \sim$ Extreme maximum temperature	3	−8.0743
		$R_t \sim$ Extreme minimum temperature	3	−0.6695
		$R_t \sim$ Mean maximum temperature	3	−1.5279
		$R_t \sim$ Mean minimum temperature	3	−0.7731
		$R_t \sim$ Mean temperature	3	−1.1596
Adult	Precipitation	$R_t \sim$ Accumulated rainfall	3	−0.8856
		$R_t \sim$ Day of year snowmelt	3	−0.7088
		$R_t \sim$ Max snow water equivalent	3	−2.7788
		$R_t \sim$ Mean snow water equivalent	3	−2.7788
	Temperature	$R_t \sim$ Extreme maximum temperature	3	−3.3465
		$R_t \sim$ Mean maximum temperature	3	−1.6039
		$R_t \sim$ Mean minimum temperature	3	−0.6702
		$R_t \sim$ Mean temperature	3	−1.4181

Note: Due to correlation between maximum and mean snow water equivalent, maximum snow water equivalent was chosen as the predictor variable during the adult life stage since the AIC values were the same between the two variable models. Bold variables indicate the best predictive weather explanatory variable among highly correlated variables to be included in each life stage model.

linear model with population change as the response revealed that none of the descriptive weather variables during the egg stage significantly explained population change (Figures 3 and 4).

Larval-pupal life stage

All explanatory weather variables were highly correlated during the larval-pupal life stage. Therefore, generalized linear models were constructed with population change as the response variable and each explanatory weather variable. AIC comparison determined that accumulated rainfall and extreme maximum temperature were the best descriptors (i.e., lowest AIC value) (Table 2) of population change during the *P. clodius* larva-pupa life stages. The full model including all descriptive weather variables, their interactions, and density dependence resulted in no

significant explanation of independent variation on population change. The same was true for the full model excluding interactions. Each descriptive weather variable was evaluated in its own generalized linear model with population change as the response. For the larval-pupal life stage, we found that extreme maximum temperature significantly explained population change ($\beta = -0.095 \pm 0.031$ (SE), $t = -3.032$, $p = 0.023$) (Figures 3 and 4; Table 3).

Adult life stage

Correlation tests determined that extreme minimum temperature during the adult stage was not highly correlated with the other explanatory weather variables and so was included in the full generalized linear model for the adult stage. Of the remaining variables, maximum snow water equivalent and extreme maximum temperature had the

TABLE 3 Akaike information criterion (AIC) comparison table for full generalized linear models including the best predictive weather explanatory variables at each life stage (i.e., egg, larval-pupal, and adult), their interactions, and density dependence on population change R_t .

Life stage	Model	F	df	AIC
Egg	$R_t \sim \log N_t + \text{Mean snow water equivalent} \times \text{Extreme maximum temperature} + \text{Mean snow water equivalent} \times \text{Mean minimum temperature}$		8	-3.3665
	$R_t \sim \log N_t + \text{Extreme maximum temperature} + \text{Mean snow water equivalent} \times \text{Mean minimum temperature}$		7	-4.2761
	$R_t \sim \log N_t + \text{Mean snow water equivalent} \times \text{Extreme maximum temperature} + \text{Mean minimum temperature}$		7	-4.8884
	$R_t \sim \text{Mean snow water equivalent} \times \text{Extreme maximum temperature} + \text{Mean minimum temperature}$		6	3.5334
	$R_t \sim \text{Mean snow water equivalent} \times \text{Extreme maximum temperature}$		5	2.0951
	$R_t \sim \text{Mean snow water equivalent} \times \text{Mean minimum temperature}$		5	1.3311
	$R_t \sim \text{Extreme maximum temperature} + \text{Mean snow water equivalent} \times \text{Mean minimum temperature}$		6	0.2423
	$R_t \sim \log N_t + \text{Mean snow water equivalent} + \text{Extreme maximum temperature} + \text{Mean minimum temperature}$		6	-6.2467
	$R_t \sim \log N_t + \text{Mean snow water equivalent} + \text{Extreme maximum temperature}$		5	-1.6514
	$R_t \sim \log N_t + \text{Mean snow water equivalent} + \text{Mean minimum temperature}$		5	-7.7721
	$R_t \sim \log N_t + \text{Extreme maximum temperature} + \text{Mean minimum temperature}$		5	-7.2273
	$R_t \sim \text{Mean snow water equivalent} + \text{Extreme maximum temperature} + \text{Mean minimum temperature}$		5	1.7033
	$R_t \sim \text{Mean snow water equivalent} + \text{Extreme maximum temperature}$		4	0.1886
	$R_t \sim \text{Mean snow water equivalent} + \text{Mean minimum temperature}$		4	0.3441
	$R_t \sim \text{Extreme maximum temperature} + \text{Mean minimum temperature}$		4	0.1655
	$R_t \sim \log N_t$		3	-3.0856
	$R_t \sim \text{Mean snow water equivalent}$		3	-1.3919
	$R_t \sim \text{Extreme maximum temperature}$		3	-0.8014
	$R_t \sim \text{Mean minimum temperature}$		3	-1.3306
	$R_t \sim 1$		2	-2.6412
	Likelihood ratio test of null model to best model	4.0271	3	0.1059
Larval-Pupal	$R_t \sim \log N_t + \text{Accumulated rainfall} \times \text{Extreme maximum temperature}$		6	-4.7182
	$R_t \sim \log N_t + \text{Accumulated rainfall} + \text{Extreme maximum temperature}$		5	-5.6658
	$R_t \sim \text{Accumulated rainfall} + \text{extreme maximum temperature}$		4	-7.6590
	$R_t \sim \text{Accumulated rainfall} \times \text{Extreme maximum temperature}$		5	-6.4838
	$R_t \sim \log N_t + \text{Extreme maximum temperature}$		4	-6.0747
	$R_t \sim \log N_t + \text{Accumulated rainfall}$		4	-1.8830
	$R_t \sim \log N_t$		3	-3.0856
	$R_t \sim \text{Accumulated rainfall}$		3	-1.3621
	$R_t \sim \text{Extreme maximum temperature}$		3	-8.0743
	$R_t \sim 1$		2	-2.6412
	Likelihood ratio test of null model to best model	9.1939	1	0.02303
Adult	$R_t \sim \log N_t + \text{Maximum snow water equivalent} \times \text{Extreme minimum temperature} + \text{Maximum snow water equivalent} \times \text{Extreme maximum temperature}$		6	-2.7225
	$R_t \sim \log N_t + \text{Maximum snow water equivalent} \times \text{Extreme minimum temperature} + \text{Extreme maximum temperature}$		6	-2.7225

TABLE 3 (Continued)

Life stage	Model	F	df	AIC
	$R_t \sim \log N_t + \text{Extreme minimum temperature} + \text{Maximum snow water equivalent} \times \text{Extreme maximum temperature}$		6	-2.7225
	$R_t \sim \text{Maximum snow water equivalent} \times \text{Extreme minimum temperature} + \text{Extreme maximum temperature}$		5	-2.3274
	$R_t \sim \text{Extreme minimum temperature} + \text{Maximum snow water equivalent} \times \text{Extreme maximum temperature}$		5	-2.3274
	$R_t \sim \text{Maximum snow water equivalent} \times \text{Extreme minimum temperature}$		4	-0.8080
	$R_t \sim \text{Maximum snow water equivalent} \times \text{Extreme maximum temperature}$		4	-4.3000
	$R_t \sim \log N_t + \text{Maximum snow water equivalent} + \text{Extreme minimum temperature} + \text{Extreme maximum temperature}$		6	-2.7225
	$R_t \sim \log N_t + \text{Extreme minimum temperature} + \text{Extreme maximum temperature}$		5	-4.7035
	$R_t \sim \log N_t + \text{Maximum snow water equivalent} + \text{Extreme minimum temperature}$		5	0.4432
	$R_t \sim \log N_t + \text{Maximum snow water equivalent} + \text{Extreme maximum temperature}$		5	-3.8363
	$R_t \sim \text{Maximum snow water equivalent} + \text{Extreme minimum temperature} + \text{Extreme maximum temperature}$		5	-2.3274
	$R_t \sim \text{Maximum snow water equivalent} + \text{Extreme minimum temperature}$		4	-0.8080
	$R_t \sim \text{Maximum snow water equivalent} + \text{Extreme maximum temperature}$		4	-4.3000
	$R_t \sim \text{Extreme minimum temperature} + \text{Extreme maximum temperature}$		4	-2.4239
	$R_t \sim \log N_t$		3	-3.0856
	$R_t \sim \text{Maximum snow water equivalent}$		3	-2.7788
	$R_t \sim \text{Extreme minimum temperature}$		3	-1.0617
	$R_t \sim \text{Extreme maximum temperature}$		3	-3.3465
	$R_t \sim 1$		2	-2.6412
	Likelihood ratio test of null model to best model	2.3194	3	0.2170

Note: Bold models indicate the top model for each life stage. Bold likelihood ratio tests indicate that the top model differed significantly from null model.

lowest AIC values (Table 2). Thus, maximum snow water equivalent, extreme maximum temperature, and extreme minimum temperature were the best descriptors of population change during the *P. clodius* adult life stage. However, including those weather variables with and without interactions along with population size in generalized linear models resulted in no explanation of significant independent variation of population change during the adult life stage and did not significantly differ from the null model ($F_{3,7} = 2.3194$; $p = 0.2170$) (Table 3). Including each descriptive weather variable in its own generalized linear model with population change as the response revealed that none of the descriptive weather variables during the adult life stage significantly explained population change (Figures 3 and 4).

DISCUSSION

Life stage hypothesis modeling of a *P. clodius* population from 2009 to 2018 identified extreme maximum

temperatures during the larval-pupal life stage as a mechanism driving population dynamics in the next generation of the population (Figures 4 and 5). These findings do not support our original hypothesis that weather conditions during the overwintering period (i.e., egg life stage) would have the greatest effect on population size. However, they clearly identify that the larval-pupal life stages are the most sensitive to changing weather conditions for the montane species *P. clodius*. When extreme maximum temperatures reach 22.5°C or above in May (i.e., larval-pupal life stage), there is a noted decline in *P. clodius* population growth rates, while additional unaccounted factors must be contributing to the deviation from this pattern observed in 2018 (Figure 5). This finding suggests that the predicted increasing frequency of short-term extreme weather events (van Aalst, 2006), especially in May, and long-term climatic changes to increasing temperatures (IPCC, 2021; Whitlock et al., 2017) could lead to future declines in *P. clodius* populations.

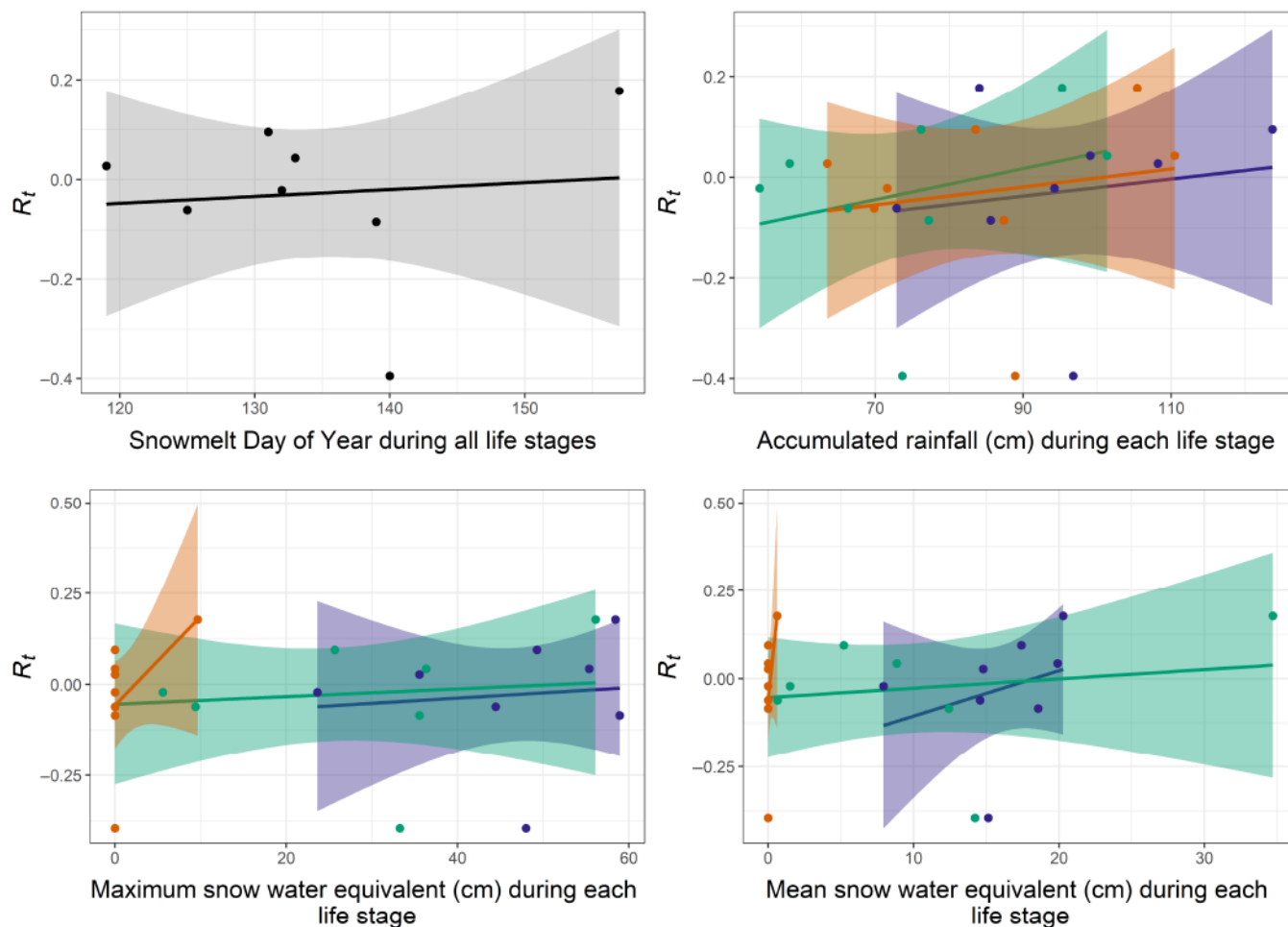


FIGURE 3 The relationship between *Parnassius clodius* population change (R_t) from 2009 to 2018 by life stage to the precipitation weather variables considered in these analyses represented by lines. The egg life stage is given in purple, the larval-pupal life stages are given in green, and the adult life stage is given in orange. Day of year snowmelt did not vary across the life stages and is given in black. Darker, thicker lines and points indicate a significant relationship between population change and a descriptive weather variable at a particular life stage. The shaded areas represent the 95% CI. Surveys were not carried out in 2012 and 2013. Overall, there were no significant relationships detected between population change and date of snowmelt, maximum snow water equivalent, mean snow water equivalent, and accumulated rainfall.

Related research investigating the response of population dynamics of the similarly non-migratory montane univoltine butterfly, *P. smintheus*, identified direct and indirect effects of weather on population growth rates. A field study showed that a quadratic interaction between extreme minimum temperature and absence of snow cover had the greatest *direct* negative effect on *P. smintheus* overwintering egg survival, with temperatures being too hot or cold and little to no snow negatively affecting population growth (Roland et al., 2021; Roland & Matter, 2016). This finding supported our hypothesis that weather during the overwintering period would primarily affect population growth; however, our findings for *P. clodius* did not identify any quadratic effects of weather but indicated that weather conditions during the larval-pupal life stages have the

greatest effect. Our research did not allow us to distinguish direct from indirect effects such as early host plant senescence on population dynamics. Increasing the years of observation and data on host plant phenology would aid in detecting a definitive relationship for *P. clodius*.

From the perspective of developing a more generalized understanding of montane insect responses to climatic variation, we can summarize the responses of these two related butterfly species by saying that the indicator life stage of *P. smintheus* is the overwintering egg, whereas the indicator life stage of *P. clodius* is the larval-pupal life stages in spring. Further, extreme summer temperatures (i.e., hot and cold) were speculated to have *direct* negative effects on *P. smintheus* adult survival (Matter et al., 2011); conversely, observed summer weather over 12 years had

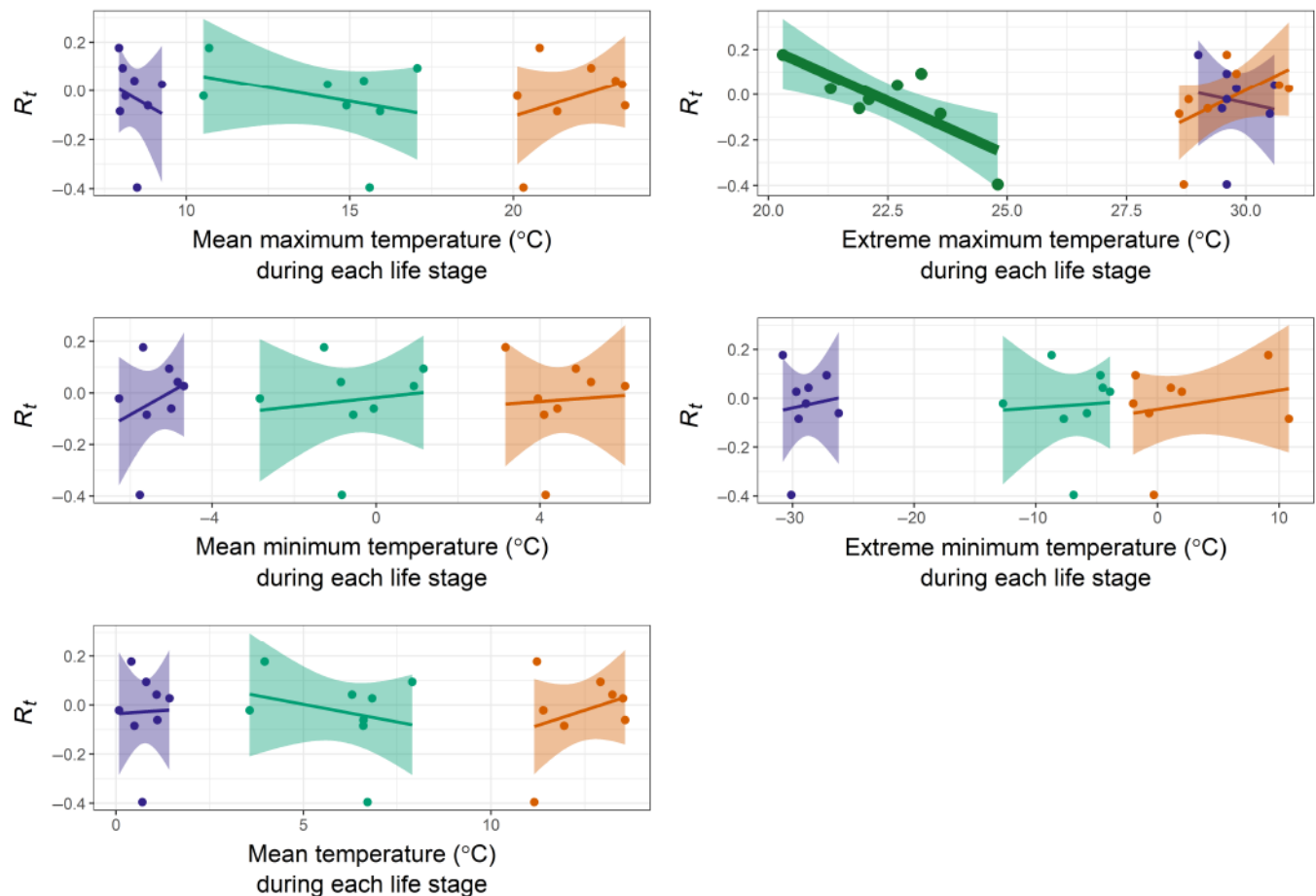


FIGURE 4 The relationship between *Parnassius clodius* population change (R_t) from 2009 to 2018 by life stage to the temperature weather variables considered in these analyses represented by lines. The egg life stage is given in purple, the larval-pupal life stages are given in green, and the adult life stage is given in orange. Darker, thicker lines and points indicate a significant relationship between population change and a descriptive weather variable at a particular life stage. The shaded areas represent the 95% CI. Surveys were not carried out in 2012 and 2013. Overall, a significant negative relationship between extreme maximum temperatures during the larval-pupal life stage and population change (R_t) was detected. There were no significant relationships detected between population change and mean temperature, mean maximum temperature, mean minimum temperature, and extreme minimum temperature.

no effect on survivorship of adult *P. smintheus* males (S. Matter, personal communication, May 2024). These results are inconsistent with our findings, suggesting that population dynamics in response to weather conditions and climate change vulnerability may not be consistent across a genus. In fact, *P. clodius* and *P. smintheus* population dynamics responded to different weather variables at different life stages.

Because of the various ways that insects use plants for larval food, nectar, and egg-laying and the importance of phenology in allowing these interactions, plant responses to a varying climate can result in both direct and indirect effects on insect distribution, population dynamics, and genetics. For example, altered temperature and precipitation affecting host and nectar plant resources had a negative *indirect* effect on *P. smintheus* presence, distribution, and genetic structure (Filazzola

et al., 2020; Matter et al., 2011). Similarly, research evaluating the reproductive success of the threatened univoltine butterfly, *Euphydryas editha bayensis*, found that later adult emergence and early host plant senescence had *direct* and *indirect* negative effects on female reproductive success (Cushman et al., 1994). Prediapause (larval life stage) starvation resulting from early host plant senescence was identified as the leading cause of *E. editha bayensis* mortality (Cushman et al., 1994). The *indirect effects* of early host plant senescence on *E. editha bayensis* population dynamics are applicable to our findings, given that the timing of host plant emergence, senescence, and survival dictated larval and pupal survival and were reflected in the population dynamics of this univoltine butterfly species. Therefore, conservation of univoltine butterfly species should be directed toward evaluating the distribution,

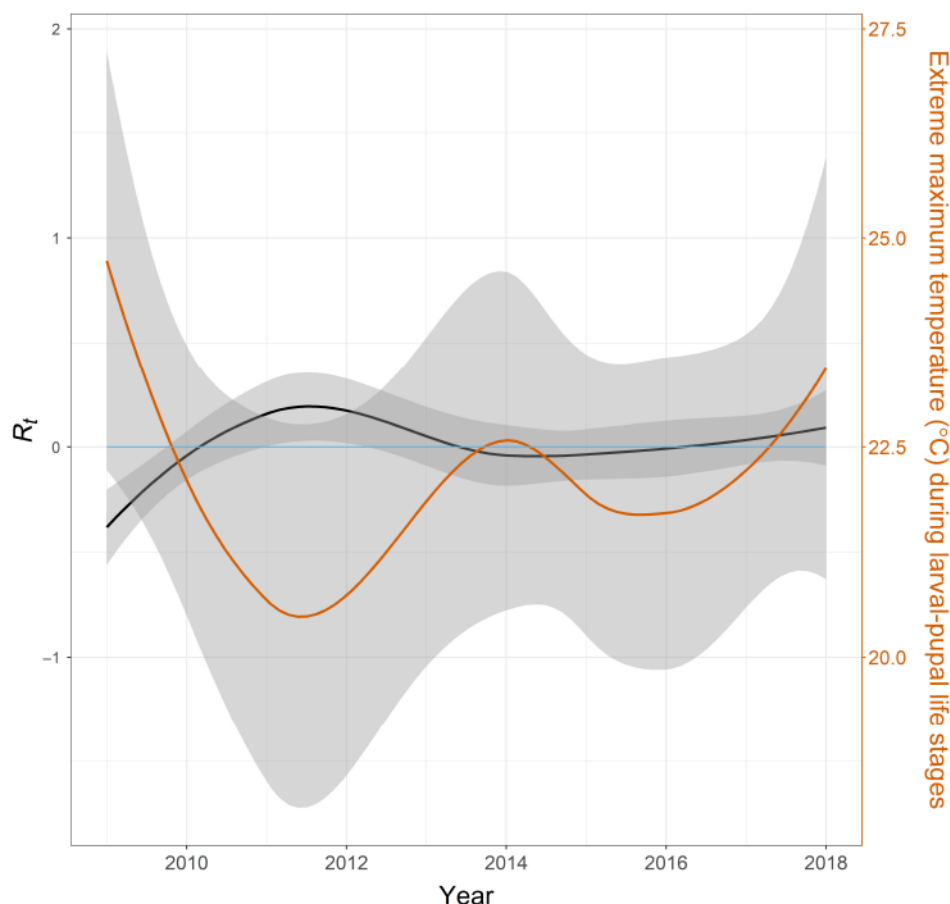


FIGURE 5 *Parnassius clodius* population change (R_t), in black, from 2009 to 2018 relative to the environments extreme maximum air temperature, in orange, during the larva-pupa life stages represented by lines. The shaded areas represent the 95% CI. The horizontal blue line represents no population change. Surveys were not carried out in 2012 and 2013.

phenology, fecundity, and survival of a butterfly species at each life stage in addition to its nectar and host plant species (Demarse et al., 2023), especially when the butterfly is specific to one host plant species.

The next steps to foster additional insights on *P. clodius* growth rates would include evaluating the distribution and phenology of its host plant, *D. uniflora*, an early-spring ephemeral forb relative to climatic data that we used in assessing *P. clodius* population dynamics. This has direct implications for the research presented here as we speculate that increasing temperatures during *D. uniflora*'s flowering duration, and *P. clodius*'s larvae life stage, could lead to early senescence thereby initiating larval starvation and declining *P. clodius* larval-pupal survival. Ultimately, increasing our understanding of *D. uniflora*'s phenology and sensitivity to climatic variation will aid in conserving both *D. uniflora* plants and *P. clodius* butterflies, and both could serve as bioindicators of weather patterns or climatic change in montane ecosystems.

Host plant life history and phenology affect the population change of numerous butterfly species, including *P. clodius* and *P. smintheus*. *P. smintheus*' primary host

plant, *Sedum lanceolatum*, is a succulent species (Roland & Matter, 2016) persisting throughout the summer months withstanding moderate drought and heat, while *D. uniflora*, *P. clodius*' host plant, is a spring ephemeral and much more vulnerable to drought and heat. The differences between these host plant's life histories influence their responses to weather conditions and phenology ultimately affecting those species that interact and depend on them. For instance, grassland and herbaceous plant communities containing *P. apollo*'s host plant, *Sedum telephium*, have experienced plant community succession toward increasing forest leading to *S. telephium* declines, indirectly affecting *P. apollo* population dynamics (Nakonieczny et al., 2007). The research presented here identified vulnerability using *P. clodius* population growth rates during the larval-pupal life stage in response to extreme heat. This could be the *direct* result of larvae and/or pupae being vulnerable to heat or the *indirect* result of host plant vulnerability leading to early senescence and larval starvation. We were unable to clearly identify at this time which metric was responding to extreme heat driving the declining

population growth trends; however, we suspect an *indirect* effect of host plant vulnerability due to *D. uniflora*'s life history characteristics. Understanding host plant life histories and potential vulnerabilities may aid in identifying indicator life stages for butterfly species.

It should be noted that the research presented here evaluates a single population of *P. clodius* from 2009 to 2018 factoring in sampling effort for each season. It is currently unknown whether other *P. clodius* populations would display the same life stage responses as observed in this particular population. However, we believe that our findings have merit as this is a relatively large population for the region (Szcudronski et al., 2018), and it was monitored over 8 years. Further, our findings identified differences in population responses to different environmental cues at different life stages between two species in the same genus. Often, findings for a single species are applied to other species within the same genus under the assumption that their life histories are similar and will therefore exhibit the same responses. This is especially true for insects. But as seen here, two butterfly species with similar life histories and within the same genus responded to different environmental cues and at different life stages. The novelty of this research lies in taking long-term and relatively continuous population data for a species and utilizing life stage hypothesis modeling to evaluate the effects of biologically significant environmental pressures on each life stage of the organism. Using results such as these, researchers can target conservation efforts more effectively.

Findings from this study and previous research demonstrate the value in assessing butterfly responses to short-term weather variation or long-term climatic changes *at each life stage* in order to protect and conserve a species and its interactions with other organisms (Buckley, 2022; Halsch et al., 2021; Radchuk et al., 2013). This research serves as a model for understanding more threatened *Parnassius* species from a global perspective, and insects in general under a changing climate. Life stage hypothesis modeling aided in identifying indicator life stages of threatened butterfly species, which could help guide conservation efforts to preserve populations. For example, host plant conservation and restoration projects in accordance with identified indicator life stages have been used to increase butterfly survival as documented in the Midwest United States with the evaluation and planting of host plant, milkweed, for monarch (*Danaus plexippus*) populations (Pocius et al., 2017). Population predictions and conservation efforts based on a single life stage could incorrectly indicate that a species is not directly at risk of global climate change (Radchuk et al., 2013). Therefore, evaluation of all life stages is warranted to correctly identify vulnerability and an indicator life stage. In addition to life stage analysis, an

understanding of host plant life histories along with data on host plant phenology in response to weather variations provides guidance for insect conservation efforts. The authors were unable at this time to include host plant phenological responses to weather variation in life stage hypothesis modeling due to a lack of available data but believe it is valuable in guiding and implementing effective conservation of butterflies. Finally, it is pertinent to evaluate species responses to extreme and/or abnormal weather fluctuations as these extreme events have been observed to have the greatest impact, especially on montane butterflies (Roland & Matter, 2013). The research presented here, using life stage hypothesis modeling, determined extreme maximum temperatures during the larval-pupal life stages of *P. clodius*—spring in this system—led to a decline in the next generation (Figure 5). As exemplified in this research, evaluating an insect species' response to external stressors by life stage reveals at which life stage conservation efforts should be focused in order to efficiently protect that species.

ACKNOWLEDGMENTS

This research was supported by grants from Decagon Devices, the Xerces Society for Invertebrate Conservation, the Center for Global and Regional Environmental Research, Iowa State University Department of Ecology, Evolution, and Organismal Biology, Iowa State University Graduate Program in Ecology and Evolutionary Biology, Montana State University, Disney Conservation Fund, and the University of Wyoming NPS Research Station. A very special thanks go to those who assisted with the field studies throughout the years: J. Sherwood, K. Szcudronski, A. McCombs, T. Proscholdt, K. McCloskey, C. Gause, A. Taylor, M. Kyer, D. Nelson, A. Binder, J. Pink, H. Pritchard, L. Crees, E. McCall, B. Sisson, L. McMahon, H. Buckbee, and K. Guajardo.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Durney et al., 2024) are available from Dryad: <https://doi.org/10.5061/dryad.w0vt4b92t>.

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How to cite this article: Durney, J. Simone, Diane M. Debinski, and Stephen F. Matter. 2025. "Life Stage Hypothesis Modeling Determines Insect Vulnerability during Developmental Life Stages to Climate Extremes." *Ecosphere* 16(1): e70147. <https://doi.org/10.1002/ecs2.70147>