

The demographic impacts of shifts in climate means and extremes on alpine butterflies

Lauren B. Buckley* and Joel G. Kingsolver

Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA

Summary

1. Climate change impacts organismal performance via both shifts in mean conditions and acute thermal stress events. Yet, we know little about the relative fitness impacts of climate means and extremes, and how phenotypes mediate these effects.
2. Here, we incorporate demography in a biophysical model of two alpine butterflies with distinct phenotypes to examine the impacts of recent climate change in the Rocky Mountains of Colorado.
3. The model suggests that shifts in available flight time (mediated by weather means) and egg viability (mediated by weather extremes) over time have varied between phenotypes and along the elevation gradient. Generally, small declines in egg viability may be more than offset by large increases in available flight time at higher elevations.
4. Interactions between environmental conditions and phenotypes may produce unexpected, individualistic responses to climate change.

Key-words: biophysical model, climate change, *Colias*, egg viability, elevation gradient, flight activity time, local adaptation, phenotype, thermal stress

Introduction

Shifts in both mean temperatures and temperature extremes associated with climate change can substantially impact organismal performance and fitness (Parmesan, Root & Willig 2000). Extreme climatic events can be identified by the presence of both an exceptional climatic driver and an ecological response (Smith 2011 and associated papers in a special issue). The relative impacts of thermal means and extremes are mediated by organismal traits (Helmuth, Kingsolver & Carrington 2005). The interaction of organismal physiology with climate variability can result in complex spatial patterns of climate change impacts. For example, thermal stress for intertidal mussels occurs as a mosaic rather than a smooth latitudinal pattern because of the interaction of climate with the timing of low tides (Helmuth *et al.* 2002). Similarly, weather means and variance differentially impact abundance of intertidal organisms (Benedetti-Cecchi *et al.* 2006), and these differential impacts across species can result in shifts in intertidal community structure (Denny *et al.* 2009). Climate change manipulation experiments have confirmed the potential for weather extremes to shift species composition, distribution and ecosystem function (Jentsch, Kreyling & Beierkuhnlein 2007).

Climate change influences organisms in multiple ways, including direct thermal stress at multiple life stages, shifting

performance or the costs of metabolic processes, and altering development (Hofmann & Todgham 2010). Characterizing the temperature sensitivity of these processes is a major challenge for forecasting responses to climate change (Chown *et al.* 2010). Most predictions of climate change impacts are based on relating mean weather conditions, often averaged annually, to species occurrences. More mechanistic approaches tend to integrate over shorter time scales, but generally ignore acute thermal stress events. Biophysical models enable translating environmental conditions into the potential body temperatures based on an organism's traits (Kearney & Porter 2009). While biophysical models are often used to understand an organism's activity time in a given environment, they have seldom been linked to demography (reviewed by Buckley *et al.* 2010). However, modelling studies have illustrated how shifts in environmental conditions along elevation gradients result in differential population growth rates (e.g. Porter 1989). Other implementations of biophysical models have revealed how geographic trait variation can influence distributions (e.g. Buckley 2008).

Here, we incorporate demography into a biophysical model to examine how shifts in mean and extreme weather conditions in response to recent climate change have influenced the performance and fitness of alpine butterflies in the Rocky Mountains of Colorado. We take advantage of the fact that Sulphur butterflies [*Colias* sp. (Pieridae: Coliadinae)] have served as a model system for biophysical ecology, population ecology and mechanisms of thermal adaptation for

*Correspondence author: E-mail: buckley@bio.unc.edu

over 40 years (Watt 2003, 2004). Collectively these data and models enable us to explore the connections among climate, phenotypic (thermoregulatory) traits, activity and population demography in this system. We combine climate data with biophysical and demographic models for two species of *Colias* along an elevational gradient to explore three main questions. First, how have changes in climate means and extremes in the past three decades affected changes in activity, egg mortality and population fitness in *Colias*? Second, how do these effects vary with elevation? Third, how do differences in thermoregulatory traits among *Colias* species alter the connections between climate variation and its ecological consequences?

Materials and methods

STUDY SYSTEM

We contrast two species of *Colias* in our studies: the high-elevation (3600 m) *Colias meadii* (Mesa Seco, Hinsdale County, CO, USA) and low-elevation (1700 m) *Colias eriphyle* (Montrose, Montrose County, CO, USA). *C. meadii* is restricted to high-elevation meadows (~3200–3700 m) (Watt *et al.* 1977), whereas *C. eriphyle* is present in high abundance at lower elevations (1400–2900 m) in Colorado (Watt, Han & Tabashnik 1979; Ellers & Boggs 2002). Both species are hostplant generalists as larvae, feeding on a variety of legumes. Although hostplant distributions are not expected to pose a strong constraint on the distributions of these two species, the primary hostplants of Colorado *C. meadii* larvae (e.g. *Astragalus alpines* and *Trifolium alpine*) are largely restricted to subalpine and alpine habitat. *C. meadii* is univoltine, while *C. eriphyle* is multivoltine in the study area; both species overwinter in a third instar larval diapause (Ae 1957, 1958; Stanton 1982). Given the general ecological similarity between the two species, we expect that the differences in adult traits explored here are primary drivers of distribution differences between *C. meadii* and *C. eriphyle*.

A key aspect of *Colias* performance is flight, which is essential for courtship and mating, nectaring, oviposition and other activities (Nielsen & Watt 1998; Watt 2003, 2004). Flight activity is restricted to body temperatures between 30 and 40 °C, and flight performance is maximized at 35–38 °C across *Colias* species and populations (Watt 1968). Adults behaviourally thermoregulate to achieve the body temperatures required for flight, but do not elevate body temperatures through endogenous heat production (Watt 1968). Butterflies use a lateral basking posture with the wings closed and the ventral hindwing surfaces oriented perpendicular to the sun to increase body temperatures. At body temperatures above 40 °C, butterflies stop flying and use a heat avoidance posture with the body and wings oriented parallel to the sun.

Colias populations and species in different climatic conditions vary in two key morphological, thermoregulatory traits (Watt 1968, 1969; Kingsolver 1983a): the degree of melanism on the ventral hindwings (VHW) (determining solar absorptivity) and the length of setae on the thorax (fur thickness). Wing absorptivity is determined by the relative proportions of melanic (black) and pteridine (yellow or orange) scales on the wing (Nijhout 1991). *Colias* populations and species from higher-elevation and higher-latitude sites have greater wing solar absorptivity and thoracic fur thickness, enabling them to achieve the elevated body temperatures needed for flight even under cool environmental conditions (Kingsolver 1983b; Ellers & Boggs 2004). Extreme

high temperature can also affect survival and fecundity. Kingsolver & Watt (1983) found that female life span decreased significantly and the butterflies decreased egg production fourfold in response to a daily 45 °C heat shock. Importantly, *Colias* adults may be exposed to short intervals of deleteriously high body temperatures (>40 °C) even at high elevation where temperature variation can be substantial (Kingsolver & Watt 1983).

We focus our assessment of performance and demographic differences on four sites along an elevation gradient (Grand Junction: 1400 m; Altenbern: 2100 m, Cochetopa Creek: 2400 m, Climax: 3500 m). We consider 24 sites in all ranging in elevation from 1400 to 3500 m (see Table S1, Fig. S1, Supporting information). The Rocky Mountains of Colorado are already experiencing increases in summer temperatures on the order of ~0.4 °C per decade. Colorado is expected to continue experiencing substantial climate warming (see Ray, Barsugli & Averyt 2008). Climate models project that Colorado will warm by 1.4 °C (+0.8 to +1.9 °C) by 2025, relative to the 1950–99 baseline, and 2.2 °C (+1.4 to +3.1 °C) by 2050 (Ray, Barsugli & Averyt 2008). Summers are projected to warm more [+2.8 °C (+1.7 to +3.9 °C)] than winters [+1.7 °C (+1.1 to +2.8 °C)], which may particularly impact butterflies as their development and reproduction primarily occurs in spring and summer.

The temperature dependence of flight and the influence of extreme high temperatures on egg viability provide a mechanistic basis for addressing the performance and demographic impacts of climate change. We focus on the influence of temperature during the flight season, but note that both mean temperatures and variability influence other fitness components such as larval feeding and survival (Sherman & Watt 1973). We examine the performance and demographic impacts of increasing flight season temperatures (which vary between sites) along the elevation gradients since 1980. We ask how these impacts vary between species with distinct phenotypes, which addresses the potential for evolutionary adaptation to alleviate climate impacts. We investigate the interaction between shifts in available flight time (as determined by mean weather conditions) and in egg viability (as determined by weather extremes). If increasing temperatures augment available flight time but increase the incidence of extreme high temperatures that increase egg mortality, what will be the net demographic impact of climate change?

BIOPHYSICAL AND DEMOGRAPHIC MODEL

We use a biophysical model for *Colias* that was developed and field validated by Kingsolver (1983a) to predict thoracic body temperature (operative environmental temperature, T_e) based on thermoregulatory traits (body size, basal ventral hind wing solar absorptivity and thoracic fur thickness) and environmental conditions. The model successfully predicts patterns of T_e , flight activity time and heat avoidance in the field for *C. meadii* and *C. eriphyle* along an elevational gradient in Colorado (Kingsolver 1983a; Kingsolver & Watt 1984). We briefly describe the model, which is developed in detail elsewhere (Kingsolver & Moffat 1982; Kingsolver 1983a). We describe the steady-state energy flux balance of a butterfly at rest on vegetation as

$$Q_s = Q_t + Q_c$$

where Q_s is the total solar radiative heat flux, Q_t is the thermal radiative heat flux, and Q_c is the convective heat flux. Conduction of heat between the body and vegetation and evaporative heat loss are considered to be negligible. The solar radiative heat flux is

$$Q_s = Q_{s,dir} + Q_{s,dif} + Q_{s,ref}$$

$$Q_s = \alpha A_{s,dir} H_{s,dir} / \cos(z) + \alpha A_{s,ref} H_{s,dif} + \alpha r_g A_{s,ref} H_{s,tot}$$

where $Q_{s,dir}$, $Q_{s,dif}$ and $Q_{s,ref}$, are the direct, diffuse and reflected solar radiative fluxes, respectively; $H_{s,dir}$, $H_{s,dif}$ and $H_{s,tot}$, are the direct, diffuse and total solar radiative horizontal flux densities, respectively; $A_{s,dir}$, $A_{s,ref}$ and $A_{s,tot}$ are the direct, reflected and total solar radiative heat transfer surface areas, respectively; α is wing solar absorptivity; r_g is substrate solar reflectivity; and z is the zenith angle. We assume $A_{s,dir} = A_{s,ref} = A_{s,tot}$.

Thermal radiative flux including both downward radiation and reflected solar radiation is estimated as follows:

$$Q_t + 0 \cdot 5 A_t \epsilon \sigma (T_b^4 - T_{sky}^4) + 0 \cdot 5 A_t \epsilon \sigma (T_b^4 - T_g^4)$$

where A_t is the thermal radiative heat transfer surface area, T_b is the body temperature, T_g is the ground surface temperature, T_{sky} is the equivalent black body sky temperature, ϵ is butterfly thermal emissivity, and σ is the Stefan–Boltzman constant.

The convective heat flux is given by:

$$Q_c = h_T A_c (T_b - T_a),$$

where A_c is the convective heat transfer surface area, and T_a is the air temperature. We assume $A_c = A_t = A_{s,tot}$. The total convective heat transfer coefficient, h_T , is calculated as the boundary layer conductance h_c and the fur layer conduction in series:

$$\frac{1}{h_T} = \frac{1}{h_c} + \frac{(r_i + \delta) \ln((r_i + \delta)/r_i)}{k_e},$$

where δ is the thoracic fur thickness, and k_e is the thermal conductivity of the fur. The boundary layer conductance, h_c , can be estimated using the relationship between two nondimensional numbers. The Nusselt number, $Nu = h_c D / k_a$, is the ratio of convective-to-conductive heat transfer, where k_a is the thermal conductivity of air. We used the maximum width of the mesothorax as the characteristic dimension of the butterfly, D . The Reynolds number, $Re = uD/\nu$, is the ratio of inertial forces to viscous forces, where u is wind speed, and ν is kinematic viscosity. We used the Nu – Re relation for a cylinder, $Nu = 0.6 Re^{0.5}$, which is a reasonable approximation for *Colias* (Kingsolver & Moffat 1982).

We use hourly estimates of ambient temperature and radiation from weather stations (see below) to estimate body temperatures and subsequently flight probability, daily flight time, egg production and egg viability. We estimate annual population growth rate as a function of survival and fecundity. Mark, release and recapture studies with *C. meadii* and *C. eriphyle* at study sites in Colorado suggest mean adult life spans (expected residence times) of 3–7 days that do not vary consistently with elevation (Watt *et al.* 1977; Watt, Han & Tabashnik 1979; Tabashnik *et al.* 1981).

Based on these studies, we assume a daily adult survival rate, S_{daily} , of 0.6 for all populations (Watt *et al.* 1977; Watt, Han & Tabashnik 1979; Tabashnik *et al.* 1981). We assume that the probability of juvenile survival from egg to adult maturity, S_{mat} , is 0.014, based on field studies of *Colias alexandra* in near Crested Butte, CO (Hayes 1981). We calculate daily egg production per female, $Eggs$, as the product of available flight time and the rate of oviposition. We assume an oviposition rate of 0.73 eggs per minutes and that 50% of available flight time is spent ovipositing, which was estimated for *Colias* females in

Colorado (Stanton 1980). We additionally calculate egg production incorporating egg viability by multiplying daily egg production by the average of hourly viability estimates. We estimate λ by summing over days to either a duration of 5 days or reaching a maximum lifetime egg production of 700 (Tabashnik *et al.* 1981) as

$$\lambda = S_{mat} S_{daily}^{day} Eggs.$$

To simplify the comparisons among sites and species, we assume a single annual generation with a single summer flight season in our simulations. In fact, populations of some *Colias* species, including *C. eriphyle*, can have two or more generations per year at lower elevations (e.g. Tabashnik *et al.* 1981). As a result, our simulations may underestimate mean annual fitness of *C. eriphyle* at lower-elevation sites (see Discussion).

WEATHER DATA

We use daily temperatures recorded by the National Weather Service Cooperative (COOP) Program. Programme volunteers record data daily from a Maximum/Minimum Temperature System (MMTS) consisting of a thermistor in a gill radiation shield and a datalogger that records daily maximum and minimum temperatures. We chose stations that were selected by the Colorado Climate Center at Colorado State University (<http://climatetrends.colorado-state.edu/>) as having the most robust long-term records (see Appendix S1 for a description of the focal stations, Supporting information). These stations minimize potential biases because of station movement, land-use change, and shifts in recording equipment or methodology. As COOP stations are scarce at high elevations, we included two stations at the Niwot Ridge Long-Term Ecological Research Site (C-1 and D1, http://culter.colorado.edu/NWT/site_info/site_info.html).

We estimated hourly air temperatures (T_a) using a diurnal temperature variation function based on maximum and minimum temperatures and the Julian date as modelled by Parton & Logan (1981). Daytime temperatures were fit using a sine wave, while nighttime temperatures were modelled using an exponential function (Appendix S2, Supporting information). We confirmed the sine-exponential fit to our weather stations using four of the weather stations that are additionally included in the Integrated Surface Hourly data set (<http://www.ncdc.noaa.gov/oa/climate/climatedata.html#hourly>). We assume that ground temperature, T_g , is equal to T_a ; sensitivity analyses indicate that predictions of T_c are robust to this assumption (Kingsolver 1983a) (see Discussion).

We use hourly total radiation data from the NREL Solar Radiation Research Laboratory (SRRL) located in Golden, CO (1829 m, 39.742°N, 105.18°W, http://www.nrel.gov/midc/srrl_bms/). Total radiation was measured using a Precision Spectral Pyranometer (Eppley, W m⁻²). We investigated other sources of radiation data such as the gridded NCEP North American Regional Reanalysis and determined that the higher precision and temporal resolution of the SRRL data provided more realistic model output. We partitioned the total radiation ($H_{s,tot}$) into diffuse ($H_{s,dif}$) and direct ($H_{s,dir}$) components using the polynomial function of a clearness index, k_t , developed by Erbs, Klein & Duffie (1982) (Appendix S2, Supporting information). We assume clear skies ($k_t = 1$) for our analysis. We confirmed our partitioning of direct and diffuse radiation data using corresponding data from the SRRL. We estimated the diffuse fraction in our analysis as the radiation components were not available throughout our study period.

SPECIES DATA

Our parameterization with species data follows Kingsolver (1983a) (Table 1). We calculate total effective surface area of a butterfly as a cylinder with diameter D without ends: $A_{s,ttl} = 2\pi D$. We estimated the probability of flight as a plateauing function of operative environmental temperatures, T_e : $P_{flight} = \exp(-0.5*(abs(T_e - 35))/4.5)^5$. The function is based on flight data for *C. eriphyle* in Montrose (Kingsolver 1981) (Fig. S2, Supporting information). Egg viability was modelled as exponential decay from 1 at 40 °C to 0 at 50 °C. This assumption is based on laboratory studies, showing that the egg viability for *C. eurytheme* was quartered when exposed to 45 °C for a 2-h period (Kingsolver & Watt 1983). In a related analysis, Kingsolver & Watt (1983) assumed that fitness drops to zero if T_{es} exceeded 40 °C for more than 1% of the total time. We assume a single generation per year. We calculate T_{es} for both a basking and heat avoidance position and assume that the butterfly will behaviourally thermoregulate to its thermal optima for flight (35 °C). In a heat avoidance position, we assume that the butterfly's effective surface area is halved (Kingsolver & Watt 1983).

Results

We first use weather data from July 2009 to illustrate how the interaction of environmental conditions with species' traits determines butterfly flight performance and ultimately egg production. Radiation elevates the butterflies' daily maximum operative environmental temperatures, T_e , above ambient temperatures (Fig. 1 top). The T_{es} are more elevated for the higher-elevation *C. meadii* because of its higher degree of wing melanism. As a result of these differential body temperatures, *C. meadii* is predicted to have less flight time available at lower elevations but more flight time available at higher elevations relative to *C. eriphyle* (Fig. 1 middle). *C. eriphyle* is predicted to have very limited flight time in Climax (3514 m). Conversely, the incidence of extreme high temperatures at low elevation reduces egg viability of *C. meadii* below that for *C. eriphyle* (Fig. 1 bottom). A reduced incidence of extremes at high elevations results in high levels of egg viability. We estimate egg production as a function of available flight time and detriment egg production by egg viability. Consequently, we predict that egg production will be greatest for the lower-elevation *C. eriphyle* at lower elevation and greater for *C. meadii* at higher elevations (Fig. 1 bottom).

We then consider the implications for increasing summer (15 June–15 August) temperatures since 1980 on butterfly performance and demography. Some sites have experienced significant increases ($P < 0.05$) in either or both minimum

and maximum daily temperatures (Fig. S1, Supporting information), but the occurrences of temperature increases are spatially variable. In contrast, the majority of sites have experienced significant increases in the proportion of days on which hourly operative environmental temperatures exceed thresholds (40, 42.5 and 45 °C) of thermal stress and decreased egg viability (Fig. S2, Supporting information). How then do these shifts in mean and extreme environmental conditions impact butterfly fitness across species and elevations?

Each of our focal sites has experienced significant increases since 1980 in mean annual ambient and operative environmental temperatures (Fig. 2 top). Yet, the implications for available flight time and population growth rates vary across elevation. At the lowest elevation site, a nonsignificant trend towards declining flight time exists. This trend is significant for *C. meadii* at a nearby weather station in Grand Junction (Fig. S3, Supporting information). The less melanistic *C. eriphyle* has greater estimated flight durations at the two lower-elevation sites, whereas the more melanistic *C. meadii* can fly longer at the two higher-elevation sites (Fig. 2 middle). Since 1980, available flight time increases significantly for *C. eriphyle* in Altenbern (2073 m) and for *C. meadii* in Cochetopa Creek (2438 m) and Climax (3514 m). Egg viability declines most severely over time at the lowest elevation site and for the more melanistic *C. meadii* (Fig. 2 middle).

We estimate that recent climate change has resulted in population growth declines at the lowest elevation (1409 m) and population growth increases at higher elevations (Fig. 2 bottom). At Grand Junction (1409 m), shifting in available flight time does not produce significant changes in population growth rates. However, once the decrease egg viability over time is accounted for, population growth rates for *C. meadii* are predicted to decline. For example at Altenbern (2073 m), the significant increase in available flight time for *C. eriphyle* results in increase population growth rate. A nonsignificant increase in available flight time for *C. meadii* is counteracted by the significant decline in egg viability, yielding no trend in population growth rate over time. The significant increases in available flight time for *C. meadii* at Cochetopa Creek (2438 m) and Climax (3514 m) and near absence of extreme high temperatures to decrease egg viability result in significant increases in population growth rates over time. Our model may underestimate lambda at the highest elevations as neither species is predicted to persist at Climax ($\lambda < 1$).

The performance and population growth trends predicted for the four focal sites are representative of predictions across all sites (Fig. S4, Supporting information). Available flight time, egg viability and population growth rates decline through time at the lowest elevations, particularly for the more melanistic *C. meadii* (which is absent at low elevations). At intermediate elevations, the species predicted to have greater available flight time shifts from *C. eriphyle* to *C. meadii*. Significant declines in egg viability accrue for both species at low and moderate elevations (see Fig. S5 for recent trends in the incidence of stressful temperatures). Declines in egg viability are more severe for *C. meadii* because of its greater wing

Table 1. Parameter values (means and standard deviations when applicable) from Kingsolver (1983a) used in the analysis

	<i>Colias eriphyle</i>	<i>Colias meadii</i>
Wing solar absorptivity, α (%)	53.7 (1.0)	64.9 (2.0)
Fur thickness, δ (mm)	0.82 (0.10)	1.46 (0.22)
Thoracic diameter, D (mm)	3.3 (0.3)	3.6 (0.2)
Fur thermal conductivity, k_e	1.3 mW cm ⁻¹ K ⁻¹	
Substrate solar reflectivity, r_g (%)	30	

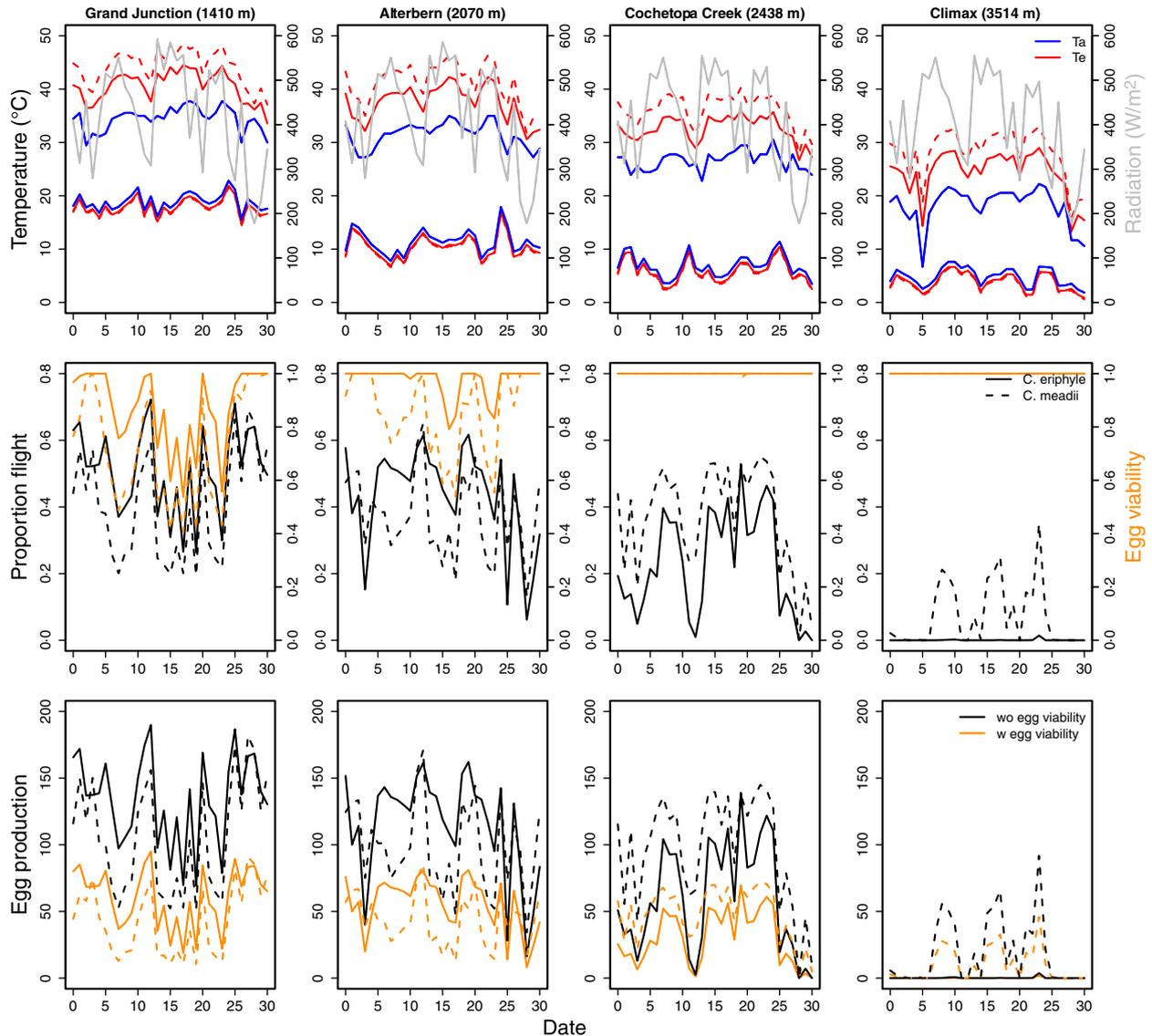


Fig. 1. An illustration of our analysis using daily weather data for July 2009 for stations at low (Grand Junction, column 1), intermediate (Alterbern, col. 2; Cochetopa Creek, col. 3) and high (Climax, col. 4) elevation. The figure contrasts the responses of *Colias* species from lower (*Colias eriphyle*: solid lines) and higher elevation (*Colias meadii*: dashed lines). Row 1: Minimum and maximum air temperatures (blue) and mean radiation (horizontal solar radiative flux density) during daylight hours (grey, data from the Solar Radiation Research Laboratory, Golden, CO) are plotted for each day during July 2009. The corresponding operative environmental temperatures (T_c) for both species (red), computed from minimum and maximum air temperatures and hourly radiation data, are also shown. It should be noted that the T_c values corresponding to daily minimum air temperatures are indistinguishable between species as they occur at night when radiation does not interact with phenotypes to influence T_c . Row 2: The daily mean proportion of the time during daylight hours in which flight can occur (black lines), and proportion of eggs can be viable (orange lines) and are computed for both species using the weather data and operative temperatures. Row 3: Daily egg production resulting from oviposition during flight activity is computed both with (orange lines) and without (black lines) accounting for reductions in egg viability because of overheating.

absorptivity. At most moderate and higher elevations increases in available flight time overwhelm decreased egg viability to result in increased population growth rates, particularly for *C. meadii*.

Discussion

Our study illustrates how mean and extreme weather conditions and species' phenotypes interact to determine the fitness

implications of climate change. Climate change responses will vary across elevation gradients along which both weather conditions and phenotypes vary. Predicting these responses is complicated by complex patterns of climate change at high elevations, where increases in daily minimum temperatures are more pronounced than increases in daily maxima (Diaz & Bradley 1997).

Our predicted elevational ranges for each species correspond qualitatively to observed distributions and flight

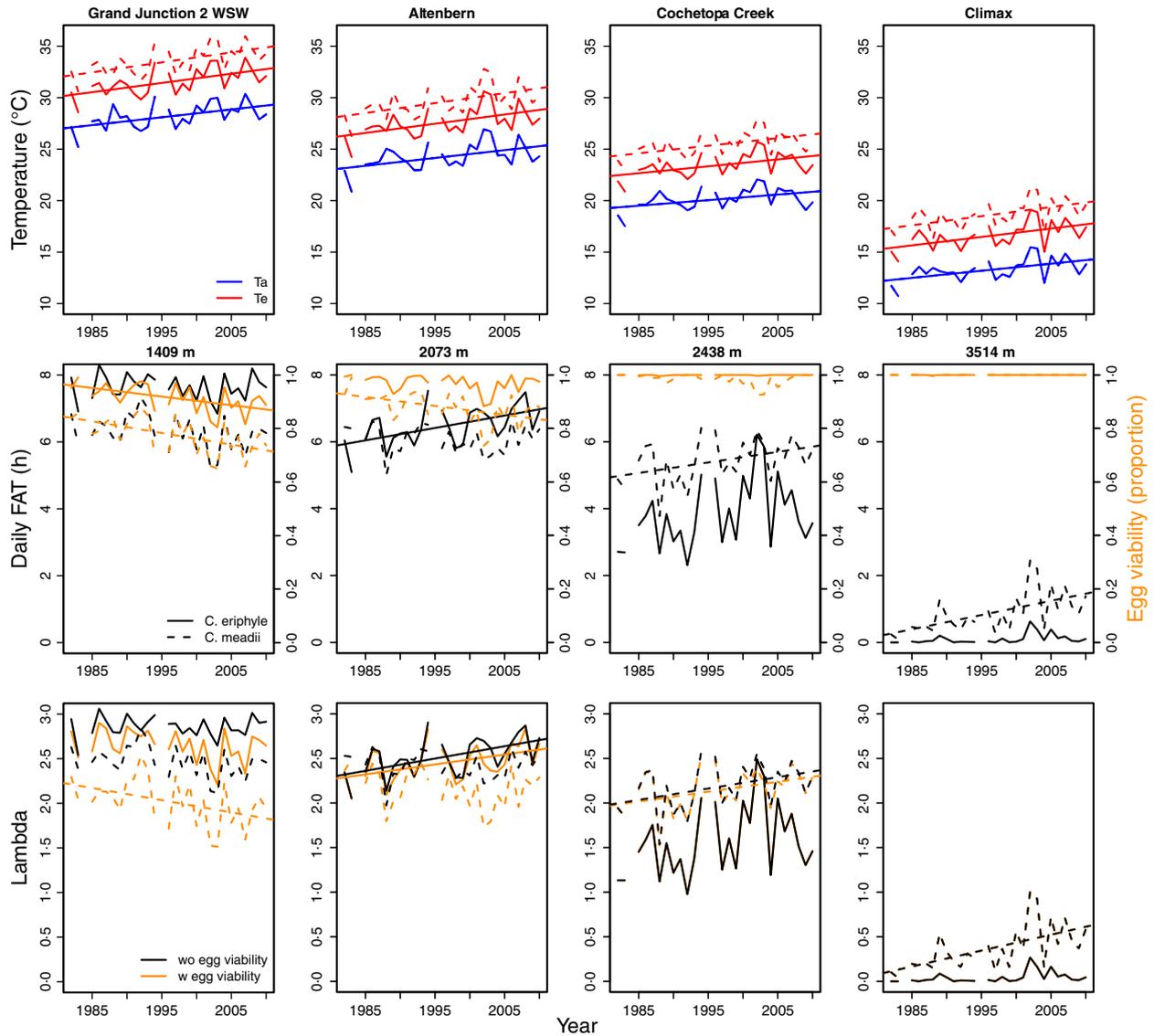


Fig. 2. An analysis of temperatures, performance and demography during the flight season (June 15–August 15) for the four focal weather stations (columns 1–4) for each year from 1980 to 2010. The figure contrasts the responses of *Colias* species from lower (*Colias eriphyle*: solid lines) and higher elevation (*Colias meadii*: dashed lines). Row 1: Seasonal averages of daily mean air temperatures during daylight hours (blue) and the corresponding operative environmental temperatures (T_e) for both species (red) are depicted. Row 2: Seasonal averages for daily flight activity time (black lines: FAT, hours) and for egg viability (orange lines) are depicted. Row 3: Seasonal averages for population fitness (lambda) both with (orange lines) and without (black lines) accounting for reductions in egg viability because of overheating. In each plot, significant trends ($P < 0.05$) are indicated with lines corresponding to the linear regressions.

activity (Kingsolver 1983a) in this region. We predict that *C. eriphyle* will not persist ($\lambda < 1$) above ~ 2500 m in elevation, which roughly corresponds to the approximate upper limit of its distribution (2900 m). We find that recent warming has elevated λ values above 1 in some sites. Those low-elevation (< 1500 m) sites in which *C. eriphyle* is expected to experience increased thermal stress (decreased flight time and egg viability) as a result of recent climate change are near the approximate lower limit of distributions (1400 m). We predict that *C. meadii* can persist at lower elevations than its observed distribution (~ 3200 – 3500 m). We also underestimate its population growth rate ($\lambda < 1$) at our only weather

station that actually falls within its observed range (Climax, 3514 m).

Our underestimates of population growth rates at higher elevations likely result from three factors. First, our data for air temperature and wind speed are measured at 2–3 m height above the surface (Appendix S1, Supporting information), whereas basking butterflies experience temperature and wind speeds near the top of vegetation (Kingsolver 1983a). Strong temperature and velocity profiles near the ground, especially during sunny, midday conditions, will increase air temperatures and decrease wind speeds experienced by butterflies, increasing operative temperatures (Porter *et al.* 1973;

Kingsolver 1983a). These effects may be particularly important at higher elevations, where maximum solar radiative heat fluxes are greater. As a result, our model likely underestimates operative temperatures, flight time and egg production at these sites. Unfortunately, estimating temperature and velocity profiles are challenging in the absence of data on surface temperatures. Second, field data suggest that *C. meadii* may initiate flight at operative basking temperatures as low as 26–28 °C (Kingsolver 1981), lower than that detected for *C. eriphyle* (Kingsolver 1983a; and Fig. S2, Supporting information). This would increase the predicted flight times at higher elevation. However, our current field data are not sufficient to estimate the complete flight function for *C. meadii*, so to be conservative, we have used a single function for both species. Third, *C. meadii* primarily utilizes larval hostplants that are restricted to subalpine and alpine habitats in Colorado (e.g. *Astragalus alpines* and *Trifolium alpinum*). Whether weather or hostplant limits the lower elevational limits of *C. meadii* in this region is unknown.

A key result from our studies is that differences in phenotypes among species complicate the association between mean temperature increases – ‘global warming’ – and population fitness and elevational shift under climate change. Thus, interactions between environmental conditions and phenotypes may produce unexpected, individualistic responses to climate change. Numerous recent resurvey projects have demonstrated elevation shifts in distributions and abundance, but researchers are just beginning to understand the functional drivers of these responses. For example, the optimum elevations of forest plant species have shifted upward at a mean rate of 29 m per decade between 1905–1985 and 1986–2005 (Lenoir *et al.* 2008). This shift was most pronounced for mountain habitat specialists and those with rapid life cycles. Since 1949–1951, montane herbaceous communities shifted to those characteristic of drier climates, including a shift towards smaller leaf areas (Harrison, Damschen & Grace 2010). Age and size at maturity were observed to predict depth and distribution shifts of marine fish in response to warming since 1962 (Perry *et al.* 2005). Limitations on activity time because of thermal stress associated with thermal tolerances may result in lizard extinctions (Sinervo *et al.* 2010).

Insects have been prominent in the pursuit of a functional understanding of climate change responses. Both temperature increases and grasshopper phenological advancements since 1959–1960 were most pronounced at higher elevations along an elevation gradient in Colorado (Nufio *et al.* 2010). Additionally, stronger late-season warming yielded more pronounced phenological shifts among late-developing species. Growing degree days prior to emergence were constant across time, suggesting that thermal limits on development are an important determinant of climate change responses. The shift towards earlier phenology in an Australian butterfly corresponded to the predictions of a biophysical model of environmental influences on development (Kearney *et al.* 2010).

The importance of physiologic traits for forecasting species’ responses to climate change has been demonstrated in

several other systems. Historic data on body temperatures and the temperature dependence of performance for two tropical lizard species suggest that they may have been differentially impacted by recent climate change (Huey *et al.* 2009). The authors predict that open-habitat lizards may move into the forest to evade thermal stress and competitively displace the nonbasking forest species. The potential for evolutionary changes in the egg desiccation resistance of mosquitoes was found to be a major determinant of whether climate change would result in range expansions (Kearney *et al.* 2009). The link between physiologic traits and thermal stress suggests that evolutionary shifts in phenotypic traits are likely to be an important determinant of climate change impacts (Hoffmann & Sgrò 2011).

One important prediction from our analyses is that small declines in egg viability will be more than offset by large increases in available flight time at higher elevations. However, this finding depends on our assumption that radiation fluxes are constant (based on a site at 1800 m) across the elevation gradient and that surface temperatures are equivalent to ambient temperatures. In contrast, higher radiation values and elevated surface temperatures are likely at higher elevations, particularly at the alpine sites with limited vegetation cover. More generally, the current models do not capture short-term (1–100 min) variability in microclimatic conditions that can affect both flight (Kingsolver 1983a) and overheating (Kingsolver & Watt 1983) in butterflies, especially at higher elevation. Further study of the fitness consequences of short-term overheating and the environmental conditions that cause them is needed. Additionally, weather stations do not fully capture temporal trends in microclimate in topographically diverse regions (Scherrer, Schmid & Körner 2010). Such local topographic features can have important impacts on phenology and fitness of butterfly populations (Dobkin, Olivieri & Ehrlich 1987; Weiss, Murphy & White 1988; Weiss *et al.* 1993). Nevertheless, our analysis succeeds in illustrating how organismal response to mean and extreme temperatures can counteract each other in determining fitness consequences.

Acknowledgements

We thank Jessica Higgins, Heidi MacLean and anonymous reviewers for useful comments on an earlier version of the manuscript and Joseph Grigg for assistance with processing the radiation data. We appreciate Colorado State University’s efforts to make Colorado weather station data available. The Whiteley Center provided an ideal venue for analysis and writing for JGK. Research supported in part by NSF grants DEB-1120062 to LBB and JGK and IOS-1120500 to JGK.

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Received 19 October 2011; accepted 23 January 2012
Handling Editor: Art Woods

Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1. Description of focal sites.

Appendix S2. R code for diurnal temperature variation function.

Fig. S1. Topographic map of Colorado showing weather stations.

Fig. S2. Proportion butterfly flight time as a function of temperature.

Fig. S3. Trends in flight season means of minimum and maximum daily temperatures.

Fig. S4. An analysis of temperatures, performance and demography during the flight season.

Fig. S5. The proportion of extremes for daily hourly operative environmental temperatures.

Table S1. The weather stations used in the analysis.

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