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The response of two butterfly species to climatic variation at the edge of their range and the implications for poleward range shifts

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Abstract To predict changes in species' distributions due to climate change we must understand populations at the poleward edge of species' ranges. Ecologists generally expect range shifts under climate change caused by the expansion of edge populations as peripheral conditions increasingly resemble the range core. We tested whether peripheral populations of two contrasting butterflies, a small-bodied specialist (*Erynnis propertius*) and a large-bodied generalist (*Papilio zelicaon*), respond favorably to warmer conditions. Performance of populations related to climate was evaluated in seven peripheral populations spanning 1.2° latitude (160 km) using: (1) population density surveys, an indirect measure of site suitability; and (2) organismal fitness in translocation experiments. There was evidence that population density increased with temperature for *P. zelicaon* whose population density declined with latitude in 1 of 3 sample years. On the other hand, *E. propertius* showed a positive relationship of population density with latitude, apparently unrelated to climate or measured habitat variables. Translocation experiments showed increased larval production at increased temperatures for both species, and in *P. zelicaon*, larval production also increased under drier conditions. These findings suggest that both species may increase at their range edge with warming but the preference for core-like conditions may be stronger in *P. zelicaon*. Further, populations of *E. propertius* at the range boundary may be large enough to act as sources of colonists for range expansions, but range expansion

in this species may be prevented by a lack of available host plants further north. In total, the species appear to respond differently to climate and other factors that vary latitudinally, factors that will likely affect poleward expansion.

Keywords *Erynnis propertius* · Climate change · Geographic range · Larval production · Lepidoptera

Introduction

Ecological theory suggests that climate-limited species will shift their geographic ranges under climate change, and several studies indicate that range shifts are already occurring (Thomas et al. 2001; Root et al. 2003; Parmesan et al. 2005). These shifts likely arise because conditions conducive for population growth are altered across a species' range (Webb and Bartlein 1992). As the climate shifts, conditions at the equatorial range boundary become increasingly marginal and conditions at the poleward range boundary become more favorable (Parmesan et al. 1999; Crozier 2003, 2004a, b; Hampe and Petit 2005; Crozier and Dwyer 2006). This response should occur if individuals at the range edge have higher fitness under conditions characteristic of the range core than they have under peripheral conditions (Hengeveld and Haack 1982; Brown 1984; Lawton 1993; Brown et al. 1996; García-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997; Case and Taper 2000; Holt et al. 2005). Not all species are shifting in response to climate, however (e.g., see Parmesan et al. 1999). A key question, therefore, is whether peripheral populations in a variety of different species actually do increase under warmer conditions, conditions that increasingly resemble the range core. If peripheral populations show

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increased performance under increased temperatures, climate change may enable population growth at the periphery and increase the opportunity for poleward expansion.

Existing evidence suggests that species have varying degrees of population differentiation across their geographic ranges, suggesting that edge populations may not have the same fitness optima as populations toward the range core (e.g., Clausen et al. 1940; Hiesey et al. 1971; Chapin and Chapin 1981; Loik and Nobel 1993; Hoffman and Blows 1994; Etterson 2004). Such population differences arise from restricted rates of gene flow among populations, from strong local selection, and/or from genetic drift due to population isolation (Mayr 1963; Hoffman and Blows 1994; García-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997). Other factors being equal, species with limited dispersal should have less inter-population gene exchange than easily dispersing species (Wright 1931, 1943; Avise 1994; Bossart and Prowell 1998; Bohonak 1999), and highly specialized species that are limited to rare or fragmented habitats also may have isolated populations (e.g., Brouat et al. 2003). Further, species with geographic barriers between core and edge populations may have greater peripheral divergence than species with contiguous ranges (García-Ramos and Kirkpatrick 1997). Following simple theory that relates life history characters to potential interpopulation gene flow, we predict that peripheral populations of a broadly dispersing generalist would be more responsive to warmer conditions than a dispersal-limited specialist.

To capture potential differences in the responsiveness of peripheral populations to climate change, we examined two ecologically contrasting butterflies that co-occur and share a poleward range boundary. Several studies have found climate-related range shifts in butterflies suggesting that temperature can be a range-limiting factor for Lepidoptera (e.g., Hill et al. 1999; Parmesan et al. 1999). Our study species reach their northern range limit on a large island so that edge populations may be genetically isolated from more southerly populations (Zakharov and Hellmann 2008). One species is a large, widely dispersing generalist [*Papilio zelicaon* (Papilionidae)], and the other is small and tends to remain in patches where its single host plant occurs [*Erynnis propertius* (Hesperiidae)].

In our investigation, we use the relationship of density, an indirect measure of site suitability, with latitude and climatic factors to determine if populations favor warmer conditions. We also quantify the degree to which resource availability determines butterfly density. Density trends can be compared between taxa, but the absolute value of density cannot because it is affected by life history traits (Thomas et al. 1998; Cowley et al. 2001). Second, we determine if larval performance is enhanced in sites closer to the range core or in warmer locations to indicate the response of

peripheral populations to warming. Taxa that respond favorably to warming at their range edge will likely have an increasing number of colonists for range expansion, assuming that biotic and abiotic conditions outside the current range become suitable in the future (Caughley et al. 1998). Species with peripheral populations that do not increase with warming are unlikely to increase their colonization rate under climate change.

Materials and methods

The Propertius duskywing, *Erynnis propertius*, is a small (wingspan = 3.5–4.5 cm) specialist butterfly whose caterpillars feed exclusively on Garry oak [*Quercus garryana* (Fagaceae)] in the northern portion of its geographic range (Scott 1986; Opler 1999; Guppy and Shepard 2001). In southerly portions of its range, it feeds on additional oak species, and its total range extends from Baja California, Mexico, through California, Oregon, and Washington in the United States and onto southeastern Vancouver Island, British Columbia, Canada. Individuals are found in close association with oak and are thought to be limited in their ability to fly long distances (Guppy and Shepard 2001). The anise swallowtail, *Papilio zelicaon*, in contrast, is a large (wingspan = 7–9 cm) generalist butterfly, and its caterpillars feed on many species in the parsley family, Apiaceae (Wehling 1994; Scriber et al. 1995; Guppy and Sheppard 2001). This butterfly can be found outside of native habitat and is a strong flier (Scriber et al. 1995; Shapiro 1995). *P. zelicaon* occurs throughout the western United States and much of western Canada. It extends south into Baja California, its furthest poleward extent occurs in eastern British Columbia and Alberta.

Both *E. propertius* and *P. zelicaon* occur in coastal savanna distinguished by the presence of *Q. garryana*, and they reach their coastal range limit at the mid point of Vancouver Island and associated islands of the Georgia Strait, British Columbia (Fig. 1; Guppy and Shepard 2001). These oak-savanna habitats are characterized by a moderate climate with cool, wet winters and warm, dry summers (Ropelewski and Halbert 1986; Klinka et al. 1996; Dettinger et al. 1998), and they contain nectar sources and the primary native host plants of both butterfly species (*E. propertius*: *Q. garryana*; *P. zelicaon*: *Lomatium* spp.). Additional hosts are available for *P. zelicaon* in the study region outside of Garry oak habitats (e.g., *Heracleum lanatum*, *Daucus carota*, and *Conium maculatum*).

Study sites were selected along a latitudinal gradient within Vancouver Island that approaches the northernmost occurrence of intact, native oak-grassland (MacDougall 2005). Seven sites were selected: S1 (48°19'N, 123°32'W), S2 (48°25'N, 123°20'W), S3 (48°27'N, 123°28'W), S4

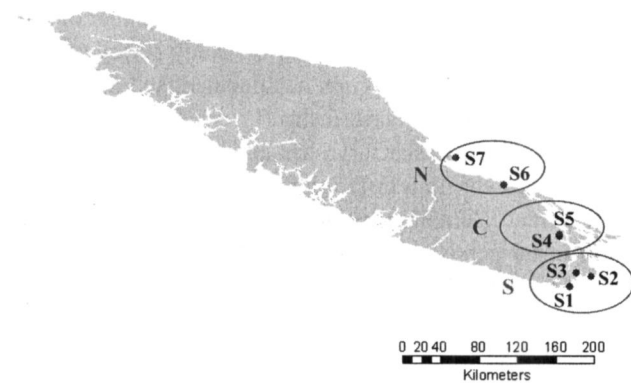


Fig. 1 Study sites on Vancouver and Hornby Islands, British Columbia, Canada. Sites are numbered S1–S7 from south to north and were grouped into three regions [southern (S), central (C), and northern (N)] for translocation experiments

(48°47'N, 123°38'W), S5 (48°48'N, 123°37'W), S6 (49°16'N, 124°9'W), and S7 (49°31'N, 124°36'W) (Fig. 1). The straight-line distance between the southernmost site (S1) and the northernmost site (S7) is 160 km. Sites were chosen from among the largest available habitats that have been minimally disturbed by humans and invasive plants (MacDougall 2005). The long-term average temperature during mid May and through July in Victoria, Vancouver Island, British Columbia is 14°C. This peripheral climate contrasts with warmer and drier conditions in the range core. For example, in southern Oregon (Medford), summer temperatures are 5°C higher on average. Yet, climate also varies within Vancouver Island. Average air temperature in Victoria, near S2 (Fig. 1), and in Nanaimo, between S5 and S6 (Fig. 1), differs by approximately 1°C during the summer months, and variation in the microclimatic conditions experienced by butterflies can be considerably larger (as much as 10°C in our ground-level recordings). The gradient in annual rainfall also is large on the island, increasing by 400 mm from Victoria to Nanaimo, for example.

Population density

To estimate population density, an indirect measure of the suitability of a site to support a butterfly population, we performed transect-based visual assessments of population size (Pollard 1977; Pollard and Yates 1993; Brown and Boyce 1998) on a weekly basis over the flight season in 2003–2005. Transects were placed in a systematic fashion across each study site and were composed of 30-m segments. The number of segments surveyed per site was standardized to site size so that ~20% (actual coverage ranged from 19–26%) of each study habitat was assessed during each survey. We recorded the number of *E. propertius* and *P. zelicaon* individuals observed within 5 m of each segment during a period of 1–1.5 min on sunny days.

Density was chosen as a population metric because it enables comparisons among sites of differing size. To calculate a seasonal estimate of density in each site, we estimated the area under the curve of observed abundance versus flight date (Rothery and Roy 2001) and divided this value by the number of transect segments per site. This method accounts for an unequal number of sampling days across sites and years. Surveyors did their best to avoid double-counting of individuals, but recounting of individuals between sampling periods is possible. We assume that double-counting is equal among sites and minimized by weekly separation of surveys. In 2004, the phenology of the oak-savanna was accelerated due to unseasonably warm conditions, and the earliest portion (~8–10 days) of the flight season was missed. Estimated population size in this year, therefore, is depressed relative to 2003 and 2005. Comparisons among sites are still possible, however, because the entire study region experienced the warm spring.

Habitat measures

To explore the role of climate and habitat factors in determining population density, we measured temperature, total precipitation, and plant resource availability at each site. Weather was recorded at ground level using temperature data loggers and rain tipping-buckets with event data loggers (Onset Computer Corporation and Davis Instruments). Temperature loggers were shaded with white dishes to capture the conditions for butterflies on the ground. Using these data, we calculated maximum, minimum, and average daytime temperature (1000–1600 hours) and total precipitation over two time periods for each species: the flight season and the period during which larval experiments were conducted.

Vegetation was assessed once per season using transects placed systematically across each study site. Each transect was composed of 1 × 1-m quadrats spaced 20 m apart, and the total area surveyed for plants was standardized by site size such that each hectare was represented by ~20 (actual coverage ranged from 18–24) sampling quadrats. In each quadrat, we surveyed the percent cover of forbs, grasses, shrubs, bare ground and grazing (browsing evident or not evident). Percent cover was assessed as <25, 25–50, 50–75, or >75%, and the mid point of each range was substituted for data analysis. In addition, we counted the number of *Lomatium* spp. and nectar plants [*Camas* spp. (2003–2005) and *Vicia* spp. (2004–2005)] in each quadrat, assigning each quadrat to the lower end of a base-3 categorical interval (e.g., 1, 4, 11, 31, ...). Finally, the abundance of *Q. garrayana* was estimated by the percentage of survey quadrats containing oak cover. All of the plants, cover types, and presence/absence of grazing were relatively constant over

the 3-year study period; therefore, we used an average value in all analyses.

Translocation experiments

To investigate the performance of individuals under a variety of climatic conditions, we examined biomass production of caterpillars in translocation experiments. Translocation experiments were conducted during May and through July in 2004 and 2005. Eggs were collected for both species from gravid females at each study site, and seven to 21 eggs were placed in mesh cages with at least three replicates per site. Translocation sites were identified by grouping the seven study sites into southern (S1, S2, and S3), central (S4 and S5), and northern (S6 and S7) regions within the range edge (Fig. 1). Cages were placed at each population's natal site and were translocated to sites in the other two regions. For example, *E. propertius* individuals from S7 (northern region) were reared at S7 and at S5 (central region) and S1 (southern region) in 2004. An insufficient number of eggs were collected for experimentation at S2 for both species in both years and from S4 for *P. zelicaon* in 2004. For *P. zelicaon* in 2005, individuals were caught only at S4 and S6 and were reared at their natal sites and every other study site except S2 and S5.

Cages of *E. propertius* (41 cm diameter \times 60 cm length) were placed directly onto *Q. garryana* trees. Cages of *P. zelicaon* (30.5 cm each side) contained potted parsley (*Petroselinum crispum*) and were placed on the ground. All parsley plants were purchased from a single, commercial nursery. This host plant design ensured that plant material was fresh and abundant for both species and was necessary because potted *Q. garryana* have relatively few leaves, and rooted, native hosts of *P. zelicaon* senesce each summer. This design does potentially confound sites with host plant for *E. propertius*, however (see "Discussion"). At each site, cages were placed in close proximity on trees with similar exposure (*E. propertius*) or in a flat area with similar exposure (*P. zelicaon*) so that variation in sunlight and humidity among cages within a site was minimized. Competitors and predators were removed from all cages.

We monitored cages weekly and measured the total biomass of all surviving individuals at the end of the experiment (end of July). We report total biomass production per cage (g/no. stocked eggs) as that measure captures growth, survivorship and factors correlated with fecundity such as body size (Sharpe and DeMichele 1977; Huey and Stevenson 1979; Ratte 1984; Kingsolver 1989; Slansky 1993; Hellmann 2001, 2002; Bale et al. 2002). This metric assumes that units of biomass correlate with potential reproductive output such that a few, large individuals and several, small individuals could have similar reproductive capacity. To address this assumption, we quantified varia-

tion in larval production as a function of the number of survivors in each cage. By the end of the study period (end of July), all surviving *P. zelicaon* had pupated, and *E. propertius* had reached the fourth instar (Prior and Hellmann, in review). A fourth instar larva has approximately one-third of its full-grown, sixth instar biomass. In growth chambers, size differences among treatment groups that appear by the fourth instar persist until pupation if temperature is maintained (unpublished data).

Data analysis

To meet assumptions of normality, estimates of seasonal population density were square-root transformed. These values then were regressed against latitude to reflect position at the edge of the range. Density estimates of zero were included in analyses if a species was ever observed at that site. Density was also regressed against climatic variables recorded during the flight season for each species. Due to strong correlations between minimum, average, and maximum temperatures and uncertainty about which parameter is important in determining butterfly performance, a principal component analysis was used to collapse these variables; the factor scores of the principal components were then used in multiple linear regression with rainfall during the flight season as an additional variable. To determine if habitat quality explains population patterns, we regressed butterfly density against vegetation characteristics. Each vegetation characteristic was analyzed separately because there was little correlation among variables (all correlation coefficients less than 0.7). For all vegetation variables except the density of *Q. garryana* and grazing intensity, we used the mean rank score in regression analyses due to the non-normality of these data.

Translocation data (i.e., larval production) were arcsine, square root-transformed for both species to meet assumptions of normality. Data were then analyzed using general linear models, comparing production in natal versus non-natal sites (one-way ANOVA) and among source and rearing populations (two-way ANOVA). The ANOVAs were performed separately for 2004 and 2005 in the case of *P. zelicaon* because it was sampled differently in each year. The one-way ANOVA tests for local adaptation at the level of the regional groupings; the two-way ANOVA tests for site-level differences. We also performed a principal components analysis for each species of latitude, precipitation falling during the larval experiment and maximum, minimum, and average temperature recorded during the experiment. We then regressed larval production against the first and second principal components of these factors for all cages independent of source site. This test quantifies the role of climate in production using all caterpillars at their rearing location and enables a more powerful test of the

direct influence of climate on larval performance. For *P. zelicaon*, values of the second principal component did not initially meet the assumption of linear regression so they were made positive by adding the number 2 and transforming with natural log. A backward selection procedure was used to remove variables from the regression model.

Results

Population density

E. propertius

Six of the seven study sites contained *E. propertius* (Table 1). S2 contains the necessary resources for this species and the butterfly historically occurred there, but the population appears to be extirpated. The density of *E. propertius* showed a positive relationship with latitude such that the northernmost sites had the highest density (Table 2; Fig. 2a). One principal component ($PC1_{epd}$) accounted for 87.6% of the total variance of average, maximum, and minimum temperature during the flight season of *E. propertius* (Table 3). After regression using backwards selection with $PC1_{epd}$ and rainfall, however, no climatic variables remained as significant explanatory variables of *E. propertius* density ($F = 0.06$, $df = 1, 11$, $P = 0.95$). We found only one statistically significant relationship between the density of *E. propertius* and the various measures of habitat quality: a positive relationship between density and percentage cover of grass in 2004 ($r^2 = 0.07$, $n = 6$, $P = 0.04$).

P. zelicaon

All of the study sites contained *P. zelicaon* at some point during the 3-year study period (Table 1). In 2004, *P. zeli-*

Table 1 Estimates of population density based on repeated transect surveys

Site	<i>Erynnis propertius</i>			<i>Papilio zelicaon</i>		
	2003	2004	2005	2003	2004	2005
S1	5.35	5.27	5.74	0.18	2.10	0
S2	0	0	0	0.61	2.18	0.35
S3	8.18	13.1	4.17	1.19	2.62	1.17
S4	13.02	23.33	10.34	0.13	1.57	0.11
S5	20.43	20.56	5.98	0	0.44	0
S6	31.73	25.49	12.99	0.31	0.85	0.37
S7	26.38	44.33	30.13	1.63	0.57	0

Density was estimated as the area under the curve of observed individuals against time divided by the number of transect segments surveyed per site

caon showed a negative relationship between population density and latitude such that the most southern locales had the highest abundance (Table 2; Fig. 2b). There was no relationship between density and latitude for this species in 2003 and 2005 (Table 2). One principal component ($PC1_{pzd}$) accounted for 89.5% of the total variance of average, maximum and minimum temperature during the flight season of *P. zelicaon*. After regression using backwards selection with this component and rainfall, $PC1_{pzd}$ remained the only significant explanatory variable of *P. zelicaon* density ($F = 5.77$, $df = 1, 19$, $P = 0.03$, $r^2 = 0.19$). Specifically, density was highest where temperature ($PC1_{pzd}$) was highest. There were no statistically significant relationships between the density of *P. zelicaon* and vegetation characteristics except for negative relationships with the percentage cover by grass in 2004 ($r^2 = 0.78$, $n = 7$, $P = 0.008$) and the abundance of *Vicia* spp. in 2005 ($r^2 = 0.77$, $n = 7$, $P = 0.009$). Thus, no single vegetation factor is consistently predictive of population size in either species, although χ^2 analysis suggests that sites differed in quality

Fig. 2a, b The relationship between population density and population location in degrees of latitude (Table 2). A positive relationship existed in all study years between the index of population density (see “Materials and methods”) and latitudinal position for *Erynnis propertius*. Data shown are for 2004 (a). A significant, negative relationship exists between population density and latitudinal position for *Papilio zelicaon* in 2004 only (b)

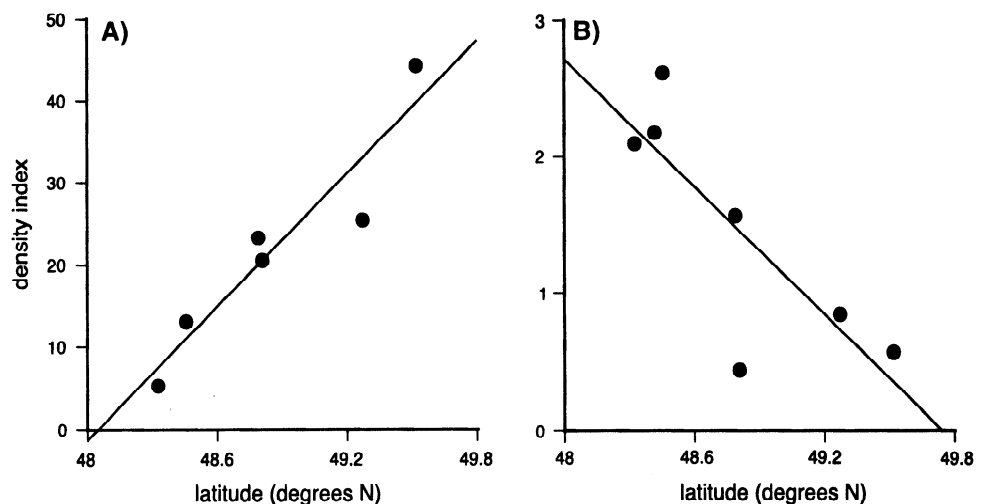


Table 2 Results of regression analyses for a population's density (square-root transformed) and its location in degrees of latitude

Year	<i>E. propertius</i> (<i>n</i> = 6 sites)			<i>P. zelicaon</i> (<i>n</i> = 7 sites)		
	r^2	Slope	<i>P</i>	r^2	Slope	<i>P</i>
2003	0.86	2.63	0.008	0.07	–	0.58
2004	0.88	2.98	0.006	0.64	–0.67	0.03
2005	0.81	2.46	0.015	0.08	–	0.55

Table 3 Mean and SD of temperature (°C) and total rainfall (mm) among sites recorded during the flight period of adults (~mid April–mid June; *F*) and during the translocation experiment with larvae (~mid May–late July; *L*). Data shown are for *E. propertius*. The phenology of the two species is similar, but *P. zelicaon* pupates in June or July while *E. propertius* larvae continue growing. Avg Average, Precip. precipitation

Year	Minimum temperature	Maximum temperature	Avg temperature ^a	Precip.
2004	F: 18.2 ± 1.8	F: 26.2 ± 1.9	F: 22.5 ± 1.7	F: 52.7 ± 17.0
	L: 23.0 ± 2.3	L: 31.4 ± 2.2	L: 27.8 ± 1.9	L: 44.5 ± 16.6
2005	F: 16.5 ± 1.2	F: 24.4 ± 2.3	F: 20.7 ± 2.0	F: 58.1 ± 19.3
	L: 19.6 ± 2.4	L: 28.8 ± 3.5	L: 24.4 ± 3.1	L: 48.3 ± 21.2

^a Mean of values recorded between 1000 and 1600 hours

for all measures ($df = 6$, $P < 0.0001$) except for the coverage of *Q. garryana* ($df = 6$, $F = 3.65$, $P = 0.06$).

Translocation experiments

We use larval production as a metric of fitness, a value that captures both survivorship and fecundity if two assumptions are met. First, we assume that late-instar (*E. propertius*) and pupal (*P. zelicaon*) biomass is indicative of fecundity, an assertion generally supported for insects (Honěk 1993). Second, we assume that the potential reproductive capacity of biomass is independent of the number of individuals. Our analyses are robust to this latter assumption because the variation in production among cages with similar numbers of surviving individuals was small. A linear regression of production versus number of individuals per cage explained a high percentage of the variance (*E. propertius*—2004 65%, 2005 55%; *P. zelicaon*—2004 86%, 2005 95%).

E. propertius

A comparison of larval production for *E. propertius* between natal versus non-natal sites showed no significant differences ($F = 1.17$, $df = 2.71$, $P = 0.32$). Additionally, source site (population) ($F = 1.31$, $df = 5.68$, $P = 0.27$) and rearing site ($F = 1.36$, $df = 5.68$, $P = 0.25$) had no signifi-

cant effect on performance. No interaction of source and rearing site could be analyzed, however, due to limited df .

Of five abiotic and position variables recorded during the larval experiments with *E. propertius*, two principal components (PC1_{epi} and PC2_{epi}) accounted for 63 and 21% of the total variance. Average, minimum, and maximum temperature exhibited high positive loading on PC1_{epi} while rain and latitude were strongly negatively correlated with PC2_{epi}. In multiple linear regression analysis with larval production, a positive relationship with PC1_{epi} remained in the model after backward selection ($F = 12.63$, $df = 1.76$, $P < 0.001$, $r^2 = 0.13$; Fig. 3a).

P. zelicaon

A comparison of larval production for *P. zelicaon* between natal and non-natal sites showed no significant differences in either year (2004, $F = 0.32$, $df = 2.30$, $P = 0.73$; 2005, $F = 2.25$, $df = 2.31$, $P = 0.12$). In 2004, source site had a significant effect on larval production ($F = 5.04$, $df = 4.24$, $P = 0.004$) while rearing site had a marginally significant effect ($F = 2.52$, $df = 4.24$, $P = 0.07$). Post hoc pairwise comparisons revealed that caterpillars from S1 had significantly lower production across treatments than those from three of the four remaining sites (S1 vs. S3, $P = 0.12$; S1 vs. S5, $P = 0.002$; S1 vs. S6, $P = 0.04$; S1 vs. S7, $P = 0.03$). Sites other than S1 were not significantly different from one another. Results were similar in 2005; source site and rearing site had marginally significant effects on larval production (source site, $F = 3.16$, $df = 4.28$, $P = 0.09$; rearing site, $F = 2.21$, $df = 4.28$, $P = 0.09$). Again, an interaction between source population and rearing site was not included in the model due to limited df .

Two principal components (PC1_{pzi} and PC2_{pzi}) accounted for 64 and 24% of the total variance of five climatic variables recorded during larval experiments with *P. zelicaon*. Average, minimum, and maximum temperature exhibited high positive loading on PC1_{pzi}, while rain and latitude were strongly negatively correlated with PC2_{pzi}. In multiple linear regression analysis with larval production, both components remained in the model after backward selection ($F = 4.68$, $df = 2.63$, $P = 0.01$, $r^2 = 0.10$; Fig. 3b). PC1_{pzi}, a component positively related to temperature, remained as a significant and positive predictor of larval production ($P = 0.03$), while PC2_{pzi}, a component negatively related to rain and latitude, was marginally and negatively significant ($P = 0.08$).

Discussion

The threat of climate change compels us to understand the fitness of poleward, peripheral populations because individ-

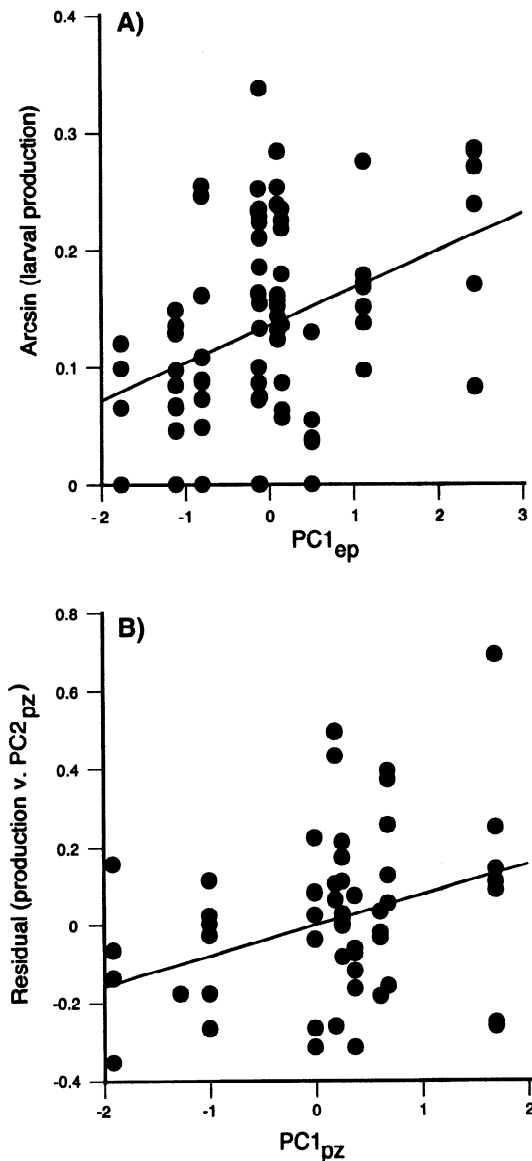


Fig. 3 Relationship between climatic factors and organismal fitness measured as larval production in *E. propertius* (a) and *P. zelicaon* (b). In a, a statistically significant relationship ($r^2 = 0.14$, $P = 0.0007$) between temperature, reflected in the principal component $PC1_{ep}$, and the arcsine, square root-transform of larval production is shown. In b, a statistically significant relationship ($r^2 = 0.12$, $P = 0.005$) between temperature, reflected in the principal component $PC1_{pz}$, and the residuals of a statistically significant relationship ($r^2 = 0.06$, $P = 0.04$) between arcsine, square root-transformed larval production and $PC2_{pz}$, a principal component negatively correlated with rainfall and latitude, is shown. The data in b capture the influence of two principal components, temperature and rainfall, on larval production of *P. zelicaon*

uals in these populations will likely lead geographic range shifts if they occur. Taking a comparative approach between contrasting species, we find support for our prediction that peripheral populations of a large generalist are more responsive to climatic variation than a small-bodied specialist. Abundance of *P. zelicaon* is positively related to

temperature, and larval production was affected positively by warmer conditions. Larval production also trended toward higher values under drier conditions. Larvae of *E. propertius* also responded positively to warmer conditions, but they did not respond to variation in precipitation. The population density of this species also did not vary with climatic factors. These results suggest that both species may increase at the edge of their range with warming, but we found stronger evidence that the density of *P. zelicaon* increases under conditions that are increasingly similar to the range core.

Previous studies of butterfly abundances also suggest that species display a variety of dynamics at their range boundaries. For example, Thomas et al. (1998) found variation in density across the ranges of six butterfly species, including at the range margin. One of these species was an *Erynnis*, *E. tages*, and it showed no statistically significant trend in density with latitude. Previous studies involving habitat modeling of peripheral populations of butterflies and other insects also suggest that ranges could expand if peripheral habitats become more suitable or more available due to warming (e.g., Thomas et al. 1999). Our study draws similar conclusions using both density data and empirical experiments of fitness.

The simplest theory of a species' range change under climate change evokes a single ecotype distributed over space with fitness diminishing gradually with increasing distance from the range center (Brown 1984; Caughley et al. 1998). Climate envelope modeling that aims to project future range boundaries also typically assumes a single ecotype per species and uses occupancy as an overall indicator of a species' preferences and tolerances (see e.g., Pearson and Dawson 2003). This single ecotype view assumes relative maladaptation to the range edge, and it may describe *P. zelicaon* because this species decreases in abundance with decreasing distance to the range boundary and shows increased fitness under conditions that are more like the range core. Gene swamping from core locales could be the explanation for these observations (Avise 1994; Bossart and Prowell 1998; Kirkpatrick and Barton 1997; Davis and Shaw 2001). But this simple expectation does not describe *E. propertius* because population size does not diminish with decreasing distance to the range boundary and fitness in edge populations is somewhat robust to variation among sites within the range periphery. In fact, population surveys performed in the range core indicate that edge densities are as high or higher than in regions further to the south (unpublished data). A number of alternative dynamics could be at play in peripheral populations of *E. propertius*. We discuss three possible explanations and their implications for range change under climate change.

First, peripheral populations of *E. propertius* could be adapted to local conditions. If this is the case, climatic

change could perturb locally adapted forms and require long-distance dispersal from southern locales or assisted migration by people to facilitate range change (McLachlan et al. 2007). Alternatively, natural selection may need to increase the frequency of southerly adapted forms that may be present at low frequency within edge populations or select for genotypes with enhanced dispersal capability to enable range shifts (Thomas et al. 2001). This possibility for local adaptation to the range edge in *E. propertius* requires further study, including translocations over a greater range of temperature and geographic distance.

Second, the high suitability of habitats at the periphery of the species' range suggests that it is limited by some factor that changes in step-wise manner at the range boundary (Caughley et al. 1998; Case and Taper 2000). In particular, host plant availability will limit range expansion in this species because oak shares a range boundary with *E. propertius* (e.g., see Merrill et al. 2008). Accordingly, it is possible that this species is not constrained by climate at its range edge, and this could explain the generalized performance of this species among our study sites. Other biotic factors also could act in a step-like fashion at the boundary of *E. propertius*. We are not aware of any competitors or significant predators at or beyond the range boundary, however, and these interactions could not have occurred without host plants existing further to the north. Further, large peripheral populations might provide a source of colonists for future range expansion, but the probability of long-distance dispersal per individual of this species is not known. We are currently pursuing studies to reveal if climate outside the species' range is viable for population establishment provided that colonists are available.

Third, high densities at the periphery of this species' range could be explained by the relative isolation of suitable habitats. As suggested by Päävinen et al. (2005), it could be that only the best habitat patches are occupied and because they are high quality, they support large populations. This does not seem like a likely explanation given the spatial scale of our study, however. The pattern in density that we found occurs close to the range boundary, though the pattern may also persist over larger spatial scales (see below/above). Further, we found no relationship between measures of habitat quality and density, but an analysis of relative habitat isolation along our latitudinal gradient could reveal more information to test this hypothesis.

We used a translocation approach because translocations are a powerful way to examine differences in population fitness (Crozier 2004a, b). For example, a recent study considered covariation among fitness traits in *Chamaecrista fasciculata* and uncovered differing genetic architecture in differing populations (Etterson and Shaw 2001; Etterson 2004). Other studies have considered boundaries between ecotypes or subspecies within a species' range, revealing

selective pressures that reinforce locally adapted forms (Eckhart et al. 2004; Geber and Eckhart 2005). And a collection of studies with plants in reciprocally sown trials have demonstrated growth and other fitness differences among individuals grown in native versus non-native sites (e.g., Chapin and Chapin 1981; Chapin and Oechel 1983; Schmidt and Levin 1985). Because climate change has the potential to alter geographic range boundaries and dynamics at range edges, a great deal more translocation studies are needed to test theories about local adaptation (e.g., Kirkpatrick and Barton 1997) and density (see Gaston 2003) in these key locations.

Our own analysis of peripheral populations relies on several assumptions and considerations. To supply adequate food resources for our study organisms, we potentially confounded host plant and climate in our experiment with *E. propertius* as both vary among sites. We saw minimal differences among sites in our experiment with *E. propertius*, however, suggesting that neither host plant or climatic differences among sites are strong limitations on larval performance. Further, preliminary analysis of leaves collected from sites across Vancouver Island indicate strong seasonal differences in nitrogen and carbon content but no significant differences among individual trees or sites (unpublished data). As plants for *P. zelicaon* were drawn from a common source and randomly placed among sites, this experiment did not test the effect of local host plant quality or host plant species. Nonetheless, host plants could be a mediating factor in the range expansion of *P. zelicaon* as well. In particular, climate change could affect the onset of summer drought, affecting the late-season availability of host plants for *P. zelicaon*.

Our experiment also assumes that larval performance is a good metric of population fitness and potential changes in population size. Previous studies suggest that this conclusion is reasonable for butterflies because the larval stage is a key survivorship bottleneck (Stearns 1992; Benrey and Denno 1997; Bernays 1997; García-Barros 2000; Fordyce and Shapiro 2003; but see Clancy and Price 1987) and fecundity is often correlated with final caterpillar biomass (Boggs 1986; Karlsson and Wickman 1990; Oberhauser 1997; García-Barros 2000). Climatic factors in other seasons also could affect larvae, however, including overwintering survival (e.g., see Crozier 2003). The role of minimum temperature in setting the northern range boundary of these species requires further study. We assume that the removal of predators and competitors in experimental cages does not confound our results. Predators, including parasitoids, can be important factors in the dynamics of butterfly species (e.g., Clancy and Price 1987; vanNouhuys and Hanski 2004), but climate also is consistently influential in the dynamics of insects (Kingsolver 1989; Hellmann 2001). If these assumptions are valid, our study demon-

strates that phylogenetically similar species vary at their range boundaries in a way that can affect their potential for range shifts under climate change.

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