Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change

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There is a pressing need to predict how species will change their geographic ranges under climate change. Projections typically assume that temperature is a primary fitness determinant and that populations near the poleward (and upward) range boundary are preadapted to warming. Thus, poleward, peripheral populations will increase with warming, and these increases facilitate poleward range expansions. We tested the assumption that poleward, peripheral populations are enhanced by warming using 2 butterflies (*Erynnis propertius* and *Papilio zelicaon*) that co-occur and have contrasting degrees of host specialization and interpopulation genetic differentiation. We performed a reciprocal translocation experiment between central and poleward, peripheral populations in the field and simulated a translocation experiment that included alternate host plants. We found that the performance of both central and peripheral populations of *E. propertius* were enhanced during the summer months by temperatures characteristic of the range center but that local adaptation of peripheral populations to winter conditions near the range edge could counteract that enhancement. Further, poleward range expansion in this species is prevented by a lack of host plants. In *P. zelicaon*, the fitness of central and peripheral populations decreased under extreme summer temperatures that occurred in the field at the range center. Performance in this species also was affected by an interaction of temperature and host plant such that host species strongly mediated the fitness of peripheral individuals under differing simulated temperatures. Altogether we have evidence that facilitation of poleward range shifts through enhancement of peripheral populations is unlikely in either study species.

Lepidoptera | range center | range expansion | range periphery

The biological impacts of climate change are likely to be multifaceted, involving behavioral change, evolutionary change, and local and global extinction, but a well-documented response is geographic range change. Given a species that is completely occupying its thermal niche, warming should open poleward (or upward) territory to population establishment (1, 2). In most cases we would expect establishment to be driven by populations at the poleward (or elevational) periphery of a species' range. If these peripheral populations are preadapted to warmer conditions, due to gene swamping from the center of the range or historical selection under warmer conditions, we would expect them to increase with warming and thereby enhance the colonization process (3, 4). The assumptions underlying this "peripheral enhancement," however, have not been tested despite their significance in determining geographic range change under climate change.

A number of factors could prevent peripheral population enhancement. Resource availability and quality in peripheral locales could limit the growth of poleward populations or the colonization of poleward locales. In herbivorous insects, for example, interactions with host plants could change under climate change, potentially counteracting any direct effects of warming (5). The colonization of new sites also could be limited by host plant availability in species that share their range boundary with host resources (6).

In addition, populations at the range edge could be locally adapted. Previous studies suggest that isolation, genetic drift, and local selection can lead to locally adapted forms, including at the range edge (7–9). If peripheral populations are not preadapted to warmer climates that are characteristic of their range center, climate change may not enhance peripheral populations (10–12). Without enhancement to increase the number of potential colonists, poleward colonization could be restricted (3, 4, 13). Range contraction at the poleward boundary is even possible if peripheral populations decline and fail to colonize new locations.

These limitations on peripheral enhancement and associated implications for the colonization of new habitats are generally not considered in predictions under climate change (see 14–16). Yet, this process demands consideration just as natural and human-caused dispersal limitation and lack of available habitat can constrain geographic range change (17). Furthermore, because fitness is an integration of the total experience of an individual, life stages may differ or even counteract one another in their responses to climate change. For example, in *Papilio canadensis* (Lepidoptera: Papilionidae), increased temperatures are beneficial to growth and development rates when they occur during the growing season (18), but they can have detrimental effects on mass and survivorship when they occur during late autumn, winter, or spring (19).

In this study, we employ field and lab experiments to test the assumption of peripheral enhancement that underlies many projections of climate-driven geographic range shifts. We examine the performance of 2 butterfly species, *Erynnis propertius* (Lepidoptera: Hesperiidae) and *P. zelicaon* (Lepidoptera: Papilionidae) at the poleward periphery and latitudinal center of their shared coastal geographic distribution. These species differ in resource specialization and interpopulation gene flow from the center to the periphery of the species' ranges (3). Zakharov and Hellmann (3) found that peripheral populations of the smaller-bodied and more specialized species, *E. propertius*, are strongly differentiated from their central counterparts whereas *P. zelicaon* exhibits more gene flow across its geographic range. We expected to find that peripheral populations of *P. zelicaon* are more likely than *E. propertius* to be enhanced by warming because we hypothesize that local adaptation occurs in *E. propertius* (4). Further, *P. zelicaon* can move poleward without host plant limitations while lack of host plants

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will prohibit immediate colonization of poleward habitats by *E. propertius*.

Erynnis propertius (Propertius duskywing) is a small-bodied (4-cm wingspan) oak (*Quercus* spp. [Fagaceae]) specialist that ranges along the coast from Baja California, Mexico to southeast Vancouver Island, British Columbia (20). It overwinters as a sixth instar caterpillar and is univoltine in most of its range (21). In the southern portion of its range, it consumes a wide range of oak species including *Q. agrifolia* and *Q. kelloggii* (22). Northward of southern Oregon, the butterfly feeds only on *Q. garryana* (Garry oak) (20, 23), and there are no suitable host plants beyond its current range boundary. The geographic distribution of *Q. garryana* is expected to shift poleward under climate change (24), but the differential dispersal abilities and generation times of *E. propertius* and *Q. garryana* will likely create a lag, initially prohibiting *E. propertius* from colonizing poleward locales.

Papilio zelicaon (Anise swallowtail) is a larger (8-cm wingspan) butterfly that feeds on plants in the Apiaceae family including both native (e.g., *Lomatium* spp.) and non-native plants (e.g., garden plants such as parsley, carrot, etc.) in a variety of habitats (20, 25). It occurs throughout western North America and overwinters in pupal diapause (26). Host plants that are potentially suitable occur northward of the current range limit. Populations throughout the species' range vary in voltinism, depending upon weather and host plant phenology (23). The 2 butterflies share a coastal, northern range limit where open, oak-dominated habitats transition to wetter and colder coniferous forests (23, 27, 28).

To test for peripheral enhancement under climate change, we used 2 approaches. First, we performed translocation experiments between peripheral (Vancouver Island, Canada) and central (southwest Oregon, USA) locations in the field. In this design, central conditions represent a warming treatment for peripheral populations, and we can test for local adaptation to region of origin. Second, we performed a controlled experiment using environmental chambers where we determined the effects of both temperature and host plant of different geographic origin (*E. propertius*) and different species (*P. zelicaon*). This design captures the possibility that the specialist species could be locally adapted to host populations and that the generalist species could respond differently to different host species.

We examined survivorship and body size through the larval growth period in both experiments. Larval survivorship is a good indicator of potential population size, and body size is a good indicator of potential fecundity (29–32), storage reserves (33) and starvation resistance (34) in Lepidoptera and with increased population growth in many taxa (35). In the growth chamber experiment, we also examined differences in metabolic rate during the subsequent winter. Neither butterfly species feeds during the winter; thus, prewinter energy reserves sustain basic metabolic processes and fuel development and initial performance of the adult (33). Therefore, increased energy use over the winter could negatively influence adult fitness, assuming that this energy cost counteracts any accelerated development associated with higher metabolic rates during spring (36).

This study advances the field of climate change biology by directly testing for peripheral population enhancement, taking a comparative approach between 2 species, and considering the effects of climate and host plant treatments at different life stages. In doing this, we aim to increase the realism of future projections under climate change, suggest phenomena that differ among taxa, and illustrate how processes such as peripheral enhancement are complicated by complex life histories.

Results

Field Translocation Experiment. For *E. propertius*, when larvae were reared in field enclosures in a reciprocal fashion to (rearing region) and from (larval source) central (Oregon) and peripheral (Vancouver Island) locales, larval source and rearing location had no effect on survivorship (larval source: $F_{1,51} = 0.97$, $P = 0.33$; rearing region: $F_{1,51} = 0.31$, $P = 0.58$), with no significant interaction ($F_{1,51} = 2.4$, $P = 0.12$) (Fig. 1*A*). Enclosures containing larvae from the range periphery had marginally higher larval mass than those from the center ($F_{1,43} = 3.2$, $P = 0.08$, Fig. 1*B*). Larvae reared in central locales had significantly higher larval mass than those reared in peripheral locales ($F_{1,43} = 9.5$, $P = 0.004$; Fig. 1*B*). There was no significant interaction between larval source and rearing region for larval mass ($F_{1,43} = 0.48$, $P = 0.49$). To determine if larval mass or survivorship varied with climate, we did backwards selection regression with temperature and precipitation. We found that temperature remained a positive, significant predictor variable for larval mass ($P < 0.001$; $r^2 = 0.24$). None of the weather variables remained as significant predictors of survivorship.

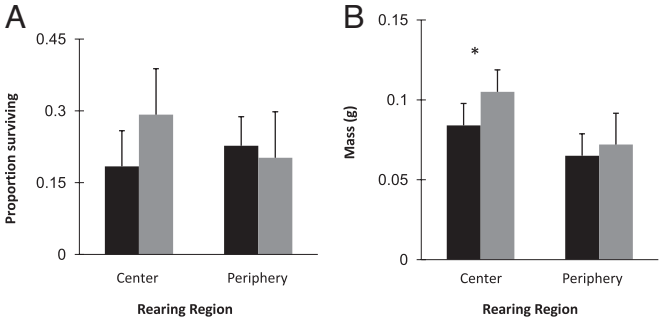

Fig. 1. Field translocation survivorship (*A*) and body size (*B*) results for *E. propertius*. Black bars show performance of larvae from the center, and gray are those from the periphery of the species' range. (*A*) Mean (±95% CI) proportion of larvae surviving to the end of the experiment in each cage. (*B*) Mean (±95% CI) of total mass of surviving fifth instar larvae in each cage. Data shown are untransformed (see *Materials and Methods*). *, denotes a statistically significant difference between rearing regions ($P < 0.05$).

For *P. zelicaon*, larval source did not affect survivorship ($F_{1,103} = 0.51$, $P = 0.48$; Fig. 2*A*). Survivorship was significantly reduced in central locales ($F_{1,103} = 8.77$, $P = 0.004$; Fig. 2*A*). There was no significant interaction between larval source and rearing region for survivorship ($F_{1,103} = 0.62$, $P = 0.43$). Enclosures with individuals from the range center had significantly higher pupal mass than those from the periphery ($F_{1,56} = 5.9$, $P = 0$ .02; Fig. 2*B*). Pupal mass was significantly reduced in central rearing locales ($F_{1,56} = 4.4$, $P = 0.04$; Fig. 2*B*). There was no significant interaction between larval source and rearing region for pupal mass ($F_{1,56} = 0.00$, $P = 0.99$). To determine if pupal mass or survivorship varied with climate, we did backwards selection regression with temperature

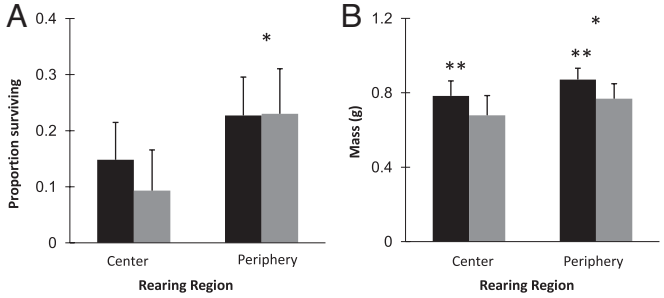

Fig. 2. Field translocation survivorship (*A*) and body size (*B*) results for *P. zelicaon*. Black bars show performance of larvae from the center, and gray are those from the periphery of the species' range. (*A*) Mean (±95% CI) proportion of larvae surviving to the end of the experiment in each cage. Data shown are untransformed (see *Materials and Methods*). (*B*) Mean (±95% CI) of total mass of all surviving pupae in each cage. *, denotes a statistically significant difference between rearing regions. **, denotes a statistically significant difference between larval source regions.

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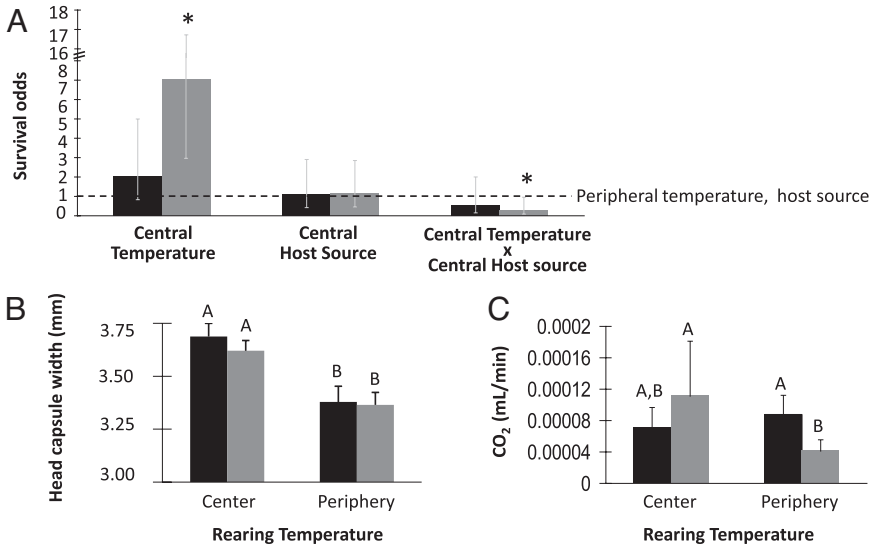

Fig. 3. Growth chamber survivorship (*A*), body size (*B*) and metabolic rate (*C*) results for *E. propertius.* Black bars show performance of larvae from the center, and gray are those from the periphery of the species' range. (*A*) Odds of larvae surviving (±95% CI) to the overwintering period in central (bars) relative to those in peripheral temperatures and/or peripheral *Q. garryana* plants (reference line). *, Instances where the confidence intervals do not overlap the reference line indicate a statistically significant difference ($P < 0.05$) between performance in central and peripheral conditions. (*B*) Mean head capsule width (±95% CI) of sixth instar, overwintering larvae. Data shown are untransformed (see *Materials and Methods*). (*C*) Mean metabolic rate, i.e., CO_2 production, (±95% CI) of overwintering larvae. Data shown are untransformed (see *Materials and Methods*). Letters denote statistically significant differences (*B* and *C*).

and precipitation. We found that temperature remained as the only significant predictor variable for pupal mass and survivorship, having a negative effect on both (pupal mass: $P = 0.04$, $r^2 = 0.07$; survivorship: $P = 0.008$, $r^2 = 0.07$).

Growth Chamber Experiment. In the chamber experiment, individuals from central and peripheral source populations were placed under central and peripheral temperatures. Nested within these treatments, individuals of *E. propertius*, the more specialized feeder, were given a single host (*Quercus garryana*) from central and peripheral locales. The more generalized species, *P. zelicaon*, was given alternate host species (*Lomatium nudicaule*, *L. utriculatum* and *Petroselinum crispum*).

For *E. propertius*, survival of individuals from central locales did not differ across temperature or host plant treatments ($\chi^2 = 3.5$, $P = 0.38$; Fig. 3*A*). Individuals from peripheral locales had significantly greater survival in central temperatures ($P < 0.001$), and there was a significant interaction between temperature and *Q. garryana* source ($P = 0.04$) such that individuals from peripheral populations had greater odds of surviving in peripheral temperatures on peripheral *Q. garryana* than on central *Q. garryana* in central temperatures ($\chi^2 = 27.6$, $P < 0.001$; Fig. 3*A*). Individuals reared in central temperatures had significantly larger head capsules (i.e., body size) at the end of the larval growth period ($F_{1,139} = 74.7$, $P < 0.001$; Fig. 3*B*). The source of larvae had only a marginal effect on head capsule width ($F_{1,\ 139} = 3.2$, $P = 0.075$), and there were no significant differences between individuals from central and peripheral populations when the experiment started (Tukey: $t_{27} = 0.979$, $P = 0.34$). There also was no significant effect of *Q. garryana* source or any of the interaction terms on head capsule width (Fig. 3*B*). Mass of overwintering larvae had no significant effect on CO_2 production (i.e., metabolic rate) ($F_{1,36} = 0.15$, $P = 0.70$). There were marginal effects of rearing temperature ($F_{1,36} = 3.2$, $P = 0.08$) and larval source ($F_{1,36} = 3.5$, $P = 0.07$) and a significant interaction between the 2 factors ($F_{1,36} = 7.8$, $P = 0.01$) on CO_2 production. For individuals from the range periphery, estimates of lipids expended during the overwintering period were 43% lower for those reared in peripheral temperatures (Fig. 3*C*).

For *P. zelicaon*, survival did not differ across temperature treatments, but host plant treatments had significant effects (individuals from central populations: $\chi^2 = 89.7$, $P < 0.001$; individuals from peripheral populations: $\chi^2 = 25.4$, $P < 0.001$; Fig. 4*A*). Individuals from central locales had lower survival on *L. nudicaule* than on *P. crispum.* For individuals from central locales, survival was higher on

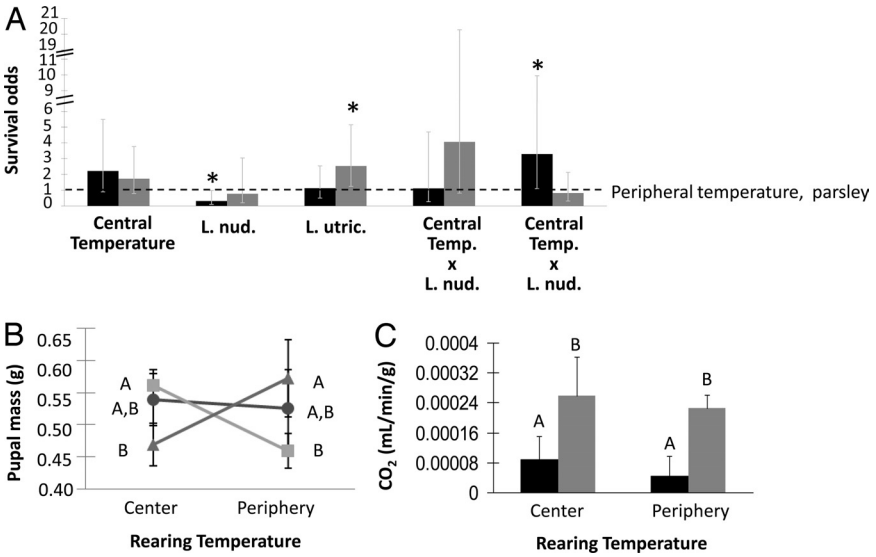

Fig. 4. Growth chamber survivorship (*A*), body size (*B*) and metabolic rate (*C*) results for *P. zelicaon.* Black bars show performance of larvae from the center, and gray are those from the periphery of the species' range. (*A*) Odds of larvae surviving (±95% CI) to the overwintering period in central (bars) relative to those in peripheral temperature and/or on *P. crispum* (reference line) *, Instances where the confidence intervals do not overlap the reference line indicate a statistically significant difference ($P < 0.05$) between performance in central and peripheral conditions. (*B*) Mean pupal mass (±95% CI) of individuals fed 3 hosts: triangles are *P. crispum*, circles are *L. utriculatum*, and squares are *L. nudicaule*. Data shown are untransformed (see *Materials and Methods*). (*C*), Mean metabolic rate, i.e., CO_2 production, (±95% CI) of overwintering larvae. Data are mass specific CO_2 values to account for variance associated with pupal mass. Data shown are untransformed (see *Materials and Methods*). Letters denote statistically significant differences (*B* and *C*).

L. utriculatum in central temperatures than on *P. crispum* in peripheral temperatures (Fig. 4*A*). Individuals from peripheral locales, however, had higher survival on *L. utriculatum* than on *P. crispum* (Fig. 4*A*). While the main effects of temperature, larval source, and host plant had no significant effect on pupal mass, the interaction between temperature and host plant did ($F_{2,286} = 15.2$, $P < 0.001$; Fig. 4*B*). Pupal mass of individuals reared on *P. crispum* was highest in peripheral but lowest in central temperatures (Fig. 4*B*). Mass had a significant effect on CO_2 production ($F_{1, 24} = 8.3$, $P = 0.01$) and was used as a covariate of CO_2 production in subsequent analyses. Individuals from central locales had significantly lower CO_2 production than those from peripheral locales ($F_{1,24} = 30.9$, $P < 0.001$), with no effect of rearing temperature ($F_{1, 24} = 0.51$, $P = 0.48$) and no interaction between larval source and rearing temperature (Fig. 4*C*). Individuals from central locales used 72% less lipid per month (0.32–0.79 mg) than individuals from the periphery (1.13–2.78 mg) under similar temperature conditions.

Discussion

By examining the performance of central and peripheral populations in native and translocated conditions and on different host plants, we tested several underlying assumptions about the potential for geographic range change under climate change. We found evidence that the simple assumption of enhancement in poleward, peripheral populations (i.e., increased population size and colonization potential) under warming does not adequately capture the character of peripheral populations in these species. Therefore, this assumption could lead to misguided management decisions under climate change.

We hypothesized that the species with greater host plant usage and higher rates of gene flow (*P. zelicaon*) would be more likely to be enhanced by warming at the poleward range edge. In contrast, we speculated that the other species (*E. propertius*) could be locally adapted and thus less likely to benefit from warming in peripheral locales. We did find greater evidence for local adaptation in *E. propertius* with respect to overwintering metabolism and performance on local host plants under native climatic conditions. However, peripheral populations of *E. propertius* seem to benefit from warming in the summer months. Meanwhile, we did not find any evidence for peripheral enhancement in *P. zelicaon*. In addition, interactions with host plants appear to strongly mediate the future trajectory of peripheral populations in both butterfly species.

We found in both the field and chamber experiments that performance (body size in the field and body size and survivorship in the chambers) of peripheral populations of *E. propertius* was enhanced by warming during the larval growth period. Individuals were 7 times more likely to survive (chamber experiment) and grew 8–40% larger (chamber and field experiments, respectively) in warmer, central conditions than in peripheral conditions. This finding supports the assumption that poleward populations will increase under warming. However, increases in fitness of *E. propertius* during larval growth may be negated by higher metabolic costs during the overwintering period, assuming that overwintering costs persist under climate change despite winters becoming shorter (37). We found that *E. propertius* individuals from peripheral sites used 43% less energy in their current versus warmer conditions during the middle of winter, suggesting that there is a tradeoff in overwinter metabolism resulting from local adaptation to peripheral conditions (38).

The survivorship advantage of warmer conditions observed for *E. propertius* in the chamber experiments was not found in field conditions. This difference between the 2 experiments may be attributed to differences in temperature exposure. During the field experiment, an extreme heat wave occurred throughout the Pacific Northwest, and temperatures, as recorded by our temperature loggers (see *Materials and Methods*), reached up to 45 °C (36 °C average) for 3 days and 49 °C (47 °C average) for 4 days in peripheral and central sites, respectively. These extreme temperatures were not captured in the chamber experiment, where long-term average temperatures were used with maximums of 21 °C (peripheral chambers) and 34 °C (central chambers). In the case of *E. propertius*, this result suggests that mean warming may be beneficial but extremes could reduce or possibly eliminate survivorship advantages of warming in peripheral populations.

For *P. zelicaon*, we found that survivorship and body size in the field experiment were reduced under warming, findings that do not support the assumption that poleward populations will increase under climate change. In central sites, survivorship was only 48% of that in peripheral locales and pupae were 11% smaller. We speculate that the ability of *P. zelicaon* larvae to thermoregulate in the field experiment could have been constrained by the enclosures, that is, larvae were unable to crawl into the shade or air flow was reduced. *E. propertius* larvae, in contrast, use leaf rolling to modify their microclimate and thus may be better suited to warmer, even extreme, temperatures (21, 39). In addition, *P. zelicaon* also may be more vulnerable to desiccation than *E. propertius* due to its larger surface area (40). During the heat wave, all *P. zelicaon* larvae had reached at least the third instar, and more than 50% of these individuals died. This mortality was substantially higher than that of late instar larvae that were reared in growth chambers. In the chambers, mortality from the third through sixth instars was less than 5%. Further, we found no main effect of temperature on *P. zelicaon* performance in the growth chamber experiment. This result confirms a lack of peripheral enhancement and supports the assertion that temperature extremes were likely responsible for poor performance under central conditions in the field experiment. An increase in extreme temperature events is expected under future climate change (41, 42); thus, species with limited ability to modify their thermal environment could be negatively affected.

The chamber experiment also revealed a host plant effect on survivorship and body size in *P. zelicaon*. While body size of central and peripheral individuals was highest on *P. crispum* in peripheral temperatures, those feeding on either *Lomatium* species were 20% larger in the warmer, central temperatures. Survivorship of central and peripheral populations also differed across host plants, with central populations having greater odds of surviving on *P. crispum* than on *L. nudicaule* across temperatures and *L. utriculatum* than on *P. crispum* only in warmer temperatures. For peripheral populations, however, survivorship was higher on *L. utriculatum* than on *P. crispum* across temperature treatments but survivorship on *L. nudicaule* did not differ from that on the other plants. The 2 *Lomatium* species used in this study contain lower levels of toxic furancoumarins than *P. crispum*, and these differences could be related to differences in *P. zelicaon* performance in our experiment (43). Because plants in our experiment were reared in a common environment before being placed in the chambers for immediate feeding, the changes in host suitability in different temperatures are likely due to changes in larvae, rather than in the host plants themselves. For example, temperature may affect feeding behavior and/or metabolism that alters the rate of ingestion or the ability to detoxify furanocoumarins (44).

In *P. zelicaon*, increasing winter temperatures also may have a disproportionate effect on winter energy use in peripheral populations. The average metabolic rate of *P. zelicaon* from central populations was lower at both rearing temperatures than the metabolic rate of those originating from the periphery of the range. This suggests that selection has acted upon central populations to reduce energy use during winter. We hypothesize that this selection pressure comes from the heat stress in the late summer and autumn after development has ceased. This also is consistent with the results from the field translocation experiment, where insects from both regions raised in the periphery had higher survivorship and pupal mass, but individuals originating from central populations achieved larger sizes than those from the periphery. We are not aware of behavioral differences in diapause site selection between source regions in the field or temperature treatments in our experiment,

although there is variation in overwintering microhabitat within sites (e.g., on or slightly off of the ground) for *P. zelicaon*. Such behavioral differences could moderate the effect of overwintering temperature if it were a consistent response to rearing condition. For *E. propertius*, in contrast, there is less variation in diapausing behavior as all individuals overwinter in hibernacula created from leaf folding (21).

Conclusion

We have amassed evidence that facilitation of simple poleward range shifts from enhancement of peripheral populations is unlikely, or at the least, complicated, in these 2 butterfly species. *Erynnis propertius* populations could increase under warming due to the increased fitness of peripheral populations under central conditions during the growing season, but increased overwinter energy use may reverse these apparent benefits. In contrast, warming will not likely benefit *P. zelicaon* at either life stage: performance during larval growth was substantially reduced in the warmest conditions. In both species, host plants strongly mediate peripheral responses to warming. In *E. propertius*, the lack of host plants outside the species' current range precludes range expansion. In *P. zelicaon*, differential changes in host plant suitability resulting from temperature change may affect successful poleward movement.

Ideally, studies such as this one need to be conducted on multiple species with differing traits to glean a general understanding of factors that limit range shifts under climate change. Previous studies have demonstrated that habitat or resource specialization increases the risk of population decline under climate change (17, 45), and our findings suggest that the ability of individuals to modify their microclimate also is important (46). Evolutionary changes promoting range expansions have not been shown to be common (47, 48), but ecologists have only just begun to consider this process under climate change (49). Our results suggest that evolutionary change in heat tolerance, overwintering efficiency, and/or host usage may reduce or eliminate constraints on peripheral population enhancement or poleward colonization in our study species.

We must move beyond simple assumptions about geographic range change to project future impacts of climate change on biodiversity. It is imperative that we gain a more mechanistic understanding of species' potential for range shifts under climate change because asynchronous changes across species will alter community composition and ultimately affect ecosystem services (6, 50, 51).

Materials and Methods

Field Translocation Experiment. Three study sites in southern Oregon were selected to represent the center of the species' distribution: OR_1 (42° 8′ N, 123° 3′ W), OR_2 (42° 13′N, 123° 10′ W), and OR_3 (42° 28′ N, 122° 56′ W). These sites are biased to the north of the species' latitudinal mid-point so that *Q. garryana* could be used as the host plant for *E. propertius* in both central and peripheral treatments. Three sites were selected on Vancouver Island, British Columbia to represent the periphery of the species' ranges: VI_1 (48° 19; N, 123° 32′ W), VI_2 (48°48′ N, 123° 37′ W), and VI_3 (49° 16′ N, 124° 9′ W). The 2 regions are separated by approximately 800 km. The average temperature recorded by our temperature loggers (HOBO H8 Proseries, Onset Computer Corporation) at central sites during the field experiment (May–July, 2006) was 5 °C warmer than at peripheral sites (central avg. = 22 °C, SD = 1; peripheral avg. = 17 °C, SD = 1). This difference does not occur during the summer months; for example the averages recorded November 2007–March 2008 by our temperature loggers (iButton thermochron DS1992L, Maxim-Dallas Semiconductor) at the central sites were slightly lower and much more variable than at the peripheral sites (central avg. = 3.5 °C, SD = 7.6; peripheral average = 5.1, SD = 2.2).

Eggs were collected from wild-caught females and placed in replicated field enclosures, creating 4 treatment groups: central individuals reared in central sites (control 1), central individuals reared in peripheral sites (translocation and cooling treatment), peripheral individuals reared in peripheral sites (control 2), and peripheral individuals reared in central sites (translocation and warming treatment). We divided sibs between treatments. Enclosures contained eggs from 1 or several populations.

At least 9 *E. propertius* or 12 *P. zelicaon* eggs were stocked per enclosure on 4 occasions between May 18 and June 3, 2006. Each deployment was separated by fewer than 3 days between regions. Enclosures were made of Dacron chiffon mesh (4 cells/mm). *Erynnis propertius* enclosures were 41 cm in diameter and approximately 60 cm long and hung in *Q. garryana* trees with sufficient, natural plant material to avoid resource shortage. *Papilio zelicaon* enclosures were 30 × 30 × 30 cm cubes and placed on the ground with potted parsley (*Petroselinum crispum*) that was watered regularly and replaced if depleted. We did not use local, rooted plants for *P. zelicaon* because they could not be fully enclosed to prevent larval escape.

We used survivorship and body size of late-instar larvae (*E. propertius*) and pupae (*P. zelicaon*) for fitness comparisons. At the completion of the field experiment (July, 2006), all *P. zelicaon* larvae had pupated, and *E. propertius*, which overwinters in the larval stage, had reached at least the fourth of 6 instars [the average instar per enclosure was the same (4.8) in both regions at this time, suggesting that development times did not differ between regions]. Survivorship and mass of pupae (*P. zelicaon*) and survivorship and mass of fifth instar larvae (*E. propertius*) were compared among treatment groups using 2-way ANOVA at the enclosure level to determine the effect of source and rearing region. We limited larval mass comparisons to fifth instar *E. propertius* larvae to evaluate differences at the same stage across all treatments; larval size is highly variable across instars but survivorship beyond the fourth instar is less variable and higher. Survivorship data for *P. zelicaon* were arcsine square-root transformed, and mass data for *E. propertius* were transformed with natural log to meet assumptions of ANOVA.

To determine the role of abiotic variables in larval performance, we performed multiple linear regression with temperature and precipitation against body size and survivorship for both species. Temperature and precipitation data were recorded using field-deployed temperature and precipitation data loggers (HOBO H8 Proseries, Onset Computer Corporation and Rain Collector II, Davis Instruments). Using these data, we then calculated the average daytime temperature (10:00–16:00) and total precipitation occurring during the study (May 18–July 26, 2006).

Growth Chamber Experiment. For both species, eggs were collected from multiple sites in the center and periphery of the species' ranges and shipped on several occasions in May 2007 to the University of Notre Dame, where they were placed individually into environmental growth chambers (MTR30, Conviron). Eggs hatched in a greenhouse to minimize hatching mortality before first instar larvae were placed into experimental treatments.

Replicate growth chambers ($n = 2$) were set to either central or peripheral conditions based on long term temperature data (1997–2006) from the Rogue Valley International-Medford Airport in southwestern Oregon and the Victoria International Airport in Victoria, British Columbia (The Weather Underground, Inc.). Experimental temperatures cycled diurnally between the average long-term minimum and maximum temperatures and were adjusted in 2-week intervals to reflect seasonal changes in temperature. Average summer temperatures were 15 °C in peripheral chambers and 22 °C in central chambers. All treatments were held at 12 l:12 d.

Individuals of both species were exposed to multiple host plant treatments. *Erynnis propertius* larvae were fed potted *Q. garryana* collected from the center and periphery but grown in common conditions in a greenhouse. *Papilio zelicaon* larvae were fed 3 host species: *Lomatium utriculatum*, *L. nudicaule*, and *Petroselinum crispum* (parsley). *Lomatium* species are dominant members of *P. zelicaon's* native habitat and *P. crispum* is a domestic relative of *P. zelicaon's* host family. All individuals were given clippings of their host plant held in florists' aquapics to retain leaf turgor. Plants were checked daily to ensure all individuals had adequate food supply.

After all individuals had entered the overwintering period (September), they were transported under ambient conditions to the University of Western Ontario where they were maintained under the same cycling temperature and light regime as at Notre Dame. The average temperatures during this period (September–March) were 6.5 °C and 7.3 °C in central and peripheral chambers, respectively. A flow-through respirometry system (Sable Systems International) with a Li-Cor 7000 CO_2 infrared gas analyzer was used to measure metabolic rate (as estimated by CO_2 production) for both species at 8 °C. To quantify the differences in metabolic rate, we used mean metabolic rates at 8 °C and 1 °C to extrapolate the total lipid that would be used over a 1-month period during which the daytime temperature was 8 °C for 12 h and nighttime temperature was 1 °C for 12 h. This corresponds to January temperatures for both the center and periphery of our study system. In this analysis, we used a respiratory quotient of 0.7, assuming that all energy that comes from lipid catabolism and that 2 L oxygen is consumed per milligram of lipid catabolized (52).

A 3-way ANOVA (body size) and logistic regression (survivorship) were used to determine the effects of larval source, rearing temperature, and host plant on performance at the initiation of the overwintering period for each butterfly species. We used pupal mass of *P. zelicaon* and head capsule width for *E.*

propertius for performance comparisons. We used head capsule width of overwintering larvae as a surrogate for mass in *E. propertius* because it minimizes disturbance of diapausing larvae and is strongly correlated with larval and pupal mass. A natural log transformation was applied to *P. zelicaon* pupal mass, and an inverse transformation was applied to *E. propertius* head capsule width data so that assumptions of normality were met. For survivorship in both species, we used logistic regression to detect treatment differences because the data followed a binary distribution. We did separate analyses for central and peripheral populations in both species. CO_2 data were log-transformed to meet assumptions of normality and analyzed using ANOVA to determine the effects of larval source and rearing temperature with mass as a covariate. Analyses on the effects of host plant treatments on metabolic rates and survivorship to adulthood were not included due to limited sample sizes (i.e., survival to the overwintering period).

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