Research

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Oviposition behavior and offspring performance in herbivorous insects: consequences of climatic and habitat heterogeneity

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The preference–performance hypothesis predicts that when female herbivorous insects determine where to position offspring of low mobility, they will select sites that maximize development and survival of those offspring. How this critical relationship responds to variation in climatic and habitat conditions remains untested, however, despite its important consequences for population and evolutionary dynamics. Here we report on 13 years of data totaling 1348 egg clusters of the montane Gillette's checkerspot butterfly *Euphydryas gillettii* (Lepidoptera: Nymphalidae). We used these data to test the hypothesis that, in environments with climatic and habitat heterogeneity, the oviposition behavior–offspring performance relationship should vary in both space and time. Orientation of egg clusters for maximum morning sun exposure is known to affect developmental rate. We therefore predicted female preference for morning sun orientation to be variable and a function of climatic and habitat conditions. We found that preference for egg cluster orientation on the leaf tracked the phenology of the start of the female flight season but that seasonal temperatures drove most of the variation in egg cluster development time. The relationship between behavior and performance was also dependent upon the climatic effects on survival; sun-oriented egg clusters had higher survivorship in the coldest year of the four years for which measurements were made. We also examined how conifer cover affected larval survival and female oviposition behavior in one year. Females selected oviposition sites in more open habitat. However, when egg clusters were oriented to intercept morning sun, conifer cover increased survivorship to diapause. Finally, we found that predator activity was lower for morning sun-oriented egg clusters suggesting that predation patterns may further influence habitat selection for oviposition. This study exemplifies how the relationship between oviposition behavior and offspring performance is context-dependent: habitat and climate interact to determine preference–performance outcomes.

Especially in a time when long-term and rapid climate change is in prospect (Solomon et al. 2009), it is important to understand the determinants of population change in herbivorous insects, humanity's most important competitors for food. Within those insects, the early stages of development strongly influence natural population dynamics (Stiling 1988, Cornell and Hawkins 1995). Female oviposition behavior at multiple scales determines the context within which egg and larval development take place. First, habitat selection by females for locations with particular larval host plant densities, adult nectar resources, and shade cover can influence egg and larval mortality (Friberg et al. 2008). Host plant species preference and use by females can also have large effects on the fitness of individual butterflies (Singer 2003, 2004). Finally, within host plant species, females must also assess the quality of the plant itself (Craig et al. 1989) and choose where on an individual plant to lay their eggs.

Habitat and within-plant oviposition preference can affect offspring survival in many ways. First, climatic influences can be mediated through habitat selection. For example, variation in topographic slope and aspect can influence larval growth and development by altering solar exposure (Weiss et al. 1993). Similarly, tree cover can also influence microclimate and affect egg and larval survival (Grundel et al. 1998, Bergman 1999). Within a given host plant, egg placement is one means of buffering or exploiting microclimatic factors. The orientation of butterfly eggs in relation to the sun can be one crucial determinant of egg and larval development time (Williams 1981, Grossmueller and Lederhouse 1985). Faster development time increases female fitness by lowering offspring mortality caused by predation, disease, and parasitism that often afflict the immature stages of lepidopterans (Grossmueller and Lederhouse 1985, Benrey and Denno 1997). Faster development time can also increase fitness in environments with short growing seasons by allowing development to proceed to diapause before host plant senescence (Singer 1972, Williams 1981).

However, oviposition behavior and offspring performance do not always align with one another and mismatches have been documented at all scales of oviposition behavior. With regard to habitat selection, oviposition preferences

can sometimes have little or even negative effects on larval performance (Moore et al. 1998). Oviposition preferences for host plants that are suboptimal with respect to larval preference are common in insects (Thompson and Pellmyr 1991, Larsson and Ekbom 1995, Feder et al. 1997) and selecting sites within plants to minimize development time does not always enhance survival (Williams 1999). In particular, extreme weather events can affect egg mortality and the behavior–performance relationship (Forare and Engqvist 1996, Thomas et al. 1996). For example, if larval survivorship is high on one host plant (or habitat) relative to another host, but mortality is catastrophic for the optimal host in a particular environmental context (e.g. drought events) then some amount of oviposition preference will remain for the suboptimal host (Murphy 2007). In such cases, a labile oviposition strategy would be more successful than a rigid host preference.

Any oviposition behavior–offspring performance relationship is a consequence of these environmental initial conditions and therefore, heterogeneity in the environment may significantly complicate the female's choice of prime oviposition sites. Further complicating the matter, other trophic levels (e.g. more predators in certain habitats or healthier host plants under different weather patterns) may also be impacted by environmental heterogeneity. Under these conditions of habitat and climatic heterogeneity then, we would expect variation in oviposition behavior–offspring performance relationships such that females should show plasticity in oviposition behavior and that offspring performance would be a consequence of not only that oviposition behavior but also the environmental context itself.

To examine this hypothesis we turned to the well-known checkerspot butterfly model system (Ehrlich and Hanski 2004). We collected extensive data on egg clusters of the butterfly *Euphydryas gillettii* (Lepidoptera: Nymphalidae) from an introduced population in Gothic, Colorado, ~500 km south of the historical range, with data extending back to 1981. Williams (1981) found that *E. gillettii* in Wyoming had a strong preference for ovipositing morning-sun oriented egg clusters and that this orientation significantly improved development times in their limited growth-time montane environment. We used the long-term Colorado egg cluster dataset to test: 1) do seasonal temperatures, or phenology, have an effect on egg cluster orientation preference and/ or egg cluster development? 2.) does habitat structure affect female oviposition? We then specifically addressed the relationship between oviposition behavior and egg cluster/larval performance by asking: 3) does egg cluster placement, or orientation with respect to the sun, affect egg cluster/larval development and survival? 4) how does habitat structure around selected host plants affect larval survival? The data show that the oviposition behavior–offspring performance relationship is a function of not only suitable host plant species, but also plant position/ orientation, habitat structure and seasonal weather effects.

Methods

Study site and species

The population of *Euphydryas gillettii* studied was introduced in 1977 at Gothic, Colorado (38°57'5"N, 106°59'6"W, 2912 m a.s.l.) using propagules from northwest Wyoming (Holdren and Ehrlich 1981). The two hectare site is a wet montane meadow consisting of spruce *Picea englemannii* (Pinaceae), willows *Salix* spp. (Salicaceae), and the butterfly's larval host plant *Lonicera involucrata* (Caprifoliaceae). *Euphydryas gillettii* is univoltine, with an adult flight period lasting 3–6 weeks, typically beginning in July. Eggs are laid in clusters and take approximately 3–4 weeks to develop. Larvae feed into early to mid September, and diapause for the winter as unfed fourth instar larvae.

This *E. gillettii* population remained at about 25–200 individuals through the 1980s until 2002, when the population exploded to reach over 3000 individuals and its range expanded to approximately 30 times its original size (Boggs et al. 2006). The range increase produced two subpopulations distinct from the Origin (the site of introduction) subpopulation. However, we used only data collected from the Origin subpopulation in this analysis in order to control for site to site differences that might exist among subpopulations.

Egg cluster data

We searched all *L. involucrata* plants for egg clusters within the study area during the *E. gillettii* flight seasons from 1981 to 1988 (excluding 1985) and from 2003 to 2008. We monitored each egg cluster and recorded its compass orientation and number of eggs. In 2004, 2006, 2007 and 2008 when population sizes were above 500 adults we did not sample all egg clusters in the site and subsampled approximately 200–325 clusters (Table 1). Egg clusters were checked on average every third day after initial discovery through the first two larval instars, usually about a month for each egg cluster. Egg clusters change in color through development from a light yellow when first laid, to dark gold, to reddish brown, and finally to a gray-black just before hatching (Williams et al. 1984). Egg cluster hatching typically lasts about 24 h. The first day any eggs hatch within an egg cluster, or hatch date, could be determined if monitoring fell on that day, but could also be estimated if a cluster was black (meaning hatch date was likely the following day) or if first instar larvae were very small and still in an egg cluster-like formation (meaning hatch date was likely the previous day). If an egg cluster was found while still yellow and hatch date could be estimated, then egg cluster development time was calculated as the number of days between the date when yellow egg clusters were found and the hatch date. Egg clusters turn from yellow to dark gold over a period of 2–3 days, so the estimation of lay date contains some error.

How egg cluster data were collected varied among years. Consequently we have different types of data for each year (Table 1). The number of eggs per cluster was not counted in 2003. In 2005, 2007 and 2008 egg clusters were checked on a weekly basis and thus egg development time and predation events were not obtained in those years. We recorded the presence of egg cluster predators in all of the early years (before 2003) and in 2006. Partial and complete predation of egg clusters during development is common in *E. gillettii* populations (Williams et al. 1984). Within the Gothic population, deer and elk occasionally browse *L. involucrata* leaves and the egg clusters on them. More commonly, egg clusters have small predators such as erythraid mites, which can cause mortality of roughly

Table 1. Summary statistics of egg cluster variation, oviposition behavior and weather. Standard error is shown for mean development time, clutch size (number of eggs/cluster), and cluster orientation. Sample sizes are in parentheses.

	1981	1982	1983	1984	1986	1987	1988
Egg clusters monitored (n)	76	48	38	35	12	7	16
Mean development time (in days)	27 ± 1 (23)	24 ± 1 (7)	23 ± 1 (17)	24 ± 1 (6)	27 ± 3 (2)	23 ± 2 (3)	21 (1)
Mean maximum flight season temperature (in °C)	22.6	23.3	23.9	23.3	22.3	24.4	24.7
Start flight date (Julian day)	172	195	198	195	201	181	183
Mean cluster size	171 ± 9 (69)	98 ± 6 (48)	225 ±20 (38)	184 ± 11 (35)	168 ± 16 (12)	177 ± 14 (6)	126 (16)
Mean cluster orientation (in °)	136 ± 21 (73)	287 ± 23 (48)	262 ± 99 (38)	292 ± 32 (35)	288 ± 29 (12)	198 ± 41 (6)	211 ± 36 (15)
Rayleigh test (Z) for orientation	4.77	2.91	0.17	1.60	2.14	0.41	1.62
Rayleigh test (p)	< 0.001	0.05	0.85	0.20	0.12	0.68	0.20
	2003	2004	2005	2006	2007	2008	
	30	259	29	325	231	242	
	22 ± 1 (11)	26 ± 1 (53)	–	25 ± 1 (57)	–	–	
	25.0	22.7	24.1	23.1	24.6	23.9	
	177	179	194	171	175	194	
	–	125 ± 4 (158)	141 ± 6 (28)	142 ± 3 (267)	153 ± 4 (218)	135 ± 3 (239)	
	–	–	304 ± 41 (29)	261 ± 10 (315)	250 ± 14 (225)	319 ± 24 (242)	
	–	–	0.98	15.22	7.55	2.73	
	–	–	0.38	< 0.001	<0 .001	0.07	

10–20% (but up to 100%) of any given cluster (Williams et al. 1984, Benz and Boggs unpubl.).

Survivorship to diapause is defined here as the proportion of eggs within an egg cluster surviving to diapause conditional on successful hatching of the egg cluster. From 2005 to 2008, we calculated early instar survivorship by first counting how many larvae were present in the larval diapause web at the end of the season (usually in early September). We chose only larval masses that clearly originated from a single egg cluster. We then divided the number of larvae present by the number of eggs within the egg cluster from which those larvae originated. We obtained survivorship data for 19 egg clusters in 2005, 43 clusters in 2006, 22 clusters in 2007, and 63 clusters in 2008.

The female flight season was defined as the period from the first adult female seen to the last adult female seen. Maximum temperature (mean of the daily mean maximum temperature) during the female flight season was calculated for all years from a NOAA climate station located in Crested Butte, CO, about 10 km from the study site. This was used as a surrogate for the daily temperature that the butterflies experienced while active, and was used as an index of seasonal temperature for inter-annual comparisons.

Egg cluster orientation was recorded in every year but 2003 and 2004 using a compass. True north lies 15° northeast of magnetic north and so 15° was subtracted from all compass readings. In other populations of *E. gillettii,* orientation with respect to morning sun is known to affect development such that egg clusters oriented southeast (100° to 190°) and northwest (280° to 10°) (i.e. on leaves with a surface exposed to morning sun) have a thermal developmental advantage over other egg clusters (Williams 1981). Furthermore, females clearly choose, non-randomly, the oviposition sites which most intercept morning sun (Williams 1981).

Habitat data

We determined the location of all 299 *L. involucrata* plants within the study site in 2006 using a GPS unit with sub-meter accuracy. The number of egg clusters and the identity of each egg cluster were noted for each plant. We used a 2006 aerial photograph of the site to estimate conifer cover associated with larval host plants. The orthorectified color image had a spatial grain < 1 m^2 and contained a layer of data for each of the primary colors (red, green, blue). Of the three data layers, the red layer visibly corresponded most strongly with conifer cover in the image. We judged all pixels in the image with a red value $\leqslant 45$ (on a scale of 0–255) to be conifer-covered (Fig. 1). Using this first approximation of cover, we calculated the proportion of conifer-covered pixels within a 5-m radius of each point where *L. involucrata* was found. The area within a 5-m radius of each *L. involucrata* was judged to encompass most of the conifers which could likely alter microclimate (e.g. through shade or wind blocking).

Statistical analysis

We used an ordinary least squares regression model to determine how seasonal temperature affects egg cluster development time. Circular statistics were required for oviposition orientation analysis because the data are in degrees (Zar 1999). We performed Rayleigh's test to examine

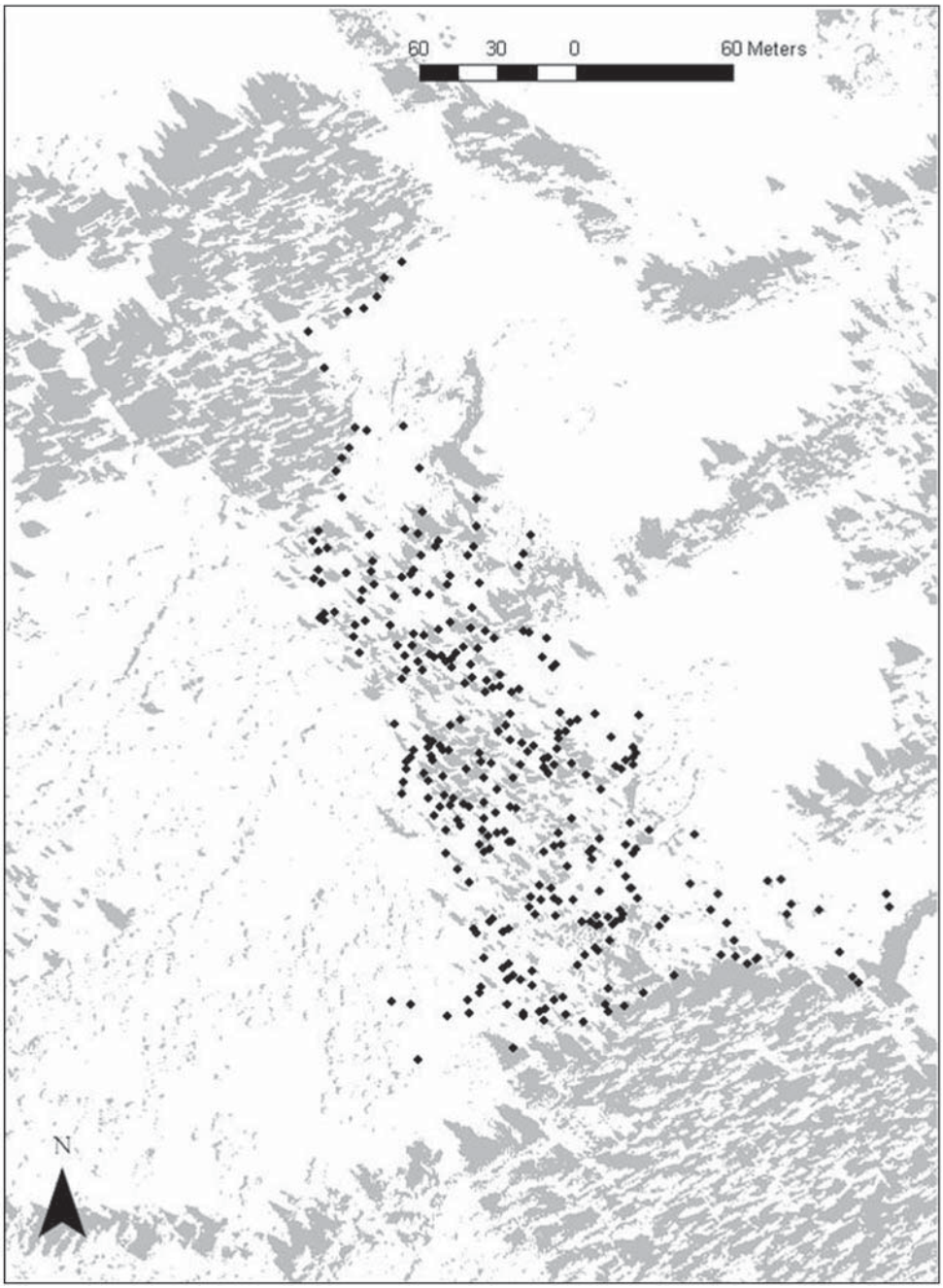

Figure 1. Map of the study site showing overlap of *E. gillettii* host plant individuals (*Lonicera involucratra*) (black diamonds) and conifer cover (grey shading).

deviation from the uniform distribution, i.e. whether or not egg cluster orientation is non-random (Table 1). We used angular-linear correlations to test relationships between egg cluster orientation and other linear data, time and seasonal temperature. For circular statistics and plots we used Oriana 2.0 (Kovac Computing Services).

We transformed habitat cover data using $x' = \arcsin(x^{0.5})$ and larval survivorship using a square root transform. We used ANOVA to test if plants with egg clusters had different percent conifer cover within 5-m than plants without conifer cover. ANOVAs were also performed to test the effect of egg cluster orientation on survivorship. We analyzed predator presence as a function of orientation (morning sun oriented or otherwise) using a χ^2-test. Finally, we also used ordinary least squares regression to examine how local conifer cover around each plant, development time, and egg cluster size affected larval survivorship. Statistical analyses were done in Systat 12 (SPSS, IL, USA).

Results

Oviposition behavior, weather and egg cluster development

We collected data on 1348 egg clusters over the 13 years studied (Table 1). Flight season mean maximum temperature

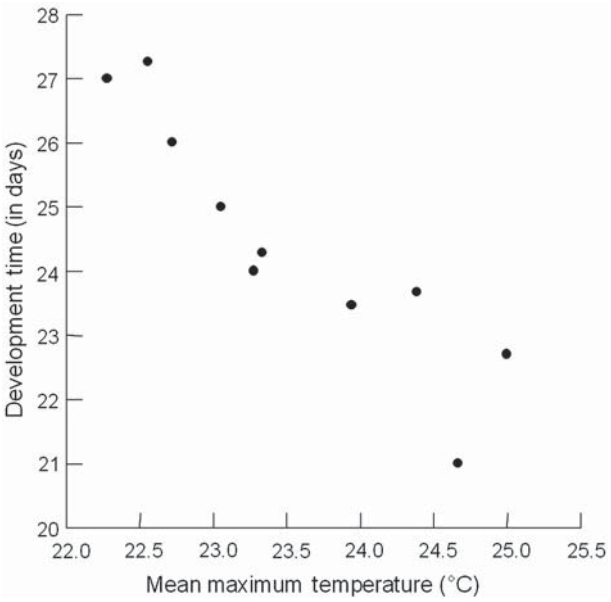

Figure 2. Relationship between flight season temperature and egg cluster development time.

varied among years (from 22.3°C to 25.0°C) as did flight phenology (30 days separate the latest from earliest start of the flight season). Egg cluster size, orientation, and development time also varied among years.

Flight season temperature accounted for 83% of the variation in egg cluster development time ($r^2 = 0.83$, $p < 0.001$, $n = 10$; Fig. 2). Egg clusters were significantly more likely to be oriented towards morning sun in phenologically late years ($r = 0.69$, $p = 0.02$, $n = 11$; Fig. 3a). Temperature had no significant correlation with cluster orientation though colder years tended to be more often associated with morning sun orientation than warmer years ($r = 0.48$, $p = 0.15$, $n = 11$; Fig. 3b). Flight season temperature was not correlated with start day of the flight season ($r = -0.12$, $p = 0.74$, $n = 11$). Preference for morning sun orientation by ovipositing females was dependent upon the flight season phenology, though egg cluster development time appears mostly determined by the seasonal temperature itself.

Oviposition behavior and habitat

Conifer percent cover ranged from 0–67% and averaged 22% ± 1% (mean ± SE) for *L. involucrata* individuals throughout the site. Plants with egg clusters had significantly less conifer cover within 5-m than did plants without egg clusters ($F_{1,297} = 31.60$, $p < 0.001$).

Egg cluster development, orientation and survival

We expected that both orientation and egg cluster size would affect the thermal conditions experienced by eggs and hence their development time and survival rates. However, egg cluster development time did not vary as a function of cluster orientation or cluster size either across or within the years 1981–1984, 1986–1988 and 2006 ($p > 0.30$). Development time to egg hatch and survivorship to diapause were also not correlated among years, although the sample size was small ($r^2 = 0.06$, $p = 0.52$, $n = 9$). When pooled among all four years in which survival to diapause data were collected (2005–2008), egg clusters oriented to intercept morning sun had no higher survival to diapause than those not intercepting morning sun ($F_{1,82} = 0.004$, $p = 0.95$).

Within years however, in 2006, egg clusters oriented to intercept morning sun had significantly higher survival to diapause than those not intercepting morning sun ($F_{1,41} = 4.05$, $p = 0.05$; Fig. 4), while no significant differences were found within 2005, 2007 or 2008 (2005: $F_{1,17} = 1.80$, $p = 0.20$, 2007: $F_{1,20} = 1.21$, $p = 0.29$, 2008: $F_{1,62} = 0.00$, $p = 0.99$; Fig. 4). Analyzed another way, we find that there is a marginally significant year by orientation interaction within a generalized linear model framework (year × orientation: $F_{3,140} = 2.56$, $p = 0.06$, year: $F_{3,140} = 1.55$, $p = 0.21$, orientation: $F_{1,140} = 0.52$, $p = 0.47$).

Habitat structure, predation and survival

Survivorship to diapause averaged 0.22 ± 0.02 (mean ± SE) in 2006. Conifer cover was not significantly correlated with larval survival ($r^2 = 0.02$, $p = 0.46$, $n = 36$). However, egg clusters in morning sun showed a positive trend between conifer cover and larval survival ($r^2 = 0.17$, $p = 0.06$, $n = 22$) while clusters not in morning sun had no correlation ($r^2 = 0.03$, $p = 0.53$, $n = 14$). One morning sun-oriented cluster was a clear outlier (studentized residual = –3.72). This cluster was one of five predator-associated egg clusters of the 43 monitored larval masses. When this outlier was removed from the analysis, the relationship between conifer cover and larval survival was strongly significant within morning sun-oriented clusters ($r^2 = 0.40$, $p = 0.002$, $n = 21$). When data were examined over all years in which predation activity was noted (1981–1988 and 2006), observed predator presence was significantly greater at egg clusters not oriented towards morning sun ($\chi^2_1 = 10.08$, $p = 0.002$).

Discussion

Our results suggest that climatic and habitat heterogeneity encouraged plastic oviposition preference in females. We found that phenology influenced female oviposition behavior and the orientation of their egg clusters. We also found that orientation influenced egg cluster survival significantly only in the coldest year studied. Therefore, females met the preference-performance expectation in the sense that in late seasons when development time was more constrained by the onset of fall and host plant senescence, egg clusters were more likely to be morning sun-oriented. With respect to temperature, we found no significant correlation between temperature and egg cluster orientation suggesting that females did not necessarily use temperature as an oviposition cue despite its importance in larval survival outcomes. Predation activity was also found to be higher on non-morning sun-oriented clusters adding another level of complication to the preference–performance relationship. Furthermore, the results illustrate that behavioral plasticity cannot fully compensate for environmental heterogeneity. Though oviposition preference is an important factor in determining larval survival (Fig. 4), temperature is a strong driver of egg cluster development time (Fig. 2) independent

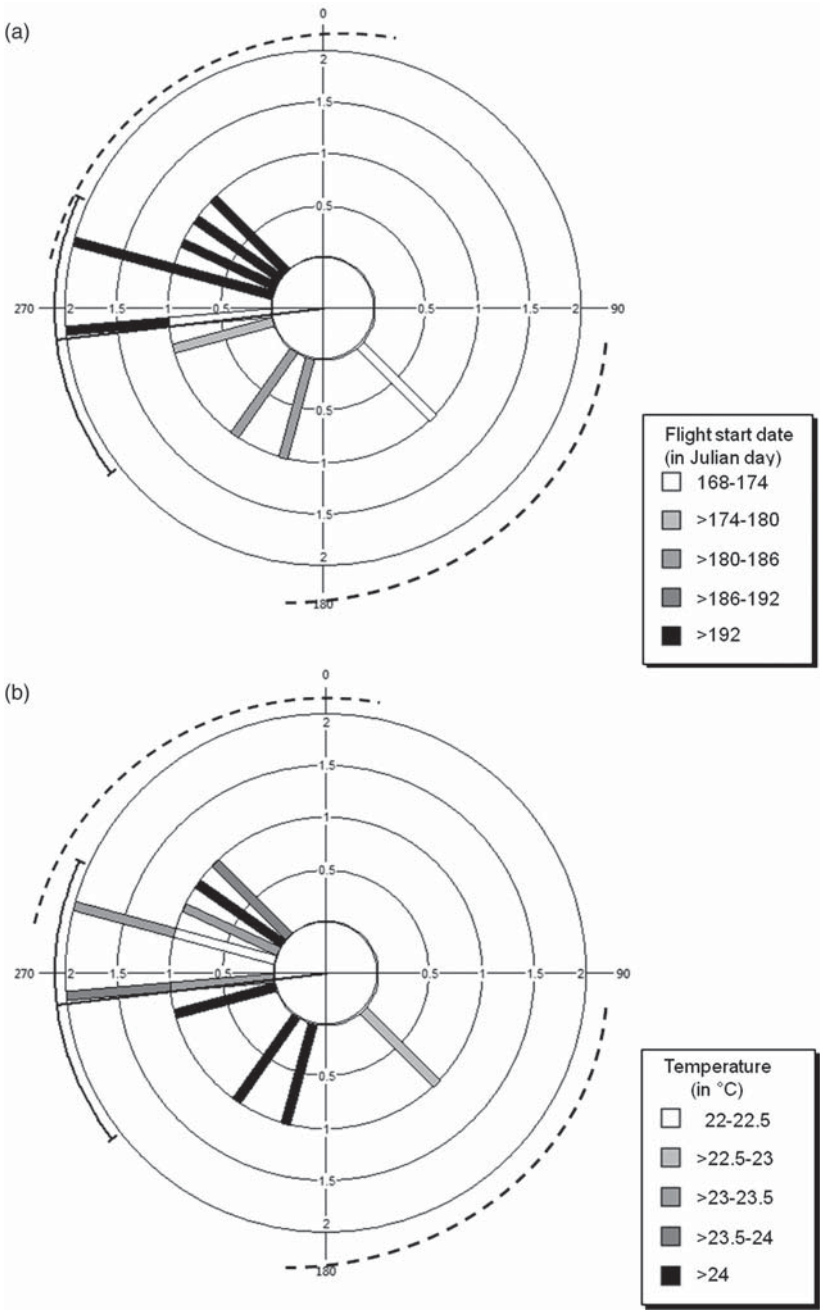

Figure 3. Correlation between yearly mean egg cluster orientation and both (a) start date of flight season and (b) mean maximum temperature. Solid arc represents overall angular mean and angular deviation of egg clusters and the dotted arcs represent the southeast and northwest axis within which egg clusters directly intercept morning sun.

of female oviposition behavior. Given the importance of egg and larval development times in the population dynamics of other herbivorous insects, we suggest that understanding the oviposition behavior–offspring performance link within populations in variable environments is critical to accurate prediction of their population and evolutionary trajectories.

Oviposition behavior and offspring performance under climatic heterogeneity

It is well established that some insect species must invest large amounts of time in selecting oviposition sites if, for example, they cluster their eggs (Stamp 1980) or have limited eggs to lay (Iwasa et al. 1984, Doak et al. 2006). We show here that phenology and temperature can also determine the importance of oviposition and offspring performance in much the same way, i.e. limited time for development will increase the importance of oviposition site selection.

In 2006, a relatively cold year (Table 1), we found that larval survival to diapause was higher when clusters were morning sun-oriented. In 2005, 2007 and 2008, relatively warm years, no statistically significant difference in survival was found as a function of orientation. This suggests that

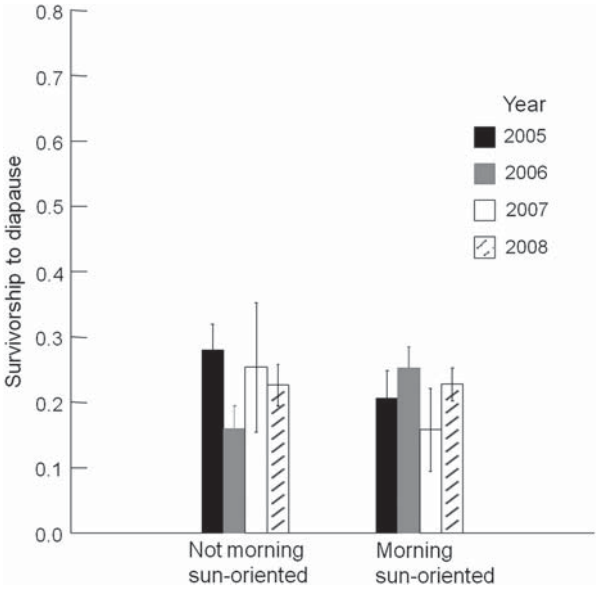

Figure 4. Survival from egg cluster to diapause was dependent on orientation with respect to morning sun in 2006, but no differences in survival were found in 2005 or 2007 as a function of orientation. See text for statistics. Error bars represent SE.

offspring benefit from oviposition preference for morning sun orientation only in colder years when thermal constraints on development time are stronger. However, factors other than development time may help explain the difference in survival found in 2006. Observed predator activity was lower on morning sun-oriented egg clusters, such that increased survival could be the result of predator preference for non-morning sun-oriented clusters (Rausher 1979). With our limited data on predator behavior, we cannot be certain of the mechanism causing the increased presence of predators on non-morning sun oriented clusters but, in any case, the results highlight the complexity that can arise due to species interactions in the explanation of oviposition behavior.

Seasonal temperature determines egg cluster development time in this butterfly population. Average development time can be accelerated by five days given warmer summer temperatures. A decrease in development time in this short growing season, montane environment could have a positive impact on population growth by enhancing larval survival. Increase in summer temperatures and the resulting decrease in early stage development time has been implicated as a cause in the range expansion of a skipper, *Atalopedes campestris*, in the Pacific northwest (Crozier 2004). Increasingly warmer summers are likely to affect *E. gillettii* similarly by affecting range and population dynamics.

Williams (1981) found strong effects of egg cluster orientation on development; clusters intercepting morning sun hatched a week earlier on average than those that did not. That we did not detect this effect over all years could be a result of differences between study sites. While the introduced Gothic, CO population of *E. gillettii* is at a higher altitude to account for the more southern latitude relative to its Wyoming donor population, the Wyoming population studied by Williams (1981) is 450 m higher (and 6°N) than the donor population. Thus, the Williams (1981) population experiences cooler temperatures than both the Wyoming donor and Gothic, CO populations. This fact is emphasized by the average development times measured by Williams (1981): 26.7 days for morning sun oriented clusters and 32.8 days for non-morning sun oriented clusters. In only two years of our study (1981 and 1986) was development time longer than 26 days, indicating much warmer conditions over all in Gothic, CO. Therefore, oviposition orientation in the Colorado population likely exerts a smaller effect on larval survival than in most of the northern populations.

Variation among years in mean egg cluster orientation correlated significantly with phenology. When the season started later, egg clusters were more likely to be morning sun-oriented. As the season progresses, day length decreases as does the time available for egg and pre-diapause larval development. Day length is a critical determinant of many insect reproductive patterns (Tauber et al. 1986) and could be the cue for the oviposition behavioral change that we observed. Though the precise mechanism is unclear, many butterflies are known to alter behavior based on changes in day length (Kemp 2000, Gotthard 2008) and it is entirely possible that *E. gillettii* have been selected to prefer morning-sun orientation more strongly when sun exposure is more limited in phenologically late years.

Oviposition behavior and offspring performance under habitat heterogeneity

Habitat heterogeneity affected larval survivorship to diapause in egg clusters that were morning sun-oriented. Clusters directly intercepting morning sun had higher survival in higher conifer cover, despite ovipositing females on the whole showing a preference for lower conifer cover. The habitat selection could be a result of apparency if host plants are more visible in lower conifer cover sites (Courtney 1982). *Lonicera involucrata* is a forest-associated species with decreased abundance and cover at edges compared to forest interior (Harper and McDonald 2002). Therefore plants in high conifer cover may be bigger or nutritionally superior to plants in the open and therefore confer fitness advantages indirectly (as for *Lycaeides meilissa*, Grundel et al. 1998). There could also be direct microclimatic consequences if, for example, higher conifer cover blocks wind, resulting in warmer egg clusters. The cause of the habitat interaction with cluster orientation is unclear but could also be the result of weather if, for example, morning sun-oriented egg clusters benefit from both nutritionally superior plants in high conifer cover and greater exposure to sun resulting in higher survival.

Empirical evidence from other study systems further suggests that habitat heterogeneity disrupts the behavior–performance link. Increasing habitat heterogeneity increased the interference in oviposition site searching (e.g. by altering host plant apparency) and subsequently weakened the oviposition behavior and offspring performance relationship in the moth species *Ochrogaster lunifer* (Floater 2001). Density dependence differences between habitats in a tree-hole mosquito species (*Ochlerotatus triseriatus*) also complicated the behavior–performance relationship (Ellis 2008). In a more homogeneous environment natural selection would likely

favor a more straightforward and positive behavior–performance outcome but variable environments complicate behavior–performance outcomes.

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