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Journal

Ecological Entomology, 40(6)

ISSN

0307-6946

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Publication Date

2015-12-01

DOI

10.1111/een.12243

Peer reviewed

Caterpillars escape predation in habitat and thermal refuges

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Abstract. 1. Climate and, therefore, abiotic conditions, are changing rapidly, and many ecological interactions depend on them. In this study, how abiotic conditions mediate a predator–prey interaction were examined.

2. Caterpillars of *Platyrepia virginalis* (Boisduval) (Arctiidae) were found previously to be more abundant in wet habitats and thick litter cover compared with drier habitats and little or no litter. We hypothesised that wet litter provided caterpillars with refuges from an important ant predator, *Formica lasioides*. It was further hypothesised that caterpillars would be able to move at lower temperatures than ants, thus providing them with a thermal refuge.

3. In the lab, caterpillars were more likely to escape ant predation and survive on wet litter and at lower temperatures. At all temperatures, ant recruitment was lower in wet litter than dry litter although ants were more active on litter than bare soil. Thus, wet litter may serve as a habitat refuge for caterpillars from ants.

4. Caterpillars were able to maintain activity at temperatures 8–14 °C lower than *F. lasioides*. Thus colder temperatures may serve as a thermal refuge for caterpillars from ants.

5. It was hypothesised that caterpillars can escape ant predation when precipitation causes wet litter and at temperatures that they experience commonly in the field. This mismatch between caterpillars and their predators in ability to tolerate wet litter and low temperatures may affect their field distribution and abundance. Expected future warmer and drier conditions may not provide these refuges.

Key words. Climate change, enemy-free space, *Formica lasioides*, habitat, *Platyrepia virginalis*, predator–prey, refuge, temperature.

Introduction

As climates change owing to human activities, species will be affected differently. Idiosyncratic responses by different species to changing regimes of temperature and rainfall have the potential to create mismatches and disrupt current species interactions (Parmesan, 2006; Tylianakis *et al.*, 2008; Gilman *et al.*, 2010). The consequences of such mismatches have recently received attention, particularly for plants and pollinators (Memmott *et al.*, 2007; Inouye, 2008). Climate change also has the

potential to change interactions between plants, herbivores, and the predators and parasites that attack them (van Asch & Visser, 2007; Singer & Parmesan, 2010). For example, rates of parasitism of spruce budworm by parasitoids that attack their eggs increased as the temperature increased (Bourchier & Smith, 1996). At higher temperatures, parasitoids were able to move more rapidly and to forage more effectively. The phenological match between predators and their prey has been recognised as an important determinant of the success and abundance of predators (Durant *et al.*, 2007; Hance *et al.*, 2007; Baffoe *et al.*, 2012).

Predators and prey often have different thermal tolerances, meaning that activity is possible over different ranges of

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temperatures. Species have different thermal optima and thresholds that allow them to move, feed, and survive under varied environmental conditions (Huey & Kingsolver, 1989; Chown & Nicolson, 2004). Invertebrates are generally considered to be poikilotherms, unable to maintain body temperatures that are independent of their environments. However, poikilotherms may regulate body temperature and temperature-dependent physiological processes by choosing microenvironments with desirable conditions that are species-specific, stage-specific, or condition-specific (Huey *et al.*, 2003). Heat is gained and lost by direct absorption of radiant energy, conduction with the air, and with surrounding substrates, and by evaporation so that shade and moisture strongly influence body temperature along with ambient temperature. Low temperatures have been implicated as important factors that limit populations of poikilotherms, particularly insects (e.g. Kingsolver, 1989; Bale, 2010). Climate change is altering the precipitation and temperature regimes along the coast of northern California (Weare, 2009; Li *et al.*, 2014).

In this study, we studied whether caterpillars of *Platyprepia virginialis* (Lepidoptera: Arctiidae), a tiger moth, and their ant predators *Formica lasioides* (Hymenoptera: Formicidae) had different tolerances for these conditions. We previously collected a long-term data set on the temporal and spatial dynamics of *P. virginialis*. Densities of caterpillars have varied by three orders of magnitude at our study site over the past 30 years (Karban & de Valpine, 2010; Karban *et al.*, 2013). We are examining the mechanisms for these dynamics through short-term experiments. Wet sites have consistently supported more caterpillars than dry ones. Wet sites tended to act as source populations with $\lambda > 1$, and dry sites tended to act as sinks with $\lambda < 1$ (Karban *et al.*, 2012b). Wet microsites supported larger caterpillars than dry microsites, suggesting that some of this effect may be driven by differences in water or other resources (P. Grof-Tisza *et al.*, unpublished). Spatial and temporal variation in caterpillar abundance may also have been driven by differential rates of predation by ants (*F. lasioides*) that attack early instar caterpillars and pupae (Karban *et al.*, 2013; Grof-Tisza *et al.*, 2015). Young caterpillars that inhabited microhabitats covered with living and dead vegetation experienced reduced ant predation relative to those inhabiting microhabitats covered by bare soil (Karban *et al.*, 2013). Other herbivore species that increased litter depth indirectly increased numbers of *P. virginialis* caterpillars, suggesting that litter may provide a refuge from ant predation (Karban *et al.*, 2012a).

In lab and field experiments reported here, we examined whether microhabitat and microclimate, both of which may be influenced by global climate change, altered predator–prey interactions. Specifically, we asked the following questions: (i) Do caterpillars and ants have different habitat- and temperature-dependent requirements for activity? (ii) Are predation rates of caterpillars by ants affected by litter, moisture, and temperature? (iii) What temperatures do *P. virginialis* caterpillars experience in different microhabitats (wet and dry sites, sun and shade) in the field? (iv) What thermal tolerances do caterpillars and ants have, and do these provide caterpillars with a refuge from predation?

Methods

Natural history of the study system

Our fieldwork on *P. virginialis* took place across several habitats at the Bodega Marine Reserve in central California. A detailed account of this reserve was provided by Barbour *et al.* (1973) and our specific sampling sites were described by Karban *et al.* (2012b). Most of the reserve is dry upland habitat occupied by grassland or dune vegetation although smaller low-lying areas are seasonally flooded and support *Juncus* rushes and other plants found in freshwater marsh habitats. *Lupinus arboreus* is the most abundant shrub on the reserve, and bushes are common in both dry and wet habitats. Young *P. virginialis* caterpillars use *L. arboreus* litter and foliage as their primary source of food at the study site.

Platyprepia virginialis is univoltine at the reserve. Eggs are deposited on vegetation during summer, and early instars hatch and feed in the litter during summer and fall. Young caterpillars are inconspicuous in the litter and move little; they are vulnerable to predation by ants during these early instars (Karban *et al.*, 2013). In February, more conspicuous later instar caterpillars move up onto the vegetation and feed on living leaves. Later instars become far more generalist in their choice of food and ultimately move from the wet sites that act as population sources to drier sites that do not commonly support young caterpillars (Karban *et al.*, 2012b). These larger caterpillars are not vulnerable to attack by ants under most circumstances. Caterpillars pupate in vegetation in late spring, during which time they suffer high rates of predation by mice and ants (Grof-Tisza *et al.*, 2015).

Platyprepia virginialis is found throughout western North America although its distribution is patchy and generally associated with wet habitats (Ferguson *et al.*, 2000; Opler *et al.*, 2014). Caterpillars are relatively tolerant of cold temperatures and survive above 50° latitude and 2000 m elevation. Other species of Arctiids are known to be capable of surviving in very cold environments (e.g. Layne, 2005).

Our initial assumption during prior studies was that ants were not particularly abundant or necessarily ecologically important in this system. Contrary to these impressions, *F. lasioides* is the most common ant species in the reserve, and it preys heavily on early instar caterpillars and pupae that are encountered by foraging workers (Harrison & Wilcox, 1995; Karban *et al.*, 2013). The distribution of *F. lasioides* is roughly similar to that of *P. virginialis*; it is widespread throughout western North America from sea level to over 3000 m (Ward, 2014). However, unlike *P. virginialis*, *F. lasioides* nests in the ground and is not associated with wet habitats (Ward, 2005).

Habitat- and temperature-dependent activity of *F. lasioides*

In order to learn about the habitat and thermal preferences of *F. lasioides*, four colonies were collected from the field site on 3 August 2013 and placed in 15-quart (14.21) plastic containers (model 3Q24; Rubbermaid, Atlanta, Georgia). Multiple queens and several hundred workers with brood were collected for each colony. Colonies were maintained in the lab and provided with water and a source of fat, sugar, and protein (pecan

shortbread cookies; Safeway, Pleasanton, California). Approximately 2–3 cm of local soil was placed at the bottom of each container, allowing the ants to construct nests.

We examined whether ants varied in their use of three different common habitat types on the reserve – wet litter, dry litter, and bare soil – at different temperatures. One of the colonies was moved in its container to a controlled environment chamber (Sanyo Versatile Test Chamber MLR-351H, Wood Dale, Illinois) and maintained on an LD 14:10 h. Three plastic deli containers (11 cm diameter) were placed on top of the soil inside the larger container that held the colony. The bottoms of the deli containers had been replaced with a fiberglass window screen mesh (with 1.1 mm spaces between parallel warp and weft). Ants but not caterpillars were able to pass through the mesh. One of the three deli containers had only a thin layer of soil, a second deli container had dry lupine litter, and a third deli container had lupine litter that was misted once a day, which kept it from ever becoming dry. Temperature was experimentally set at either 5, 10, 15, 20 or 25 °C on each day, and daily temperature was determined randomly so that each temperature level was replicated between 3 and 7 times ($n = 66$). The colony was maintained at the assigned experimental temperature for approximately 24 h, at which point we recorded the number of ants in each of the deli containers. For this experiment, we only used one *F. lasioides* colony because it had the largest number of active workers. We used different caterpillar individuals and different deli containers for each trial. We conducted an analysis of covariance on the mean number of ants in each deli container for the three microhabitats with temperature as a covariate. We tested two *a priori* hypotheses that containers with no litter would have more actively foraging ants than those with litter and that containers with dry litter would have more actively foraging ants than those with wet litter.

We evaluated the ability of ants to search for and attack caterpillar prey at varying temperatures. We estimated the critical thermal minimum (CT_{min}) for 25 workers of *F. lasioides* by subjecting them to decreasing temperatures and observing the temperatures at which coordinated movement stopped (Cowles & Bogert, 1944; Cerda *et al.*, 1998). Workers from a colony were placed individually into 1 of 16 cylindrical chambers (each 19 mm deep \times 5 mm in diameter) drilled into a copper block (38.5 \times 38.5 \times 25.5 mm³) and covered by a glass plate. The block was cooled using a thermoelectric plate (12 V, 40 \times 40 mm²) and a DC power supply (Mastech Single-Output DC Power Supply HY3003D, Pittsburgh, Pennsylvania). Temperatures were decreased from room temperature (25 °C) by 2 °C at a time. One thermocouple was placed on the outer edge of the copper block and a second thermocouple was placed in the centre of the block to monitor evenness of cooling. As a result of the high thermal conductivity of copper, temperatures across the block equilibrated within a few seconds. Ant activity was recorded for each temperature after the ants had been held at that temperature for 10 min. Each trial was stopped, and the CT_{min} was recorded when the ant became unable to attach to the copper wall and remained immobile at the bottom of the chamber. In addition to CT_{min} , we visually estimated each ant's ability to predate as the temperature was decreased, noting the temperature at which ants displayed impaired mobility.

Temperature-dependent activity of *P. virginialis*

We estimated the ability of caterpillars to forage and to escape predation at varying temperatures. We estimated the critical thermal minimum (CT_{min}) for 11 early instar caterpillars by subjecting them to decreasing temperatures and observing the activity. The procedure was similar to that described above for the ants except that caterpillars were placed individually in larger cylindrical chambers (each 19 mm deep \times 14 mm in diameter) in a copper block (38.5 \times 38.5 \times 25.5 mm³). Caterpillar movement within the cylinder was observed and recorded for each temperature. Each trial was stopped, and CT_{min} was recorded when caterpillars became unable to attach to the copper wall and remained immobile at the bottom of the chamber.

Habitat- and temperature-dependent predation of caterpillars

Rates of ant predation were measured in the lab by placing caterpillars so that ants could potentially find and consume them. Early-instar caterpillars were placed in deli containers as described above, and the deli containers were placed on top of the soil in the larger plastic containers that housed the four ant colonies. Window screen mesh on the bottom of the deli containers allowed ants to enter and exit but prevented the larger caterpillars from leaving. The inside walls of the deli containers were painted with fluon (Whitford dispersion #1, Elverson, Pennsylvania), which prevented the caterpillars from climbing out. Caterpillars were from a colony that was maintained at the Bodega Marine Laboratory.

One caterpillar was placed in each deli container, with three containers per ant colony. Rates of predation were assessed weekly by monitoring the presence or absence of the caterpillar. Often when the caterpillar was absent from the container, tufts of setae were left behind, indicating that predation had occurred. Colonies were maintained in a growth chamber with LD 14:10 h at 10, 15, or 20 °C, common temperatures at the field site. The deli containers either had no litter, a covering of the dry lupine litter or a covering of lupine litter that was misted with water every day to keep it moist. A fresh lupine leaf was added to each deli container every week to provide the caterpillar with food. Each trial was run for 1 week at which time survival of the caterpillar (presence/absence) was determined.

Caterpillar survival was analysed by fitting a generalised linear model in JMP 10.0 (SAS Institute, Cary, North Carolina) with an ant colony, temperature, and habitat (no litter, dry litter, or wet litter) as fixed effects. Each caterpillar was considered as an independent replicate and 108 caterpillars were tested. As three caterpillars were placed in each ant colony container each week (considered as a run), the caterpillars within a run may not be independent. However, including a run as a random blocking factor failed to improve the model fit (likelihood ratio test using glmer in R) and was not included in the final analysis. Presence/absence data were modeled with a binomial distribution using a logit link function and maximum likelihood estimation. None of the interactions between ant colony, temperature, and habitat were significant, and they were deleted from subsequent models. Three *a priori* hypotheses were tested using contrasts: caterpillars were hypothesised to have a

higher survival with wet litter than dry litter, a higher survival with wet litter than either dry litter or no litter, and a higher survival with any litter than bare soil (no litter).

Thermal conditions for *P. virginalis* in the field

To evaluate the field relevance of lab results, we recorded temperatures of 53 caterpillars in the field in April 2013 using an infrared laser thermometer gun (Metris Instruments, Los Gatos, California). Measurements were made between 11.00 and 16.00 hours on sunny days. Last-instar caterpillars were collected haphazardly from foliage, and temperatures were measured by pointing the gun at the black 'middle stripe' of each caterpillar from a distance of approximately 10 cm.

To evaluate possible effects of wet habitat on caterpillar temperatures, we assessed evaporative cooling on body temperatures for 33 last-instar caterpillars. Two temperature recordings were taken for each caterpillar, the first when the caterpillar was dry and the second immediately after misting the caterpillar with water from a spray bottle. A paired *t*-test was used to evaluate temperature differences between dry and wet caterpillars.

The effect of microhabitat on caterpillar body temperature was assessed by collecting 20 caterpillars haphazardly from vegetation and then placing them first on bare soil and then on top of litter (living and dead low vegetation that covered the soil). Two temperature recordings were taken for each caterpillar; temperatures were recorded 2 min after placing the caterpillar on each of the two microhabitats. A paired *t*-test was used to evaluate body temperature differences between caterpillars on bare soil and litter. The ambient temperatures of the soil and litter were also recorded.

We evaluated whether the temperatures that were being used in the lab experiments were temperatures that the caterpillars and ants were experiencing in wet and dry environments in the field. We recorded the minimum litter temperatures at five wet and five dry sites at the Bodega Marine Reserve using an iButton digital thermometer (Maxim Integrated, San Jose, California). Temperatures were recorded from 1 July 25 to August, when eggs hatch into caterpillars, and from 13 December to 31 January, when caterpillars are larger but still vulnerable to predation. We compared daily minimum temperatures for wet sites and dry sites using a mixed model with the site as a random factor using the 'nlme' package in R (Pinheiro *et al.*, 2015). Model fit was based on likelihood ratio tests (LRT). We also recorded the temperature once per hour every day at these sites and estimated the amount of time when temperatures were above and below 11 °C. We compared these field temperatures with our estimates of the temperatures at which the ants and caterpillars were mobile.

Results

Habitat- and temperature-dependent activity of *F. lasioides*

Ant activity varied by microhabitat (Fig. 1, the effect of microhabitat $F_{2,60} = 6.70$, $P = 0.002$). Even when the effects of temperature were removed, more ants were present in containers with dry litter than wet litter, and this effect was marginally

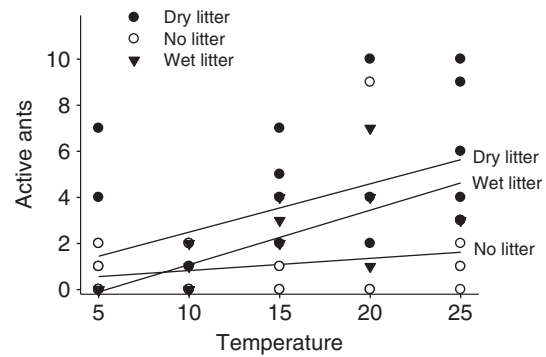


Fig. 1. Number of ants active in containers at different temperatures and microhabitats ($n = 66$).

significant (effect of microhabitat $F_{1,60} = 3.81$, $P = 0.055$). Contrary to our *a priori* expectation, fewer ants were observed foraging in containers with no litter than in containers with dry or wet litter (effect of litter $F_{1,60} = 7.95$, $P = 0.007$).

Ant activity also varied by temperature, declining as temperatures dropped. Ants were more active at higher temperatures, and few ants were seen foraging in the deli containers below 15 °C (Fig. 1, the effect of temperature $F_{1,65} = 17.6$, $P < 0.001$). This effect of temperature did not differ significantly among the three microhabitats (temperature \times habitat interaction $F_{2,60} = 2.36$, $P = 0.10$).

Differences in activity may have a physiological basis. All *F. lasioides* worker ants were active only when temperatures exceeded 11 °C. Below these temperatures workers were able to hold on to the sides of their copper chambers but displayed only limited mobility and were unlikely to be effective predators. Workers became immobile and unable to maintain their upright orientation at 2.1 ± 0.3 °C (mean \pm 1 SE). In conclusion, ants were unable to maintain activity at temperatures at which caterpillars moved and fed.

Temperature-dependent activity of *P. virginalis*

Caterpillars maintained activity at temperatures well below those where ants became inactive. All early-instar caterpillars moved around in the test chambers as temperatures decreased below 25 °C. The mean temperature (\pm 1 SE) at which they became noticeably less mobile was -1.4 ± 0.8 °C. They responded to pokes by moving until temperatures dropped to -4 °C. All movement stopped, and caterpillars dropped from the sides of the copper test cylinders at -5.6 ± 0.2 °C. All caterpillars recovered (that is, became able to move again as the temperature rose) after being exposed to -6 °C for 10 min.

Habitat- and temperature-dependent predation of caterpillars

Microhabitat affected the probability that caterpillars would be killed by ants (Fig. 2a, $\chi^2 = 9.7$, d.f. = 2, $P = 0.008$). Caterpillars were more likely to survive if they were on litter than on bare soil ($\chi^2 = 5.7$, d.f. = 1, $P = 0.02$). Litter quality also affected rates of predation; caterpillars were more likely to survive if they were

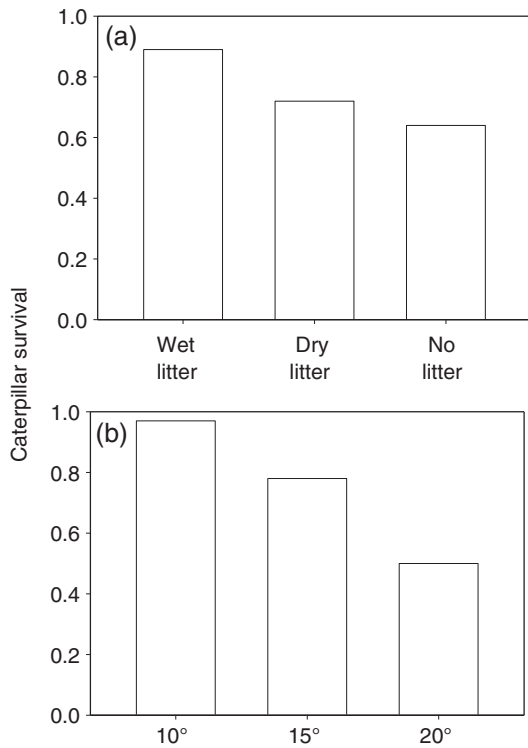


Fig. 2. The likelihood of caterpillars escaping predation when placed into the container with an ant colony under different (a) microhabitat and (b) temperature conditions.

on wet than dry litter ($\chi^2 = 4.7$, d.f. = 1, $P = 0.03$) and if they were on wet litter than on dry litter or bare soil ($\chi^2 = 8.8$, d.f. = 1, $P = 0.003$).

Caterpillars were also at a greater risk of predation at higher temperatures. More caterpillars were killed by ants at higher temperatures (Fig. 2b, $\chi^2 = 27.5$, d.f. = 1, $P < 0.001$). The four ant colonies varied in their rates of predation ($\chi^2 = 7.4$, d.f. = 1, $P = 0.007$) although interactions between ant colony and the other factors were not significant (data not shown).

Thermal conditions for *P. virginalis* in the field

Caterpillar temperatures closely matched temperatures of the substrate on which they were living in most cases (Fig. 3a). The temperature of a caterpillar on litter was not different from the temperature of the litter (95% CI: -1.9 to 0.5 °C different from the substrate). However, caterpillars on the bare soil were 4.9 ± 0.5 °C cooler than the temperature of the soil (95% CI: -3.8 to -6.0 °C different from the substrate). The effect of substrate on caterpillar temperature was large (mean difference in temperature between litter and bare soil = 9.4 ± 0.5 °C). Caterpillars were cooler on litter (living and dead vegetation) than on bare soil (paired t -test = 18.83, d.f. = 19, $P < 0.001$).

Caterpillar temperatures were influenced by the moisture in their microenvironments. Wet caterpillars were significantly cooler than dry caterpillars (Fig. 3b, paired t -test = 5.16, d.f. = 32, $P < 0.001$). However, the effect size was small

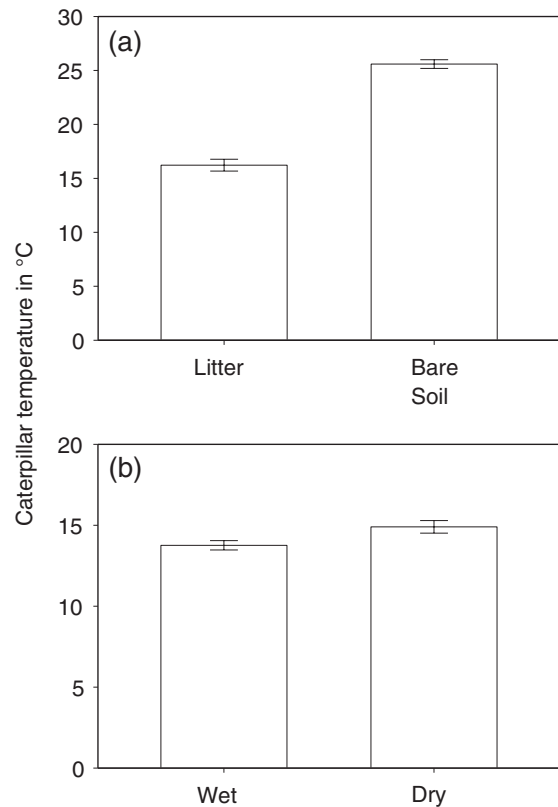


Fig. 3. Temperatures of caterpillars in different microenvironments in the field. (a) Caterpillars on litter and bare soil. (b) Dry caterpillars and caterpillars misted with water ('wet').

(the mean difference in temperature between wet and dry caterpillars = 1.1 ± 0.2 °C).

Ground temperatures at wet sites tended to be colder than at dry ones although this effect was relatively small and not statistically significant. During July and August, the mean daily minimum temperature was 14.4 °C for wet sites and 14.5 °C for dry sites ($LRT_{4,3} = 0.11$, $P = 0.74$). During December and January, the mean daily minimum temperature was 3.1 °C for wet sites and 4.4 °C for dry sites ($LRT_{4,3} = 3.035$, $P = 0.082$). Temperatures during December and January were below the 11 °C required for ant movement 66% of the time.

Discussion

In this study, caterpillars survived ant predation better under certain habitat and temperature conditions that may serve as refuges for the caterpillars. In this system, *F. lasioides* is an important predator of young caterpillars of *P. virginalis*. Early instar caterpillars were found most commonly in moist litter at wet sites (Karbon *et al.*, 2012a,b 2013). Ants also recruited more actively on litter than on bare soil (Fig. 1). There may be little chance of encountering food or other resources on the bare soil such that ants avoid it. However, ants were less active on wet litter than dry litter at all temperatures (Fig. 1). Most importantly, caterpillars experienced less predation in wet litter than in dry

litter or on bare soil (Fig. 2a). There are many potential consequences of wet litter for caterpillars; at minimum, wet habitats probably provide caterpillars with a refuge from *F. lasioides* predation although it may also slow their development.

All organisms have thermal limits that define the range of temperatures within which various activities are possible (Cowles & Bogert, 1944; Lutterschmidt & Hutchison, 1997; Rezende *et al.*, 2011). Many species interactions are possible only when the thermal requirements of the species overlap (Parmesan, 2006; Tylianakis *et al.*, 2008; Gilman *et al.*, 2010). For example, predators will only be effective when they can maintain high levels of activity. Ants are predators that may be strongly affected by the thermal regime (Cerda *et al.*, 1998; Cole *et al.*, 2010).

Formica lasioides was able to maintain activity above 11 °C whereas *P. virginalis* continued actively feeding and moving until temperatures dropped below 0 °C. The minimum critical temperature for ants was estimated at 2 °C and for caterpillars at -6 °C. These minimum critical temperatures are unlikely to be relevant to our field site where temperatures rarely drop below 0 °C (Barbour *et al.*, 1973). However, temperatures at the field site are below 11 °C for a majority of the winter months (<http://www.usclimatedata.com/climate/bodega-bay/california/united-states/>). For example, temperatures on the surface of the litter at the 10 study sites that were recorded in December and January 2013 were below 11 °C for 66% of the time. This difference in temperature-dependent activity may provide caterpillars with a thermal refuge where they are relatively unlikely to be depredated. Rates of survival for caterpillars in laboratory experiments increased from 50% at 20 °C to 97% at 10 °C (Fig. 2b). Temperature-dependent differences in activity by ants and caterpillars above and below 11 °C are likely to be far more important in shaping interactions than are minimum critical temperatures for these species.

The body temperatures of these insects were influenced by their environments. Caterpillar temperatures generally matched those of the substrate. However, caterpillars remained much cooler on litter than on bare soil (Fig. 3a). Whether or not caterpillars were wet had little influence on their body temperature (Fig. 3b). There may be other benefits of moist environments for caterpillars such as increased digestibility of food, a reduced risk of desiccation, and so on, that were beyond the scope of this study. Environmental influences on body temperature and different cold tolerance for predator and prey have two potentially important consequences. First, they may scale up to affect the distributions and population dynamics of these species (e.g. Kingsolver, 1989; Bale, 2010). *Platyrepia virginalis* is generally associated with cool, wet habitats across its range although it is capable of growing and surviving in a much wider array of habitats. For example, adults mate and oviposit in upland habitats although caterpillar survival is very low in most years at these sites (P. Grof-Tisza *et al.*, unpublished). By the time late instars become conspicuous, densities are greatly reduced in dry habitats, causing dry habitats to behave as population sinks (Karban *et al.*, 2012b). We hypothesise that greater rates of predation by ants in warm, dry habitats contribute to this habitat-specific demographic effect. This effect is likely to be accentuated by seasonal flooding, which is more frequent in low-lying wet

habitats and which may discourage nesting by *F. lasioides*. Recruitment of worker ants to baits was reduced in wet habitats compared with dry upland study sites (Karban *et al.*, 2013). We are currently testing the hypothesis that flooding events reduce ant populations and facilitate caterpillar survival and abundance.

Second, as a consequence of the different thermal tolerances of predators and prey, there may be habitats where prey can succeed but their predators cannot. These refuges require specific thermal conditions and microhabitats to create mismatches between predators and prey. Such thermal mismatches may provide small but persistent windows where prey populations can increase in most years. If prey are in fact dependent on these windows of favourable conditions, they may be at risk as seasons of above average temperatures and below average rainfall become more common. During the past few decades, the climate of coastal California has become warmer and less foggy (Weare, 2009; Li *et al.*, 2014), causing the local extirpation of insect species that rely on cool coastal conditions (e.g., Karban & Strauss, 2004).

In conclusion, abiotic conditions can allow caterpillars to escape their ant predators, or not. Continued changes in temperature and availability of moisture are likely to shift the outcomes of ecological processes such as the predator–prey interactions described in this study.

Acknowledgements

This work was conducted at the Bodega Marine Reserve, and we thank Jackie Sones and Suzanne Olyarnik for facilitating our fieldwork there. Louie Yang graciously allowed us to use his growth chamber. We thank Matthew Prebus and Jesse Karban for help in the field and Matthew Prebus, Marek Borowiec, and Phil Ward for suggestions and identifications of ants. This manuscript was improved by Marcel Holyoak. We were supported by NSF LTREB-0639885. R.K. designed the study, collected and analysed data and wrote the first draft, P.G.T. collected and analysed data, M.M. designed and conducted the CTmin experiments, and H.K. designed and analysed the iButton measurements. P.G.T., M.M., and H.K. edited the manuscript. M.H. wrote the final draft.

References

- van Asch, M. & Visser, M. (2007) Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology*, **52**, 37–55.
- Baffoe, K., Dalin, P., Nordlander, G. & Stenberg, J.A. (2012) Importance of temperature for the performance and biocontrol efficiency of the parasitoid *Perilitus brevicollis* (Hymenoptera: Braconidae) on *Salix*. *BioControl*, **57**, 611–618.
- Bale, J.S. (2010) Implications of cold-tolerance for pest management. *Low Temperature Biology of Insects* (ed. by D.L. Denlinger & R.E. Lee), pp. 342–373. Cambridge University Press, Cambridge, U.K.
- Barbour, M.G., Craig, R.B., Drysdale, R.R. & Ghiselin, M.T. (1973) *Coastal Ecology of Bodega Head*. University of California Press, Berkeley, California.
- Bourchier, R.S. & Smith, S.M. (1996) Influence of environmental conditions and parasitoid quality on field populations of *Trichogramma minutum*. *Entomologia Experimentalis et Applicata*, **80**, 461–468.

- Cerda, X., Retana, J. & Cros, S. (1998) Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. *Functional Ecology*, **12**, 45–55.
- Chown, S.L. & Nicolson, S.W. (2004) *Insect Physiological Ecology: Mechanisms and Patterns*. Oxford University Press, Oxford, U.K.
- Cole, B.J., Smith, A.A., Huber, Z.J. & Wiernasz, D.C. (2010) The structure of foraging activity in colonies of the harvester ant, *Pogonomyrmex occidentalis*. *Behavioral Ecology*, **21**, 337–342.
- Cowles, R.B. & Bogert, C.M. (1944) A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History*, **83**, 261–296.
- Durant, J.M., Hjermann, D.O., Ottersen, G. & Stenseth, N.C. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**, 271–283.
- Ferguson, D.C., Opler, P.A., Smith, M.J. & Donahue, J.P. (2000) *Moths of Western North America. 3. Distribution of Arctiidae of Western North America. Part 1. Text, Maps, and References*. Gillette Museum of Arthropod Biodiversity, Fort Collins, Colorado.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology and Evolution*, **25**, 325–331.
- Grof-Tisza, P., Holyoak, M., Antell, E. & Karban, R. (2015) Predation and associational refuge drive ontogenetic niche shifts in an arctiid caterpillar. *Ecology*, **96**, 80–89.
- Hance, T., van Baaren, J., Vernon, P. & Boivin, G. (2007) Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology*, **52**, 107–126.
- Harrison, S. & Wilcox, C. (1995) Evidence that predator satiation may restrict the spatial spread of a tussock moth (*Orgyia vetusta*) outbreak. *Oecologia*, **101**, 309–316.
- Huey, R.B. & Kingsolver, J.G. (1989) Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology and Evolution*, **4**, 131–135.
- Huey, R.B., Hertz, P.E. & Sinervo, B. (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *American Naturalist*, **161**, 357–366.
- Inouye, D.W. (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, **89**, 353–362.
- Karban, R. & Strauss, S.Y. (2004) Physiological tolerance, climate change, and a northward shift in the spittlebug, *Philaenus spumarius*. *Ecological Entomology*, **29**, 251–254.
- Karban, R. & de Valpine, P. (2010) Population dynamics of an arctiid caterpillar-tachinid parasitoid system using state-space models. *Journal of Animal Ecology*, **79**, 650–661.
- Karban, R., Grof-Tisza, P. & Holyoak, M. (2012a) Facilitation of tiger moths by outbreaking tussock moths that share the same host plants. *Journal of Animal Ecology*, **81**, 1095–1102.
- Karban, R., Grof-Tisza, P., Maron, J.L. & Holyoak, M. (2012b) The importance of host plant limitation for caterpillars of the arctiid moth (*Platyrepia virginialis*) varies spatially. *Ecology*, **93**, 2216–2226.
- Karban, R., Mata, T.M., Grof-Tisza, P., Cruisinger, G. & Holyoak, M. (2013) Non-trophic effects of litter reduce ant predation and determine caterpillar survival and distribution. *Oikos*, **122**, 1362–1370.
- Kingsolver, J.G. (1989) Weather and population dynamics of insects: integrating physiological and population ecology. *Physiological Zoology*, **62**, 314–334.
- Layne, J.R. (2005) Freeze tolerance and cryoprotection in caterpillars of the giant leopard moth (*Epantheria scribonia* Lepidoptera: Arctiidae). *Journal of Thermal Biology*, **30**, 267–271.
- Li, H., Kanamitsu, M., Hong, S.-Y., Yoshimura, K., Cayan, D.R., Misra, V. *et al.* (2014) Projected climate change scenario over California by a regional ocean-atmosphere coupled model system. *Climate Change*, **122**, 609–619.
- Lutterschmidt, W.I. & Hutchison, V.H. (1997) The critical thermal maximum: history and critique. *Canadian Journal of Zoology*, **75**, 1561–1574.
- Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007) Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, **10**, 710–717.
- Opler, P.A., Lotts, K. & Naberhaus, T. coordinators. (2014) *Butterflies and moths of North America* [WWW document]. URL <http://www.butterfliesandmoths.org/> [accessed on 1 April 2014].
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2015) *nlme: Linear and Nonlinear Mixed Effects Models*. R package, version 3.1-121. <http://CRAN.R-project.org/package=nlme>.
- Rezende, E.L., Tejedo, M. & Santos, M. (2011) Estimating the adaptive potential of critical thermal limits: methodological problems and evolutionary implications. *Functional Ecology*, **25**, 111–121.
- Singer, M.C. & Parmesan, C. (2010) Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B*, **365**, 3161–3176.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Ward, P.S. (2005) A synoptic review of the ants of California (Hymenoptera: Formicidae). *Zootaxa*, **936**, 1–68.
- Ward, P.S. (ed.) (2014) *AntWeb* [WWW document]. URL <http://www.antweb.org> [accessed on 8 May 2014].
- Weare, B.C. (2009) How will changes in global climate influence California? *California Agriculture*, **63**, 59–66.

Accepted 12 June 2015

First published online 16 July 2015