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THE SPATIAL DISTRIBUTION AND OVIPOSITION PREFERENCE OF THE RANCHMAN'S TIGER MOTH, *PLATYPREPIA VIRGINALIS* (LEPIDOPTERA: EREBIDAE)

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ABSTRACT. Despite decades of research on Ranchman's tiger moth (*Platyprepia virginalis*), little is known about the behavior and ecology of the adult life stage. To address this knowledge gap, we conducted surveys to quantify the spatial distribution of moths, and conducted laboratory and field oviposition assays as well as a field oviposition survey. We found that *P. virginalis* exhibits hill-topping behavior, a mate-locating strategy where individuals congregate on hilltops to increase the likelihood of sexual encounters. This behavior is common across many insect orders, but there are few examples of moths exhibiting this behavior. We found no evidence supporting our hypothesis that bush lupine (*Lupinus arboreus*), the primary larval hostplant within our study site, is the preferred oviposition hostplant. The opportunistic discovery of egg clutches on seaside daisy plants (*Erigeron glaucus*) led us to conduct a no-choice larval feeding assay to determine its suitability as a hostplant. We found that larvae reared on *L. arboreus* were more likely to survive compared to those reared on *E. glaucus*.

Additional key words: Hilltopping, Erebidae, mate choice, oviposition, larval survival

The Ranchman's tiger moth, *Platyprepia virginalis* (Lepidoptera: Erebidae) (Boisduval 1852), is a large, aposematically colored diurnal moth. The larva is covered with setae; late-instars are usually orange with a black band across the center part of the body with many long white hairs. *P. virginalis* ranges from Monterey Bay, California to Southern British Columbia and as far inland as Colorado (Ferguson 2000). Along the coast of California, the flight period most commonly extends from June through August. Eggs hatch shortly after oviposition in summer, but caterpillars do not become conspicuous until the following March and April, when they become large and mobile. To date, most of our ecological knowledge of *P. virginalis* comes from study of larval populations occurring within the Bodega Marine Reserve (BMR), Sonoma County, California. Researchers studying the population dynamics of the larval stage have assumed that the population is spatially structured into isolated sub-populations that correspond with the fragmented distribution of the primary larval hostplant, bush lupine (*Lupinus arboreus*: Fabaceae; English-Loeb et al. 1993, Karban and English-Loeb 1997). The density of caterpillars is highest and most temporally stable (i.e., less prone to localized extinction events) in patches of *L. arboreus* around low-lying, marsh habitat (Karban et al. 2012). This is due in part to lower predation rates of early instar caterpillars by ants in *L. arboreus* patches adjacent to marshes. Experiments demonstrated that the complex habitat substrate associated with marshes provides more predation refuges for young caterpillars (Karban et al. 2013).

Despite decades of research on this species, little is known about the biology and behavior of the adult life stage. Though a metapopulation framework has been used to understand the population dynamics of this system (e.g., Karban et al. 2012), the spatial distribution and dispersal ability of adult moths have never been determined. Similarly, despite the tight association between caterpillars and *L. arboreus*, it is not known whether this is the preferred oviposition plant. To address these knowledge gaps, we conducted surveys to quantify the spatial distribution of moths. We also conducted laboratory and field oviposition assays as well as an oviposition survey. Additionally, the opportunistic discovery of egg clutches on seaside daisy plants (*Erigeron glaucus*: Asteraceae) led us to conduct a no-choice larval feeding assay to determine its suitability as a hostplant.

MATERIALS AND METHODS

Adult Surveys

The initial distribution of tiger moths within BMR was determined using the line transect method (Pollard 1977). A network of transects was established across the reserve using established trails and walked weekly at a constant pace (10 m/min) between 10:00 and 15:00 hours during the 2010 and 2011 flight seasons (2010, June–September; 2011, June only). The GPS coordinates of moths encountered (within a 20m radius of observer) along transects were recorded as well as proximity to areas of local topographic prominence (hereafter hilltops). We manually classified observed individuals into those found on hilltops and those at least 20 m from the base of the hill (i.e., the lowest approximate contour line). To determine if moths occurred more frequently on hilltops, we compared the proportion of moths on hilltops to the proportion of surveyed habitat classified as hilltop using a Chi-square test.
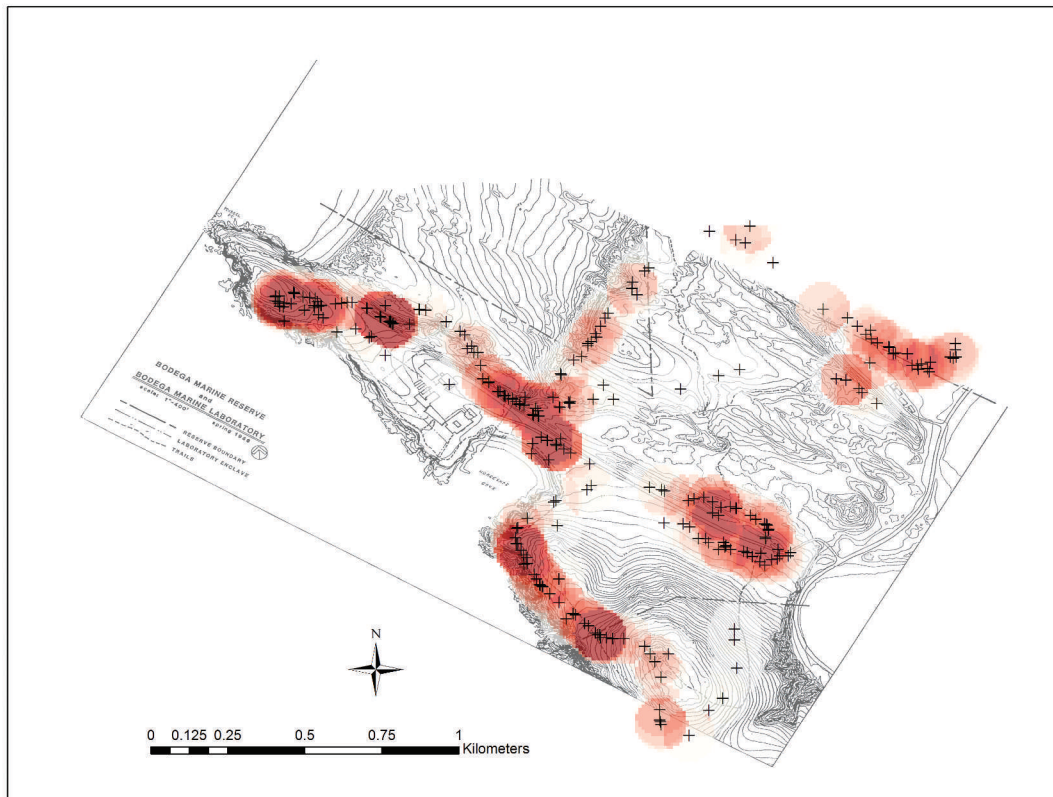
FIG. 1.Topographic map of the Bodega Marine Reserve showing moth encounters from Pollard transects. Shading intensity is directly proportional to moth density, as each encounter symbol may represent several individuals..

Oviposition preference and host plant suitability

Egg clutches are cryptic and we have rarely observed oviposition. Despite our working hypothesis that *L. arboreus* is the preferred oviposition plant due to the tight association of *P. virginalis* caterpillars with this plant, we observed three egg clutches on *E. glaucus* at one hilltop site. To test the oviposition preference of *P. virginalis* and the suitability of *E. glaucus* as a hostplant, we conducted laboratory and field oviposition assays, an egg transect survey and a no-choice larval performance assay.

We first tested oviposition preference using a choice assay in the laboratory. In June 2012, mating pairs of moths (n=11) were placed in small polyspun fiber cages with a plywood floor (30×30×50 cm). Bouquets of *E. glaucus* and *L. arboreus* of approximately equal mass were randomly placed on opposite sides of the cages and replaced every week. Moths were misted daily to prevent desiccation. Upon death of a female occupant (see Results for lifespan mean ± SD), cages were thoroughly searched for eggs. Similarly, bouquets were searched for eggs prior to replacement with fresh bouquets. Upon cage searches, we found that the majority of oviposion occurred on the walls of the cage and not on either plant species. Consequently this experiment was only used to estimate average female lifespan and total egg production.

In July 2012, we conducted an experiment examining oviposition preference. One large cage (1 m³), with an open bottom, was imbedded into the ground at 10 areas previously found to contain high densities of caterpillars (not hilltop sites). Within each cage, at least one small *L. arboreus* plant was present along with other naturally occurring plants. One pair of mating moths was placed into each cage. Upon death or escape of a female occupant, the cage and the naturally occurring vegetation was thoroughly searched for eggs. We recorded the number of eggs and the plant species on which they were found.

To determine natural oviposition preference, we conducted an egg survey by searching stems and leaves on all plants encountered along 23, 2×20 m transects. Transect locations within BMR are described by Grof-Tisza et al. (2015). To quantify larval performance on *E. glaucus* and *L. arboreus*, we conducted a no-choice field feeding assay from 30 July to 14 September 2012 in a

common garden experiment. Two-hundred and twenty, 2nd instar caterpillars were randomly caged on 11 *E. glaucus* and 11 *L. arboreus* plants (10 caterpillars/plant) where the ranges of these two plant species overlap within the reserve. Caterpillars were collected from a colony maintained in our laboratory at BMR prior to the experiment. Cages consisted of 10×15 cm sewn bridal veil mesh with a Velcro closure to prevent caterpillar escape. At the termination of the experiment, we recorded the number of caterpillars surviving. We used a generalized linear model (glm) to determine the relationship between the proportion of caterpillars surviving and host plant identity. The glm was fitted in R (version.3.0.2) using a quasibinomial error distribution (to account for over-dispersion) and logit link function (Crawley 2007).

RESULTS

Adult surveys

The density of moths censused in areas classified as hills (190 moths/ 56,540 m²) was approximately three-times greater than the density of moths in non-hill areas (65 moths/51,820 m²; χ^2 = 61.3, df = 2, P= <0.0001; Fig. 1).

Oviposition preference and host plant suitability

The average number of eggs laid per female over her life (21.1±7.4 days (mean ± SD)) was 355.0 ± 260.5 eggs (mean ± SD) across all treatments. High winds at our study site damaged all but 4 of our large cages, allowing moths to escape before oviposition. Due to the resulting low sample size, statistical analysis was not conducted. However, within the intact cages, eggs were found on *Potentilla anserina* ssp. *pacifica*, *Artemisia douglasiana*, and *Stachys rigida*. No eggs were found on *L. arboreus* in any of the cages. Similarly, no eggs were found on *L. arboreus* (n=81 plants) nor on any other plants during the oviposition field survey (the opportunistic finding of eggs on *E. glaucus* did not occur during the survey). In the no-choice larval assay, caterpillars were almost 2× more likely to survive when caged on *L. arboreus* than on *E. glaucus* (df=19, t=2.22, P=0.039; Fig. 2).

DISCUSSION

Platyprepia virginalis moths appear to exhibit hilltopping behavior, a mate-locating strategy where individuals congregate on hilltops to increase the likelihood of sexual encounters in populations occurring at a low density (Shields 1967). Hilltopping is common in butterflies and has also been observed in many other insect orders (Alcock 1987). Few examples of moths exhibiting this behavior have been documented (but see McFarland 1976, Holoway 1977). For most hilltopping species, males typically arrive first at summits and await
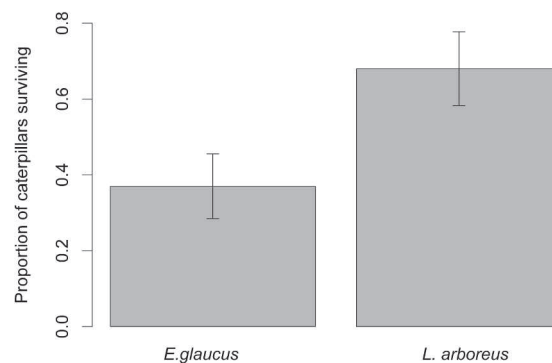

FIG. 2. Proportion of second-instar caterpillar survival in a no choice field feeding assay on *E. glaucus* and *L. arboreus*.

the arrival of virgin females. After mating, females descend to lower elevations to lay eggs. This behavior is consistent with the distribution of larvae within the BMR. Caterpillars are generally found at non-hilltop sites and often reach their highest densities in low-lying marsh habitat (Karban et al. 2012). Similar to what Baughman and Murphy (1988) found in their study of what constitutes a hill to a hilltopping butterfly, the hilltop sites varied in topographical prominence, from large hills rising 200 m above the surrounding landscape to small dunes of "seemingly insignificant topographical relief."

The opportunistic discovery of *P. virginalis* eggs at a hilltop site on *E. glaucus* deviates from the classic model of mated females descending from hilltops to oviposit on suitable hostplants. The no-choice feeding assay demonstrated that survival on *E. glaucus* was lower than on *L. arboreus*. The distribution of *E. glaucus* is generally restricted to coastal bluffs (i.e., hilltops), and *L. arboreus* is generally found within the coastal prairie (i.e., non-hilltop sites; Barbour et al. 1973). Indiscriminate oviposition across the landscape and across the hostplants available, coupled with habitat-dependent survival could account for the observed spatial distribution of larvae. Indeed, predator exclusion experiments showed that early-instar survival varies across habitats within BMR and is higher in marsh habitats (Karban et al. 2013). An alternative explanation for this seemingly suboptimal oviposition preference for laying eggs on *E. glaucus*, is that the few females involved could not return to non-hilltop larval patches due to injury, predation risk, or other limiting factors (Scheirs et al. 2000, Gripenberg et al. 2010).

Despite the close association between caterpillars and *L. arboreus*, we found no evidence to support the hypothesis that *L. arboreus* is the preferred hostplant for oviposition. In the field oviposition choice assay, only plants other than *L. arboreus* were chosen for oviposition, and no eggs were found on 81 *L. arboreus* plants that we destructively searched. During annual winter surveys, we generally observed 2nd -instar caterpillars on understory plants and not in the canopy of *L. arboreus* . Taken together, this evidence suggests that though late-instar caterpillars may prefer *L. arboreus*, it is likely not the preferred oviposition hostplant.

Most lepidopteran species are specialists (Futuyma and Moreno 1988). However, there are generalist lepidopteran species that use a broader range of hosts. Generalists tend to be fairly indiscriminate regarding hostplant choice (Shappes et al. 2015). Though late-instar *P. virginalis* caterpillars are predominantly found on *L. arboreus* at our study site, they are known to be polyphagous, and we have observed the species thriving at many sites throughout their range that lack this hostplant. Further, Karban et al. (2010) found that diet mixing enhances the performance of late-instar *P. virginalis* caterpillars. Considering that *P. virginalis* is not only polyphagous, but performs better on a mixed diet, it is not surprising that oviposition preference is not highly constrained. This is consistent with many generalist erebids that use a wide range of hosts for oviposition (Conner 2009).

Conclusion

This is the first documentation of hilltopping in *P. virginalis* and a rare example of a moth exhibiting this behavior. The multiple hilltop aggregation sites used by moths within the Bodega Marine Reserve are non-overlapping with larval habitat. We infer that our observation of the disproportionate distribution of moths on hilltops results from preference for those hilltop sites and not random movement (Baughman, Murphy and Erhlich 1988). Despite the tight association of *P. virginalis* caterpillars with *L. arboreus*, it is likely not preferred for oviposition.

Acknowledgements

Literature Cited

Alcock, J. 1987. Leks and hilltopping in insects. J. Nat. Hist. 21: 319 –328.

Barbour, M. G., R. B. Craig, R. R. Drysdale, and M. T. Ghiselin. 1973. Coastal ecology of Bodega Head. University of California Press, Berkeley, California, USA.

Crawley, M.J. 2007. The R book. John Wiley, Chichester, UK.

Conner, W.E. 2009. Tiger Moths and Woolly Bears: Behavior, Ecology, and Evolution of the Arctiidae. Oxford University Press.

Davy, B.J. 1902. Stock ranges of northwestern California. *In* US Department of Agriculture, Bureau of Plant Industry Bulletin 12. Washington DC Pp 1–81.

English-Loeb, G. M., A. K. Brody, and R. Karban. 1993. Host-plant-mediated interactions between a generalist folivore and its tachinid parasitoid. J. Anim. Ecol. 62:465–471.

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. 171 pp.

Futuyma, D.J, and G. Moreno. 1988. The evolution of ecological specialization. Annu. Rev. Ecol. Syst.19:207–233.

Gripenberg S, Mayhew PJ, Parnell M, Roslin T. insects. Ecol. Lett. 2010. A meta-analysis of preference–performance relationships in phytophagous insects. Ecol. Lett. 13:383–393.

Grof-Tisza, P., Holyoak, M. and R. Karban, 2015. Predation and associational refuge drive ontogenetic niche shifts in an arctiid caterpillar. Ecology 96: 80–89.

Holloway, J.D. 1977. The Lepidoptera of Norfolk Island: their biogeography and ecology. The Hague.

Karban, R., and G. English-Loeb. 1997. Tachinid parasitoids affect host plant choice by caterpillars to increase caterpillar survival. Ecology 78:603–611.

Karban, R., Karban, C., Huntzinger, M., Pearse, I. & Crutsinger, G. 2010 Diet mixing enhances the performance of a generalist caterpillar, *Platyprepia virginalis*. Ecol. Entomol. 35: 92–99.

Karban, R., Mata, T.M., Grof-Tisza, P., Crutsinger, G. and M Holyoak. 2013. Non-trophic effects of litter reduce ant predation and determine caterpillar survival and distribution. Oikos 122, 1362–1370.

Karban, R., Grof-Tisza, P., Maron, J.L. & M/ Holyoak, 2012. The importance of host plant limitation for caterpillars of the arctiid moth (*Platyprepia virginalis*) varies spatially. Ecology 93:2216–2226.

McFarland, N. 1976, Hilltopping and defence behaviour in a diurnal agaristid moth. Aust. Entomol. 3: 25–29.

Miller L.M. 1988. How yellow bush lupine came to Humbolt Bay. Fremontia. 16: 6-7.

Pickart, A.J, and J.O. Sawyer. 1998. Ecology and restoration of northern California coastal dunes. California Native Plant Society. Sacramento. California.

R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Found. for Stat. Comput.; 201.

Scheirs J, De Bruyn L, Verhagen R. 2000. Optimization of adult performance determines host choice in a grass miner. Proc. R. Soc. Lond. B. 267: 2065–2069.

Shapers, A., Sören, N. Carlsson, M.A., and J. Niklas. 2016. Specialist and generalist oviposition strategies in butterflies: maternal care or precocious young? Oecologia 180:335-343.

Shields O.1967. Hilltopping: An ecological study of summit congregation behavior of butterflies on a southern California hill. J. Res. Lepid. 6: 69–178.

Sholars, T. 1993. Lupines. The Jepson manual: higher plants of California. University of California, Press, Berkely. pg 622–236.