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Predation and associational refuge drive ontogenetic niche shifts in an arctiid caterpillar

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Abstract. Despite the ubiquity of ontogenetic niche shifts, their drivers and consequences are poorly understood. Different nutritional requirements and stage-specific physiological limitations have often been offered as explanations for these life history features, but emerging work has demonstrated that top-down factors may also be important. We studied the roles of predation and associational refuge in ontogenetic niche shifts for a holometabolous insect (ranchman's tiger moth *Platyprepia virginalis*), which shifts habitats and host plants to pupate. We examined the effect of pupation site selection across habitats and host plants by late-instar caterpillars on the rate of predation during the relatively vulnerable pupal stage. Studying the ontogenetic transition from mobile caterpillar to non-feeding, sessile pupa allows isolation of top-down effects from bottom-up, nutritional effects. An observational study supported previous findings that feeding caterpillars preferred marsh habitats, but pupating caterpillars preferred prairie habitats. Experiments demonstrated that caterpillars preferred to pupate within a physically defended plant species. Pupation within this defended plant species resulted in reduced predation (an associational refuge), and removal of the physical defense structures negated the reduced-predation effect. This experiment shows that ontogenetic niche shifts can be driven by predation and can involve facilitation by a host plant that provides a refuge to predation. The co-option of plant chemical defenses by animals is widely established. However, finding a clear example in which an animal exploits a plant's *physical* defense is rare, especially in the context of ontogenetic niche shifts. This work shows that facilitation mediated by refuge from predation provided by host plants and life-stage-dependent predation risk can interact to shape species' distributions.

Key words: arctiid caterpillars; associational defense; Bodega Marine Reserve, California, USA; bush lupine, *Lupinus arboreus*; complex life cycle; ecosystem coupling; holometabolous insects; ontogenetic habitat shift; predation refuge; pupal predation; ranchman's tiger moth, *Platyprepia virginalis*; thistle species.

INTRODUCTION

The course of development for nearly 80% of all animal taxa is divided into discrete ontogenetic stages that exhibit different morphological, physiological, behavioral, or ecological attributes (Werner 1988, Moran 1994). For a given organism, ontogenetic stages often use spatially distinct resources, resulting in a spatially stage-structured population. Movements to exploit stage-dependent resources are generally referred to as ontogenetic niche shifts (hereafter ONS; Wilbur 1980). ONS can have important effects at the population and community level (Werner and Hall 1988, Polis et al. 1997, Miller and Rudolf 2011). Moreover, a growing body of theoretical and empirical work indicates that ONS across habitat boundaries can indirectly couple ecosystems (Polis and Strong 1996, Sabo and Power 2002, Knight et al. 2005, Schreiber and Rudolf 2008).

Despite their prevalence and ecological implications, the drivers of ONS are still largely unexplored.

It is widely accepted that ONS are adaptations to different nutritional requirements and physiological limitations of life stages of different sizes (Moran 1994). However, both theory (Morris 2003) and recent empirical studies (Persson and Eklov 1995, Rudolf and Armstrong 2008) indicate that factors other than food, such as predation and predation refuges, are potential drivers. Theory predicts that organisms will shift niches if the ratio of growth potential to mortality risk is greater in an alternative niche (Werner and Gilliam 1984, Morris 2003). Generally, this concept is invoked when considering the importance of bottom-up factors mediating ONS. However, this same logic can be applied for top-down factors: given the ability to detect habitat-dependent mortality risk for a particular life stage, individuals will shift into less risky habitats. For example, Martin et al. (2013) demonstrated that agonistic interactions between differently sized life stages of the signal crayfish (*Pacifastacus leniusculus*

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Dana) led to ontogenetic stage structuring across two habitat types, pools and riffles. Mortality risk and inferior competitive ability of juvenile crayfish induced an escape response, resulting in their shift into riffle habitat. Many piscivorous fish species such as the Eurasian perch forage in the littoral zone of lakes during juvenile stages but shift into the pelagic zone once they reach a size threshold above which they are less vulnerable to predation (Mittelbach and Persson 1998, Woodward and Hildrew 2002). In these examples, the resource was not food, but refuge from predation (Sih 1987).

Many organisms exhibit continuous growth, in which juvenile and adult stages are morphologically similar except for a difference in body size and maturation of reproductive organs. Reaching the adult stage for such continually growing organisms is often associated with a change in resource use and trophic position (Kimirei et al. 2013). Because these developmental shifts are generally difficult to detect, organisms that metamorphose, such as holometabolous insects (which have morphologically distinct life stages and different resource requirements), are commonly used as model systems to study ONS. Additionally, although the fish and crayfish in these examples can actively assess risk and shift into less risky habitats, the pupal stage of holometabolous insects is sessile and consequently provides a good opportunity to isolate the effects of predation (Dick et al. 1990, Lucas et al. 2000). Predation of pupae by invertebrate and vertebrate natural enemies has strong effects on many lepidopteran populations (East 1974, Hunter et al. 1997, Hastings et al. 2002). Rodents, in particular, prey heavily on the pupal stage of many lepidopteran species (Varley and Gradwell 1960). However, the intensity of pupal predation often varies across habitats and host plants, an effect that is generally thought to be driven by spatial variation of natural enemy abundance (Hanski and Parvianinen 1985, Murphy and Lill 2010). The high predation rates experienced by pupae and the non-feeding, immobile traits of the pupal life stage provide an ideal opportunity to experimentally isolate and test top-down effects as contributors to ONS.

In this study, we explored the role of pupal predation and associational refuge driving ONS in an arctiid caterpillar (*Platyrepia virginalis*). During preliminary surveys, we found all *P. virginalis* cocoons in prairie habitat, which is also consistent with previous work indicating that prepupating caterpillars shifted from marsh to prairie habitat (Karban et al. 2012). An unexpected finding of the survey, however, was that the majority of cocoons were located on thistle species and none were found on bush lupine (*Lupinus arboreus*), the primary larval host plant at our study site. We tested multiple, non-mutually exclusive, hypothetical mechanisms for the ONS across habitats and host plants used for pupation (hereafter pupation plants). At the habitat scale, we tested for habitat-dependent pupal survival

independent of pupation plant and differences in natural enemy abundances across marsh and prairie habitats. At the plant scale, we tested for pupation plant preference and pupation-plant-dependent mortality. Given that thistles are physically defended, we hypothesized that thistles facilitate pupae by providing a refuge from predation (Bruno et al. 2003, Hughes 2012). Many herbivorous insects switch to host plants that provide protection from natural enemies under conditions of high predation pressure (Lima 1998). However, this is the first study that has explicitly examined the role of such facilitation in ONS, to our knowledge. We also tested for across-habitat linkages by determining whether the abundance of lupine and thistle as pupation plants varied across habitats. A higher density of pupation plants in one habitat could potentially drive ONS and link processes occurring across the habitat and plant scales.

METHODS

The study system

Surveys and experiments were conducted within the University of California's Bodega Marine Reserve (BMR), Sonoma County, California, USA. Bush lupine (*Lupinus arboreus*) is the predominant woody plant across BMR (Barbour et al. 1973) and is the primary larval host plant of the ranchman's tiger moth *Platyrepia virginalis* (Lepidoptera: Arctiidae) (English-Loeb et al. 1993). The demography of *P. virginalis* populations varies among habitats across BMR. Subpopulations in marsh habitat generally have higher caterpillar densities and are more temporally stable than those in prairie sites (Karban et al. 2012). Marsh sites are composed mostly of *Juncus* spp. rushes and poison hemlock (*Conium maculatum*) in the matrix between bush lupines and coyote bush (*Baccharis pilularis*), whereas the matrix in prairie habitat contains a diversity of grasses and forbs (Barbour et al. 1973). Both habitats contain native and exotic thistles interspersed between bush lupine and coyote bush, including bull thistle (*Cirsium vulgare*), Italian thistle (*Carduus pycnocephalus*), and milk thistle (*Silybum marianum*), the predominant thistle species within the reserve (A. Trusczyński, *personal communication*) (Appendix: Fig. A1).

Cocoon surveys

To determine the natural distribution of *P. virginalis* cocoons, we surveyed 23 transects (2 × 20 m) that were haphazardly selected in marsh ($n = 11$ transects) and prairie habitat ($n = 12$ transects). We thoroughly searched all vegetation located in each transect and counted the number of cocoons as well as recorded the plant species on which a given cocoon was found and the distance from the cocoon to the ground. For each transect, we estimated percent cover of forbs using a 1-m² quadrat and recorded the number of bush lupines searched.

To determine if cocoons occurred more frequently in particular plant species, we compared the proportion of cocoons in pupation plants to the proportion of those plant species using a chi-square test. For this analysis, we converted counts of bush lupine per transect to percent cover by multiplying the number of bush lupines by their average canopy area ($121.2 \pm 14.6 \text{ m}^2$, mean $\pm$ SE) and dividing by the total area searched (in m^2). We used generalized linear models (GLM) in R version 3.0.2 (R Development Core Team 2011) to test for differences in the percent of transect surface area covered by thistle and the number of bush lupines across habitat types as a fixed-effect factor. The function `glm` was used to fit both models. We used a quasi-binomial distribution and logit link function to model the percent thistle cover and a quasi-Poisson error distribution and log link function to model the number of bush lupines. The quasi-likelihood function was used to account for over-dispersion (Crawley 2007).

ONS across habitats

Predator exclusion experiment.—To determine that the shift in abundance of *P. virginalis* from marsh to prairie habitat was a result of movement and not differential predation, we compared the relative rates of pupal predation across marsh and prairie habitat. We also assessed the relative importance of vertebrate and invertebrate natural enemies in these habitats, independent of pupation plant, by conducting a predator exclusion experiment during June 2012. *P. virginalis* pupae were obtained by rearing field-collected caterpillars caged on bush lupine using spun polyester bags (Kleen Test Products, Mequon, Wisconsin, USA). Shortly after pupation, pupae were removed from the bags and kept in a cage until they were used in the predation experiments. To assess invertebrate predation in the field, half of the pupae were individually placed in lidded, plastic delicatesse containers (11 cm diameter) modified with a screen bottom (1.5-mm mesh) that allowed access by small invertebrate predators but not by vertebrate predators. To assess vertebrate predation rates, the same containers were used but were left unlidded. Previous experiments showed that spreading tanglefoot around the container rim was a poor barrier to ants and deterred mammalian predators. Consequently, we were not able to isolate the effect of vertebrates. The lidded ($n = 6$) and unlidded ($n = 6$) containers each containing a single pupa were placed under the edge of bush lupine canopies across prairie ($n = 9$) and all possible marsh sites ($n = 4$). Containers were situated such that they were equidistant from bush lupine stems and adjacent thistle plants. After 5 days, the number of containers that were missing pupae was recorded. The pupal stage of *P. virginalis* lasts for ~ 4 weeks (P. Grof-Tisza, unpublished data). All pupae used for this experiment were less than 2 weeks old and thus we are confident that all missing pupae resulted in predation and not eclosion.

Our model included treatment [lidded (invertebrates) or unlidded (vertebrates and invertebrates)] plus the following covariates recorded at each site to determine the best predictors of pupal predation: habitat type, vertebrate abundance, and ant abundance. Track plates, baited with *P. virginalis* pupae, were used to survey and assess the relative abundance of potential vertebrate predators of pupae. Track plates consisted of aluminum foil wrapped around 30×30 cm ceramic tiles. A thin layer of mineral oil was used to coat the aluminum sheet prior to dusting the coated surface with the tracking medium, talcum powder. Track plates were haphazardly placed at all sites and collected 5 days later. Presence/absence of the pupal bait and number of vertebrate prints were recorded. Ant abundance was estimated over two census days by placing a cotton ball saturated with a sucrose solution and 1-cm^3 of a protein source (Oscar Mayer hot dog, Kraft) on a petri dish at each site and recording the number of ants of each species on the dish after 3 hours. Prior to modeling the data, a correlation matrix between explanatory variables was constructed to check for multicollinearity.

Generalized linear mixed models (GLMM) were used to model the proportion of pupae remaining, with treatment, habitat type, rodent abundance, and ant abundance as fixed factors and site as a random effect. The GLMM was fitted in R (version 3.0.2) with the function `glmer` using a binomial error distribution and logit link function using the Laplace approximation (Breslow and Clayton 1993). Employing a stepwise deletion approach from the maximal model, the minimal adequate model was selected, which consisted of significant terms assessed by residual deviances to the chi-square distribution with residual degrees of freedom (Crawley 2007). We used *t* tests to compare ant and vertebrate (i.e., track plate prints) abundance across marsh and prairie habitat.

ONS across plants

Mesocosm experiment to assess caterpillar foraging choice and pupation plant preference.—To test the hypothesis that more cocoons were found on thistle due to caterpillar preference, a choice experiment was conducted in mesocosms in a greenhouse. Mesocosms included a transplanted Italian thistle (*Carduus pycnocephalus*) and a young bush lupine of similar size planted in a 24 cm diameter flowerpot using soil from prairie habitat (Appendix: Fig. A2). Because many cocoons were found in *C. pycnocephalus* during surveys, it was selected for this experiment. One late-instar *P. virginalis* caterpillar was added to the surface of the soil in each pot ($n = 28$). The location of each caterpillar (bush lupine, thistle, or on soil) was recorded twice a week until pupation. After removal of intact cocoons, mesocosms in which caterpillars had pupated within the first week of the experiment were reused ($n = 4$). The proportion of time that caterpillars spent foraging on each plant species and its associated confidence interval

were estimated by building a GLMM intercept model. The GLMM was fitted in R (3.0.2) with the function `glmer` using a binomial error distribution and logit link function using Laplace approximation (Breslow and Clayton 1993). To account for multiple measures of individuals and possible cues left behind by previous caterpillars, “caterpillar” and “mesocosm” were used as random effects. A similar model was constructed to determine pupation preference using “mesocosm” as a random effect to account for the nonindependence of the four reused mesocosms. One caterpillar failed to pupate during the experiment and thus was not included in the pupation analysis.

Effect of plant species and physical defenses on pupal predation

To test the hypothesis that more cocoons were found in thistle than in bush lupine due to plant-dependent mortality of pupae, we glued *Orgyia vetusta* (Lepidoptera; Lymantriidae) pupae ($n = 50$) to the stems of haphazardly selected bush lupine and thistle in July 2012. The height of pupal attachment above the ground was within 1 SD of the mean height of naturally occurring *P. virginalis* cocoons found during surveys. The number of pupae remaining was recorded after 72 h of predator exposure. This experiment was repeated in July 2013 using 44 *P. virginalis* pupae. We used *O. vetusta* pupae as a surrogate due to limited numbers of *P. virginalis* pupae in 2012; *O. vetusta* are common at our study site and share the same host plant (*L. arboreus*) as *P. virginalis* (Harrison and Wilcox 1995). Furthermore, statistical models showed that rodents consume *P. virginalis* and *O. vetusta* at similar rates (Fig. 5).

To test the mechanism by which physical defenses of thistles (prickles) provided refuge for pupae from vertebrate predators, we conducted a physical defense removal experiment and a physical defense addition experiment. In the addition experiment, we haphazardly selected 60 bush lupine plants and assigned half to either a treatment or a control group. The treatment group was given a simulated physical defense, which consisted of a $5 \times 5 \times 2$ cm Styrofoam panel with implanted, protruding sewing pins to replicate thistle prickles at a biologically relevant density and length. Pin density and length for the addition experiment are similar to prickles that are naturally occurring on *C. pycnocephalus*: 0.48 pins per cm vs. 0.58 ± 0.08 prickles per cm (mean $\pm$ SE); 10 mm pins vs. 10.2 ± 0.67 mm prickles length (mean $\pm$ SE); see Appendix: Fig. A3. The control group received Styrofoam panels without pins. After gluing a pupa to the center of each panel, we glued the panel to the stem of each plant within 1 SD of the mean height of cocoons found during surveys.

In the removal experiment, we clipped prickles from the bottom half of 23 haphazardly selected thistles using surgical scissors and selected 25 unclipped controls (Appendix: Fig. A4). We then glued one pupa to each

FIG. 1. The number of *Platyprepia virginalis* (ranchman's tiger moth) cocoons found across (a) habitats and (b) host plants where 20 transects of 20×2 m were destructively searched in the study area at Bodega Marine Reserve, California, USA.

plant within 1 SD of the mean height of cocoons found during surveys. For both experiments, we recorded the number of pupae remaining after 72 h of predator exposure.

For these experiments, we used generalized linear models (GLM) to explore the proportion of pupae remaining. The function `glm` was used to fit models in R (version 3.0.2) with a binomial error distribution and logit link function. For the plant-dependent mortality experiment, plant species was included as fixed effect. Using a stepwise deletion approach from the maximal model, the minimal adequate model was selected, which consisted of significant terms assessed by residual deviances to a chi-square distribution with residual degrees of freedom (Crawley 2007). For the physical defense manipulation, treatment (i.e., + or – prickles) was the only fixed effect.

RESULTS

Cocoon surveys

The distribution of cocoons varied across habitat type and was disproportionate to that of pupation plants. All cocoons were found in prairie habitat (Fig. 1; $\chi^2 = 22$, $df = 1$, $P < 0.001$), with 1, 4, and 17 cocoons found in a fern (*Pteridium aquilinum*), yarrow (*Achillea millefolium*), and thistle spp., respectively ($\chi^2 = 41.8242$, $df = 3$, $P < 0.001$). No cocoons were found in any bush lupine plants ($n = 81$) encountered in transects. Cocoons were located a short distance above the ground (26.5 ± 17.3 cm, mean $\pm$ SD). There was significantly higher cover of thistles ($t = 6.4$, $df = 22$, $P < 0.001$) and number of lupine bushes ($t = 3.6$, $df = 22$, $P < 0.001$) in prairie than in marsh habitat. The number of bush lupine per transect in marsh and prairie habitats was 1.36 ± 0.09 and 5.50 ± 0.11 lupines (mean $\pm$ SE), respectively. The proportion of thistle cover for marsh and prairie habitat

FIG. 2. Proportion (mean $\pm$ SE) of *P. virginialis* pupae remaining (a) after exposure to invertebrate predators only (vertebrate predators are excluded) and to both invertebrate and vertebrate predators ($n = 78$ pupae for each of the two treatments), and (b) in marsh ($n = 48$ pupae in four sites) vs. prairie habitat ($n = 104$ pupae in nine sites). Error bars based on parametric SE show the error across (a) sites and (b) habitats.

was 1.18 ± 0.4 and 8.33 ± 0.71 (mean $\pm$ SE), respectively.

Predation exclusion experiments

Access by predators to pupae was the most important factor influencing pupal mortality. However, we did not detect a difference in pupal predation across habitats (Fig. 2, Table 1). The proportion of pupae remaining after 5 days of predator exposure when rodents were excluded was 0.92 and when rodents had access was 0.38. There was an inverse relationship between the proportion of pupae remaining and ant abundance, but this factor was only moderately significant (Fig. 3, Table 1). Independent of pupal survival, track plate analysis indicated that rodent abundances were not detectably different across habitats ($t = 1.14$, $P = 0.3$), whereas there was a trend of higher ant abundance in prairie habitat ($t = 2.14$, $P = 0.056$). No adult tiger moths were observed to have eclosed in the vertebrate exclusion treatment (lidded containers), nor was there any evidence of eclosion in the open containers, confirming that pupae

absent from containers in the field were removed by predators.

Mesocosm choice experiment to assess caterpillar foraging and pupation plant preferences

Caterpillars were roughly two times more likely to be found on bush lupine than thistle while foraging (Fig. 4, Table 2). Although caterpillars preferred to forage on bush lupine, they were 2.4 times more likely to pupate on thistle ($n = 19$ caterpillars in 19 thistle plants) than on bush lupine ($n = 8$ caterpillars in 8 lupine plants).

Effect of plant species and physical defenses on pupal predation

Predation was dependent on plant species; pupae in thistle were 97% more likely to remain than those in bush lupine (Fig. 5, Table 3). Including insect species (*P. virginialis* and *O. vetusta*) as a factor did not improve model fit ($\chi^2 = -0.31$, $df = 1$, $P = 0.57$) and was consequently dropped from the minimal adequate model, which only included plant as a fixed effect. Not finding a difference between lepidopteran species suggests that *O. vetusta* is a reasonable surrogate for *P. virginialis* for pupal predation experiments.

Pupae in thistles where prickles were removed were 15% more likely to be consumed compared to a non-manipulated thistle control (Fig. 6, Table 4). The physical defense addition experiment in which we experimentally simulated prickles on bush lupine bushes did not reveal an effect on predation rates as compared to the control.

DISCUSSION

Ontogenetic niches shifts (ONS) are common across taxa and can have strong ecological effects (Polis et al. 1997, Sabo and Power 2002, Knight et al. 2005, Miller and Rudolf 2011). Yet until the last decade, empirical studies mostly focused on bottom-up factors as explanations for this life history feature (Moran 1994). Recent work, however, indicated that top-down forces can also favor ONS in some species (Rudolf and Armstrong 2008, Martin et al. 2013). Most of this research has focused on continually growing species that eventually reach a size refuge and become less vulnerable to predation. This change in vulnerability alters habitat-associated risk such that individuals often shift into previously risky habitats. For example, a study com-

TABLE 1. Results of generalized linear mixed-effects models for the minimal adequate model predicting proportion of pupae of *Platypreria virginialis* (ranchman's tiger moth) remaining.

Factor	Estimate	SE	Z	P
Lidded (intercept)	3.6415	0.9683	3.761	1.7×10^{-4}
Unlidded	-3.7438	0.9440	-3.966	7.32×10^{-5}
Ant abundance	-0.0473	0.0246	-1.927	0.0540

Notes: The maximal model included the following predictor variables: rodent abundance, ant abundance, treatment (unlidded vs. lidded), and habitat. All models included site as a random effect. Predictor variables not present in table were not significant at $P < 0.05$. Parameter estimates are on a logit scale.

FIG. 3. The relationship between ant abundance and proportion of *P. virginalis* pupae remaining ($n = 156$ pupae). Ant abundance was estimated over two census days by recording the total number of ants that recruited to a carbohydrate and protein bait after 3 h at each site. The fitted lines come from a general linear model with binomial errors and a logit link function (LMER model with site as a random factor fitted in R). The dashed line represents the 95% CI.

paring bottom-up and top-down drivers of ONS found that predation risk for three species of juvenile coral fish was the primary inhibitor of ONS into higher-quality adult habitat (Kimorei et al. 2013). Our study showed that an ONS occurred across habitats and host plants and that this shift was consistent with differences in predation risk at the host-plant scale. Our experiments showed differences in preference and in predation risk across pupation plant species, with predation differences resulting from physical plant defenses. Our work is novel in showing that the host plant facilitated pupal survival and that this was driven by physical plant defenses. The net effect was that refuge from predation for pupae provided by the host plant can explain the observed ONS and, hence, the distribution of *P. virginalis* through time.

ONS across habitats

Predation of pupae by invertebrates (Hunter et al. 1997) and vertebrates (East 1974, Hastings et al. 2002) is common and previous work has shown that the intensity of pupal predation can vary by habitat (Hanski and Parviainen 1985, Murphy and Lill 2010). Finding all cocoons in prairie habitat, coupled with previous work showing that pre-pupating caterpillars move out of marsh and into prairie habitat demonstrated that ONS occurred across habitats. However, contrary to our hypothesis, we did not detect habitat-dependent pupal predation (Fig. 2). The predator exclusion experiments indicated that rodents, and to a lesser extent ants, were the predominant pupal predators in this system (Fig. 2). We were unable to isolate

the effects of vertebrate predators, but assuming treatment additivity, 87% of the total pupal mortality was attributable to vertebrate predators, nearly seven times that of invertebrates. Effects of multiple predators may make actual levels of predation differ from these rates, which were calculated assuming that predators act independently (Sih et al. 1998). We failed to detect a difference in rodent abundance across habitats, but in congruence with a previous study (Kurban et al. 2013), we found a trend of higher ant abundance in prairie habitat, and marginally fewer pupae remained where ant abundance was higher (Fig. 3). However, the difference in ant abundance between habitats was not large enough to significantly affect pupal survival, as we did not detect an interaction between ant abundance and habitat.

One shortcoming of the predator exclusion experiment was its inability to distinguish between habitat-dependent predation resulting from differences in predator abundances and predation intensity. Hanski and Parviainen (1985) showed that pupal predation intensity of the pine sawfly (*Neodiprion sertifer*) varied across habitats due to differences in alternative prey items. Thus, although we did not detect differences in rodent abundance across habitats, we cannot rule out differences in habitat-dependent attack rates. Consequently, higher pupal predation intensity in marsh habitat could cause late-instar caterpillars to move out of marshes and into the less risky prairie habitat. However, our work at the plant level suggests that, at the very least, something else is occurring.

FIG. 4. The proportion of *P. virginalis* caterpillars (a) foraging ($n = 28$) and (b) pupating ($n = 27$) in a greenhouse mesocosm experiment where penultimate-instar caterpillars were placed on the soil in a flowerpot with two transplanted plants, bush lupine and thistle, and observed until pupation.

ONS across plants

Many holometabolous insects leave their host plants to pupate in alternative sites associated with reduced predation risk, because the pupal stage is particularly vulnerable to enemy attack (Price 1975, Dick et al. 1990, Lucas et al. 2000). Although other life stages can escape natural enemies or display defensive behaviors, pupae are sessile and depend on chemical defenses, physical

TABLE 2. Parameter estimates with 95% confidence intervals of generalized linear models for the proportion of caterpillars foraging and pupating on lupine and thistle in a mesocosm choice experiment.

Preference	Estimate	Lower (5%)	Upper (95%)
Foraging			
Lupine	0.6592	0.5720	0.7369
Thistle	0.3407	0.2631	0.4280
Pupating			
Lupine	0.2962	0.4900	0.1558
Thistle	0.7037	0.5100	0.8442

Note: Confidence intervals do not overlap 0.5, indicating that caterpillars prefer to forage in lupine but pupate in thistle.

FIG. 5. The proportion of *P. virginalis* (black bars; $n = 44$, in 2013) and *Orgyia vetusta* (gray bars; $n = 50$, in 2012) pupae that remained in three plants, bush lupine, and thistle, after 72 hours of exposure to natural predation. Each experimental plant received one pupa.

defenses, crypsis, or enemy-free space (such as pupating underground) to decrease predation (Soluk 1990, Brodeur and McNeil 1989). Our experiments and cocoon survey demonstrated that *P. virginalis* caterpillars shift host plants prior to pupating. The mesocosm experiment showed that caterpillars preferred to feed on bush lupine, but left it to pupate in thistle (Fig. 4). This finding was consistent with field survey results, which showed that thistles contained the highest proportion of cocoons (Fig. 1). In the predation experiments, experimentally affixed pupae in bush lupine were 97% more likely to be attacked than those located in thistle (Fig. 5). These findings show that caterpillars leave bush lupine to pupate in thistle, and when they do they are more likely to survive.

The pattern of pupal mortality in bush lupine and thistle plants was markedly similar to the cocoon distribution (Figs. 1 and 5). This observation supports the hypothesis that caterpillars choose plants for pupation that will minimize their risk of predation. Thus, it is likely that both caterpillar preference and the

TABLE 3. Results of generalized linear models for the proportion of pupae remaining in two different host plants after 72 hours of predator exposure.

Plant	Estimate	SE	Z	P
Lupine (intercept)	-2.1282	0.4731	-4.499	6.83×10^{-6}
Thistle	3.5686	0.6010	5.938	2.89×10^{-9}

Note: Parameter estimates are on a logit scale.

FIG. 6. The proportion of *P. virginalis* pupae that remained in an experiment where physical defenses were (a) removed from thistle and (b) added to bush lupine after 72 h of exposure to natural predation. Thistles were either left as controls ($n = 25$) or had their thorns removed ($n = 23$). Bush lupine were either left as controls ($n = 30$) or were given a physical defense ($n = 30$) by affixing a Styrofoam panel that contained a pupa surrounded by pins at a constant density to simulate thistle prickles.

predation risk associated with pupation plants play a role in generating the cocoon distribution.

Associational refuges, in which species susceptible to predation associate with those that are not, are common in plant communities (Hay 1986, Hughes 2012). Less common are examples in which animals exploit the structural defenses of other organisms, such as ants that use the thorns of *Acacia* host plants (Janzen 1966) and clownfish that seek refuge in the nematocyst-armed tentacles of sea anemones (Fautin 1991). We hypothesized that the survival advantage afforded by thistles to pupae was probably attributable to the plants' physical defenses, namely prickles. Testing this facilitation hypothesis, we found that the presence of prickles decreased the proportion of pupal predation, suggesting that thistles provide refuge to pupae (Fig. 6). This is the first study, to our knowledge,

to implicate facilitation as a driver of ONS. The facilitative effect of thistles was spatially and temporally dependent: spatially dependent because thistle abundance varied across habitats and temporally dependent because only the pupal stage of *P. virginalis* utilizes the predation refuge provided by thistle. Finding evidence for spatially dependent facilitation supports the maturing theory that positive species interactions, including commensalism (the likely relationship between *P. virginalis* and thistles) can shape community structure and composition (Bertness and Callaway 1994, Bruno et al. 2003). This spatiotemporal facilitation could couple marsh and prairie habitat dynamics. For example, an ecosystem subsidy, in this case the mass movement of caterpillars into prairie habitat, could potentially affect trophic control and temporal stability of prairie habitat food webs.

Across-habitat linkages

We found little evidence of a link between ONS occurring at the habitat and plant scales. There was eight times more thistle cover in prairie habitat than in marsh, which could potentially cause the observed shift of caterpillars out of marsh habitat if pupation sites were limiting (Karban et al. 2012). However, if this spillover effect were driven by contest competition and resource limitation, we would expect that the majority of thistles in marsh habitat would be occupied by cocoons. However, we found no cocoons in marsh habitat, suggesting that something other than habitat-dependent abundance of pupation plants was involved in the ONS from marsh to prairie habitat. One possible explanation of ONS across habitats is the interaction of habitat patch arrangement and pre-pupation behavior. Marsh habitat is embedded within surrounding prairie habitat. Thus, a correlated random walk by a caterpillar to increase distance between conspecifics would eventually result in the caterpillar transitioning into prairie habitat, regardless of the initial direction of movement. Clumped distributions of insects can produce an aggregative numerical response of predators and a shift from random search to area-restricted search by predators (Frazer 1988). Consequently, maximizing distance between conspecifics prior to pupating increases the likelihood of survival in some species (Hassell 1978).

TABLE 4. Results of generalized liner models for the proportion of *O. vetusta* pupae, a surrogate for *P. virginalis* pupae, remaining on thistle and bush lupine plants where prickles were removed (–), simulated with pins (+), or unmanipulated to serve as a control (intercept).

Defense status and plant	Estimate	SE	Z	P
Thistle (intercept)	2.3026	0.7416	3.105	0.0019
–Thistle	–1.7636	0.8810	–2.002	0.0453
Lupine (intercept)	0.1335	0.3660	0.365	0.715
+Lupine	0.8781	0.5517	1.592	0.111

Note: Parameter estimates are on a logit scale.

Conclusion

Thistles were physically defended non-preferred food plants that facilitated pupae by providing refuge from rodent predators. In contrast to many previous studies, this work shows that top-down factors can drive ONS for an organism that exhibits discrete stage structure. However, we contend that the relative influence of bottom-up and top-down factors contributing to ONS are probably stage and species dependent. This study also demonstrates the importance of facilitation and presents a novel interaction whereby an insect herbivore exploits the physical defense of a plant. Facilitation may be an understudied driver of ONS and, consequently, may play a larger role in food web dynamics and community structure than previously expected. This work shows that associational refuge and stage-dependent predation risk can interact to shape species' distributions.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: <http://dx.doi.org/>

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