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Intraplant Movement of Generalist Slug Caterpillars (Limacodidae: Lepidoptera): Effects of Host Plant and Light Environment

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ABSTRACT Insect herbivores frequently move about on their host plants to obtain food, avoid enemies and competitors, and cope with changing environmental conditions. Although numerous plant traits influence the movement of specialist herbivores, few studies have examined movement responses of generalist herbivores to the variable ecological conditions associated with feeding and living on an array of host plants. We tested whether the movement patterns of two generalist caterpillars (*Euclea delphinii* Boisduval and *Acharia stimulea* Clemens, Limacodidae) differed on six different host tree species over 10 d. Because these tree species vary in the range of light environments in which they commonly grow, we also compared the movement responses of *E. delphinii* caterpillars to two contrasting light environments, sun and shade. For both caterpillar species, multiple measures of movement varied significantly among host tree species. In early censuses, movement rates and distances were highest on red oak and black cherry and lowest on white oak. Site fidelity was greatest on white oak and lowest on black cherry. Movement of both caterpillar species varied inversely with mean predator density on five of the six host trees. Other ecological predictors (e.g., leaf size and the density of other herbivores) were unrelated to movement. Light environment altered behavior such that caterpillars in the shade moved and fed more often, and moved greater distances, than caterpillars in the sun. Although the mechanism(s) promoting or inhibiting movement under these different conditions requires further study, the consequences of increased movement for caterpillar development and mortality from natural enemies are discussed.

KEY WORDS behavior, dispersal, foraging, herbivore, polyphagy

Most free-feeding insect herbivores are required to move about on their host plant during the course of development. Herbivores may move about the host plant for a variety of reasons, including local food depletion, feeding-based changes in food quality (i.e., local induced responses, Haukioja and Niemela 1979, Paschold et al. 2007), interactions with competitors and natural enemies, and the amelioration of stressful abiotic conditions (May 1979, Willmer et al. 1996). When herbivores are resting or molting, they may move away from damaged leaves to disassociate themselves from feeding-related cues (e.g., plant volatiles, frass, or physical damage) that increase their risk of attack by natural enemies (Heinrich and Collins 1983, Odell and Godwin 1984, Mauricio and Bowers 1990, Bernays 1997), but evidence for this is relatively scarce and somewhat contentious (Bergelson and Lawton 1988). Several studies have found that feeding damage tends to be overdispersed, which indicates that herbivores move frequently between feeding bouts, avoid previously damaged leaves, or both (Edwards and Wratten 1985, Mauricio and Bowers 1990, Wold and

Marquis 1997), but other studies have found no evidence for overdispersion of feeding damage (Bergelson and Lawton 1988). Finally, herbivore movement can be regulated by changes in insect hormones, such as juvenile hormone and ecdysone, that regularly occur before molting or when juvenile holometabolous insects enter the prepupal stage and exhibit characteristic “wandering behaviors” (Jones and Hammock 1985).

Intraplant movement by insect herbivores may also be strongly affected by host plant architectural traits, such as structural complexity, internode distance, leaf size, stem or twig diameter, and the distribution of plant physical defenses, such as trichomes (Levin 1973, Alonso and Herrera 1996, Valverde et al. 2001, Kaitaniemi et al. 2004, Riihimaki et al. 2006, Cribb et al. 2010). Most studies examining intraplant movement of insect herbivores have focused on how intraspecific variation in plant traits, such as trichome density (Wilkens et al. 1996), plant architecture (Kareiva and Sahakian 1990, Hanley et al. 2007), leaf age (Stamp and Bowers 1992), or induced plant defenses (Hoy et al. 1998, Paschold et al. 2007) alter movement patterns of specialist insects on a single host plant species. However, a few comparative studies have studied intraplant movement on multiple host plant species. Mauricio and Bowers (1990) showed that

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Pieris rapae (L.) caterpillars move greater distances on radish than on broccoli plants, and Hannunen and Ekblom (2001) demonstrated differential interplant mobility of a generalist mirid bug among wheat and mayweed host plants; these studies suggest that host plant differences may alter patterns of insect movement and foraging. Because both habitat- and host plant-mediated differences in movement are predicted to influence the fitness of generalist herbivores via their effects on herbivore growth rate and mortality (Nathan et al. 2008), investigations of the ecological determinants of herbivore movement are necessary to improve our understanding of herbivore foraging ecology and host use. In feeding on a diverse array of host plant taxa, generalist herbivores are likely to be exposed to the different microclimatic environments where these host plants grow.

One important environmental variable in forest environments is light availability; sharp contrasts in light environment commonly occur temporally and spatially due to the changing angle of the sun both diurnally and seasonally, overstory composition and structure, the occurrence of sun flecks, and light gap dynamics (Raich 1989, Chazdon and Pearcy 1991, Montgomery and Chazdon 2001, Battaglia et al. 2002). Although the consequences of variation in light availability for plant growth, survival, physiology, and plant defensive chemistry have been well-documented (Lambers et al. 2008), fine-scale responses of insect herbivores to light microenvironments have been infrequently characterized (Schultz 1983, Whitman 1987, Harrison and Fewell 1995, but see Perkins et al. 2008). Because insects are ectothermic, variation in local light environments can have important implications for their movement and behavior. Thermoregulation and the maintenance of water balance in insect herbivores are critical environmental challenges (May 1979, Huey and Kingsolver 1993) that have likely contributed to an array of adaptations, including shelter building (Willmer 1980, Lill and Marquis 2007), internal feeding (leaf mining and gall formation), polyphenism (Kingsolver and Wiernasz 1991, Kingsolver 1995), group feeding (Klok and Chown 1999), and stereotypical basking or light avoidance behaviors (Casey 1993). Due to its demonstrated macroevolutionary importance as a selective force, understanding how insect herbivores cope with temporal and spatial variation in irradiance can be useful in explaining patterns of host plant use and selection in nature.

The aim of this study was to test the null hypothesis that movement patterns of generalist caterpillars do not differ when feeding on a suite of ecologically and taxonomically diverse host plants. Although numerous plant traits are known to influence the movement of specialist herbivores, few studies have examined movement responses of generalist herbivores to the variable ecological conditions associated with feeding and living on a wide array of host plants. Because previous studies have found strong associations between movement and fitness, rigorously quantifying movement responses of generalists to the differing host plants and associated habitats they commonly

encounter is a critical first step in developing our understanding of the evolutionary ecology of host use in generalist herbivores.

Additionally, the few studies that have compared movement responses of herbivores among multiple plant species have focused on two plant species at a time. Here we test the movement responses of two generalist caterpillars on six different host plants. Our first experiment compared intraplant movement of two generalist caterpillars, *Acharia stimulea* Clemens and *Euclea delphinii* Boisduval (Limaconidae), on a suite of six co-occurring host tree species growing syntopically in a shaded understory setting. Our second experiment compared diurnal patterns of intraplant movement by one of these generalist caterpillars on a common host plant growing in two contrasting forest light environments.

Materials and Methods

Study System. We investigated the movement of two species of slug caterpillars (Lepidoptera: Limaconidae) native to the deciduous forests of the eastern United States: *A. stimulea*, commonly known as the saddleback caterpillar, and *E. delphinii*, known as the spiny oak-slug caterpillar (Wagner 2005). Both caterpillar species are polyphagous, feeding on a wide variety of trees and shrubs from at least eight plant families throughout their range (Wagner 2005), but both prefer smooth-leaved species (Lill et al. 2006). Larval development is protracted, requiring one to several months (Murphy et al. 2011). Both species are brightly colored and are defended as caterpillars (Murphy et al. 2010); spiny tubercles project from the caterpillar's dorsum and contain an urticating toxin that is released upon contact with potential predators. In the Washington D.C. metropolitan region, both species are reported to have only a single generation (although *E. delphinii* appears to be facultatively bivoltine; J.T.L. and S.M.M., unpublished data) and are categorized as late-season herbivores; adults fly in June and July and caterpillars are found from August through October (Murphy et al. 2011). Voucher specimens of moths of *E. delphinii* and *A. stimulea* are deposited in the Smithsonian Natural History Museum in Washington, D.C.

Field Experiment 1: Effect of Host Plant Species on Caterpillar Movement. In June of 2008, we marked 15–20 understory saplings of each of six common, co-occurring host plants—black cherry (*Prunus serotina* Ehrhart Rosaceae), American beech (*Fagus grandifolia* Ehrh.; Fagaceae), black gum (*Nyssa sylvatica* Marsh; Nyssaceae), pignut hickory (*Carya glabra* (Miller) Sweet.; Juglandaceae), northern red oak (*Quercus rubra* L.; Fagaceae), and white oak (*Quercus alba* L.; Fagaceae)—in Little Bennett Regional Park (Clarksburg, MD), a second-growth oak–hickory–beech forest. Each of the six tree species used in the study serves as a host for a variety of caterpillars in the family Limaconidae, including the two study species. All study trees were <4 m tall to allow us access to the entire crown of each tree. The total number of leaves

on each tree was recorded on 16 June, and any overlapping branches of adjacent trees were pruned to prevent lateral movement of experimental caterpillars to adjacent plants. The following week, five individuals of each of the six tree species were selected randomly from the larger set of marked trees and assigned to receive cohorts of either *E. delphinii* or *A. stimulea* for a total of 30 trees per caterpillar species (60 trees total).

Caterpillars used in the experiments were obtained from laboratory matings of locally collected moths and reared caterpillars from all six host plant species. Upon hatching, caterpillars were placed on a high quality common host plant, redbud (*Cercis canadensis* L.). Once the neonates had established and were actively feeding, cohorts of caterpillars derived from at least 10 different females were transferred to cut foliage from each of the six experimental tree species and allowed to feed and acclimate to their assigned hosts for approximately 2 wk before being transferred to the field.

On 30 June and 21 July of 2008, we placed five early-instar caterpillars of *E. delphinii* and *A. stimulea*, respectively, on each assigned tree in the field (5 caterpillars per tree \times 5 trees per plant species \times 6 plant species = 150 \times 2 caterpillar species = 300 total caterpillars); these dates were chosen to match the natural phenology of the caterpillar species in the field (Murphy et al. 2011). The caterpillars allocated to each tree were the offspring of at least two different females, with a maximum of three siblings per tree. Caterpillars were haphazardly placed on the leaves of separate branches using a paintbrush, distributing them throughout the crown to allow us to keep track of individuals (caterpillars cannot be marked). The body length of each caterpillar was measured to the nearest 0.1 mm with dial calipers, and these initial sizes were also used to distinguish among individuals. For each deployed caterpillar, the petiole of the leaf was marked with a loop of colored wire; we used a different color for each caterpillar placed on a tree. Each caterpillar was initially placed on the underside of its assigned leaf and monitored until it had adhered to the leaf. The only exception to this protocol was that caterpillars were initially placed on the top surface of pignut hickory (*C. glabra*), because the fine pubescence present on the underside of the leaves of this species inhibited the adherence of early instars. The mean (± 1 SE) initial sizes (body lengths) of *E. delphinii* and *A. stimulea* caterpillars were 3.54 ± 0.07 mm and 4.63 ± 0.07 mm, respectively. Limacodid instar number is variable (8–11; Nagamine and Epstein 2007), and cannot be reliably measured because head capsules are covered by the prothorax; therefore, body length is used as a proxy for developmental stage (Murphy et al. 2011). Before deploying experimental caterpillars, each tree was searched and any “wild” *E. delphinii* and *A. stimulea* caterpillars were removed. Natural densities of these caterpillars are extremely low (<0.1 caterpillar per 10 square meter foliage; Stoepler et al. 2011), and larval development is very slow; therefore, we are confident that no additional

“wild” caterpillars colonized the trees during the study.

We conducted whole-tree censuses after 1, 3, 8, and 10 d in the field for *E. delphinii* and 1, 3, 7, and 10 d in the field for *A. stimulea*. During each census, we recorded the status (present or absent), body length (to the nearest 0.1 mm), and position (top of the leaf, bottom of leaf, stem) of each caterpillar. During the first census, which was 24 h after placing the caterpillars in the field, we also recorded whether or not each caterpillar had fed upon its original marked leaf (early-instar caterpillars feed by skeletonizing the epidermis in small characteristic patches). The distance traveled (in cm) by each relocated caterpillar was measured by running a measuring string from the petiole of the previously occupied leaf, which was marked by the loop of colored wire, to the petiole of the currently occupied leaf; we followed the shortest linear path along the branches of the tree, which is a conservative estimate of actual movement trajectories, as caterpillars tend to meander. Identifying wires were moved to the new location for each relocated caterpillar.

To explore possible mechanisms that may explain differences in movement among host plants, we recorded the average leaf size for each host plant species, the average density of arthropod predators on each host plant, and the average density of other leaf-chewing herbivores on each host plant. Leaf size was hypothesized to affect caterpillar foraging patterns via its joint effect on substrate and food availability (Bell 1990). Scanned images of undamaged leaves ($N = 100$ per plant species) were collected from understory trees at the study site and leaf area was measured to the nearest 0.01 cm^2 using SigmaScan software. Caterpillar movement may also be affected by competition (direct or indirect) with other insect herbivores and is predicted to vary in response to perceived risk (Bell 1990), prompting us to examine host plant-specific predator densities post hoc. Mean arthropod predator and insect herbivore densities (per square meter foliage, based on leaf counts) were recorded based on visual censuses of additional marked trees ($N = 5$ trees per species) at the study site during two censuses in June and July of the previous year. Only chewing insect herbivores were considered, and these were identified to species; arthropod predators were identified to family and summed to derive predator densities for each individual tree.

Field Experiment 2: Effect of Forest Light Environment on Caterpillar Movement. In July of 2012, we marked saplings of a single host plant, white oak (*Q. alba*) found naturally growing in sunny light gaps ($n = 5$) and adjacent shaded understory forest ($n = 5$) at Little Bennett Regional Park. Light gap and understory habitats had been previously censused hourly from 9 a.m. to 4 p.m. to ensure they obtained a minimum number of hours of direct sun or full shade per day, respectively (mean, light gap—5.4 h sun per day, understory—6.3 h shade per day, Stoepler and Rehill 2012). On each of three sunny days (7 July, 12 July, and 16 July, 2012), we placed five late-instar,

lab-reared *E. delphinii* caterpillars onto each of the light gap and shaded understory trees for a total of 25 caterpillars per light environment per day (a different set of larvae was used each day). The body length of each individual was measured and recorded (mean \pm SD; body length: 15 ± 2 mm; caterpillar age: 44 ± 7 d old), and the original placement location of each individual caterpillar was marked with a uniquely colored plastic hair clip to allow us to track individuals. Caterpillars were placed on the top of a leaf and distributed throughout the sapling canopy. Caterpillars were allowed to acclimate for 15 min after deployment before observations began. Each day, a team of three to four observers censused all caterpillars approximately every 10 min during the peak daylight hours of 10 a.m.–3 p.m. ($n = 30$ – 40 censuses per caterpillar per day). At each census, we recorded the caterpillar's 1) position on the plant (top of leaf, bottom of leaf, stem or petiole), 2) behavioral state (resting, moving, or feeding), and 3) the distance moved since the previous census (in cm; using the shortest stem path, as described in the host plant species experiment). The hair clip marking each individual's position on the plant was moved to track the caterpillars as needed. We chose 10-min census intervals based on our preliminary observations that showed that caterpillars generally do not switch behavioral states within these short time periods.

Data Analysis. *Field Experiment 1: Effect of Host Plant Species on Caterpillar Movement.* Movement data were examined in several different ways. First, we calculated the "movement rate" as the distance moved per day. The number of days between censuses varied from 1 (for the first census) to 5 (average = 2.5 d for both experiments). Although we monitored caterpillar survival for several weeks, we only examined movement rate data for the first 10 d because caterpillar mortality on some host plants approached 50% by this time. Thus, we have a complete set of movement rate data from all six host plants for the first 10 d, which corresponds to four census periods. The only exception to this is that for *A. stimulea* we had to harvest the caterpillars from northern red oak (*Q. rubra*) after three censuses due to very high mortality rates; thus, analyses of host plant effects for *A. stimulea* in the fourth census only compared five of the six host plants. Because movement rate data were highly heteroscedastic, nonparametric ANOVAs (Kruskal–Wallis tests) were used to compare movement rates among host plants (for each census separately) and among censuses (for each host plant separately). Because nonparametric data use ranks, we report median values instead of means.

In addition to movement rate, we calculated the "cumulative distance" each caterpillar moved over the first two censuses (the first three days). These distances were also heteroscedastic, but were $\log_{10}(x + 1)$ transformed, which served to homogenize the variances (as indicated by nonsignificant Bartlett's Tests), and allowed us to compare the transformed means with one-way ANOVA. Means comparisons of these

transformed data were made using the Least Significant Difference (LSD) test (Zar 1999).

Many caterpillars failed to move at all between censuses; thus we also compared the frequencies of caterpillars showing "site fidelity." Caterpillars showing site fidelity remained on the same leaf or leaf cluster (adjacent leaves originating from the same meristem which could be accessed without traveling onto the woody stem of the plant). Here we combined binary data from all censuses (425 movement bouts for *E. delphinii* and 294 movement bouts for *A. stimulea*) to test for overall differences in the propensity of caterpillars to move between censuses on different host plant species. The number of relocated caterpillars that did versus did not show site fidelity on each host was compared among host plants using χ^2 contingency tables. To test the association between movement and our three ecological predictors, we regressed cumulative movement on average leaf size, predator density, and insect herbivore density calculated for each host plant for both *E. delphinii* and *A. stimulea* as well as for the combined data (since the two species showed similar trends).

Finally, the resting position of caterpillars on the plant when they were relocated during each census (top or bottom leaf surface or stem) was compared among host plants for each caterpillar species using χ^2 contingency tables.

Field Experiment 2: Effect of Forest Light Environment on Caterpillar Movement. Because movement data in this experiment were collected over a different time scale (consecutive 10-min censuses) resulting in a large number of short-duration censuses, we compared the propensity to move (and feed) between sun and shade light environments using the proportion of total censuses an individual was moving or feeding, respectively. These data were also highly heteroscedastic and were thus analyzed using nonparametric Mann–Whitney *U* tests. We also compared movement distances per census by individual caterpillars in sun and shade habitats using Mann–Whitney *U* tests. The position of caterpillars (top or bottom of leaf surface) was compared among light environments using χ^2 contingency tables. The number of caterpillars that did versus did not show site fidelity over the course of each day's observations was compared between light environments using χ^2 contingency tables.

Results

Overall, host plant species and forest light environment both had strong effects on caterpillar movement behaviors. Whether movements were quantified using categorical measures (site fidelity and proportion of censuses moving or feeding) or quantitative measures (movement rate and distance moved), caterpillars showed a significant response to both host plant and light environment. Moreover, host plant effects on movement variables were fairly consistent between the two generalist herbivore species examined.

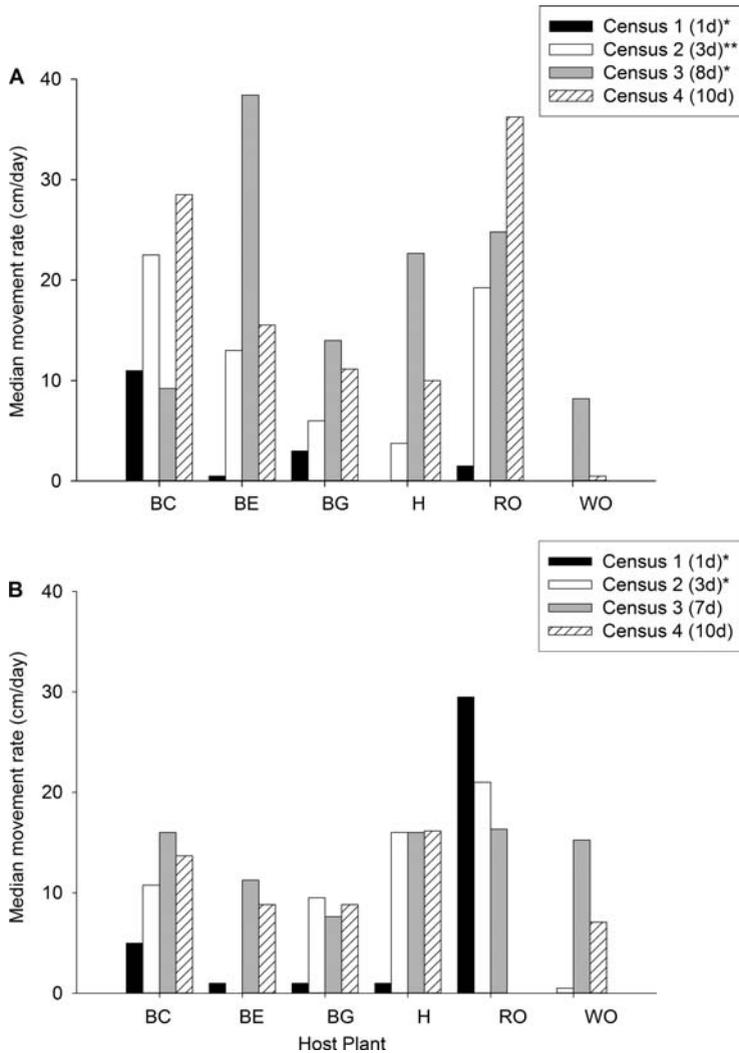


Fig. 1. Net movement rates of *E. delphinii* (A) and *A. stimulea* (B) caterpillars on each of six host plants during four census intervals. Bars depict the median movement rate (cm/d) of each caterpillar cohort since the previous census date. Host plants: BC, Black cherry; BE, American beech; BG, Black gum; H, Pignut hickory; RO, Northern red oak; WO, White oak. Censuses in which the movement rates differed significantly among host plants (results of nonparametric Kruskal-Wallis ANOVA) are indicated with an asterisk (*) in the figure legend (* $P < 0.05$; ** $P < 0.005$). Missing bars indicate censuses where the median movement rate was zero. Sample size ranges (means) for number of caterpillars, reflecting attrition rates: *E. delphinii*: Census 1, $N = 22-25$ (23.8); Census 2, $N = 16-24$ (19.2); Census 3, $N = 9-22$ (14.2); Census 4, $N = 9-21$ (13.7). *A. stimulea*: Census 1, $N = 12-25$ (20.5), Census 2, $N = 7-22$ (17.2), Census 3, $N = 7-18$ (13.0), and Census 4, $N = 11-17$ (14.2; no final census for RO due to high attrition rates).

Field Experiment 1: Effect of Host Plant Species on Caterpillar Movement. Average movement rates for *E. delphinii* caterpillars differed significantly among host plants for each of the first three census intervals (Census 1: $H = 11.44$, $df = 5$, $P = 0.043$; Census 2: $H = 15.87$, $df = 5$, $P = 0.007$; Census 3: $H = 11.33$, $df = 5$, $P = 0.045$; Fig. 1A). Cumulative mortality of caterpillars in both experiments dramatically reduced the sample sizes in later censuses, which likely reduced our power to detect host plant-specific differences in movement rates. After one day (census 1), the median movement rate of *E. delphinii* was highest on black

cherry (median movement = 11 cm) and lowest on white oak and pignut hickory (both of which had median movements of 0 cm). Between the first and second censuses, the median movement rate increased substantially for all host plants except white oak, which remained at zero. During this second interval, *E. delphinii* caterpillars on black cherry and northern red oak moved the most (median ≥ 20 cm/d). Movement rate calculated at the third census was highly variable, but peaked for four of the six host plants (American beech, black gum, pignut hickory, and white oak).

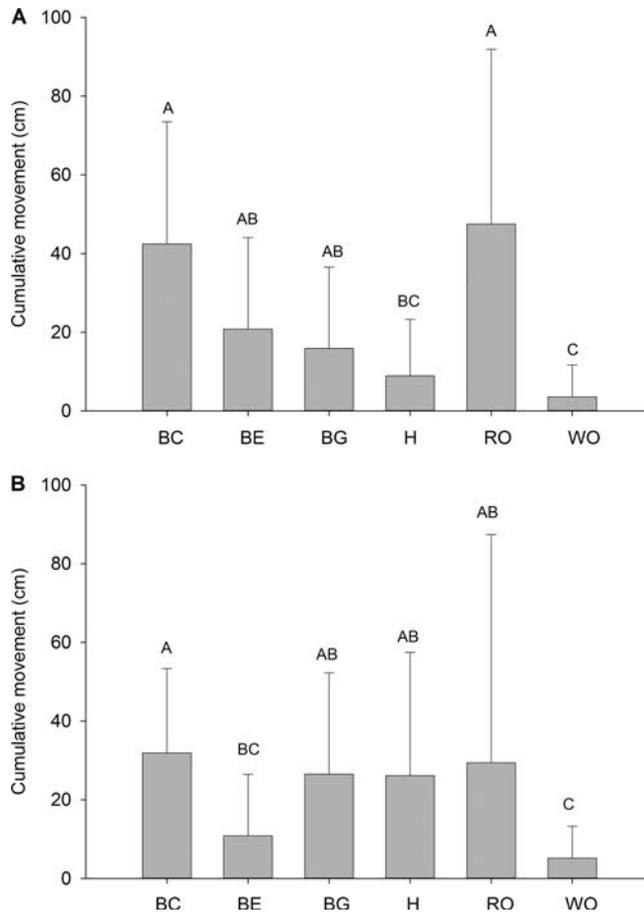


Fig. 2. Cumulative movement of individual *E. delphinii* (A) and *A. stimulea* (B) caterpillars on each of six tree species after 3 d. Data were $\log(x + 1)$ transformed before analysis to homogenize variances and analyzed with one-way ANOVA. Bars are back-transformed means and errors bars are + 95% CIs. Host plants: BC, Black cherry; BE, American beech; BG, Black gum; H, Pignut hickory; RO, Northern red oak; WO, White oak. Average cumulative-movement distances differed among host plants for both caterpillar species (*E. delphinii*: $F_{5,110} = 5.15$; $P = 0.0003$; *A. stimulea*: $F_{5,97} = 2.95$; $P = 0.016$). Means with the same letter were not significantly different based on the LSD means comparison test ($\alpha = 0.05$). Sample sizes are the same as in Fig. 1.

For *A. stimulea*, movement rates differed significantly among host plants for the first two censuses only (census 1: $H = 13.7$, $df = 5$, $P = 0.018$; census 2: $H = 13.02$, $df = 5$, $P = 0.023$) and were not significantly different for censuses 3 and 4 (Fig. 1B). For *A. stimulea*, the median movement rate in the first census was extremely high for northern red oak (>30 cm/d) compared with the other host plants. Once again, the median movement rate on white oak was 0 cm. During the second census interval, the median movement rate more than doubled for three host plants (black cherry, black gum, and pignut hickory), decreased slightly for northern red oak (which still had the highest rate), and remained very low for both white oak and American beech.

The cumulative distance moved by *E. delphinii* caterpillars over the first 3 d of the experiment also differed significantly among host plants ($F_{5,110} = 5.15$; $P = 0.0003$; Fig. 2A), with caterpillars moving the

farthest (>40 cm on average) on black cherry and northern red oak and the least (<10 cm) on white oak and pignut hickory (other host plants were intermediate). Based on the initial starting size of ≈ 3.5 mm, these data suggest that caterpillars on black cherry and red oak on average moved over 100 times their body length in 72 h. Cumulative movement of *A. stimulea* caterpillars over the same time period (3 d) also differed significantly among host plants ($F_{5,97} = 2.95$; $P = 0.016$) but followed a slightly different pattern; *A. stimulea* caterpillars moved similar average distances on red oak, black cherry, pignut hickory, and black gum, but moved significantly less on white oak and American beech (Fig. 2B). Although leaf size varied more than 10-fold between the tree with the largest leaves (pignut hickory; mean = 219 cm²) and that with the smallest leaves (black cherry, mean = 19.88 cm²), leaf size was unrelated to average cumulative movement of *E. delphinii* ($r^2 = 0.04$, $F_{1,5} = 0.17$, $P = 0.70$)

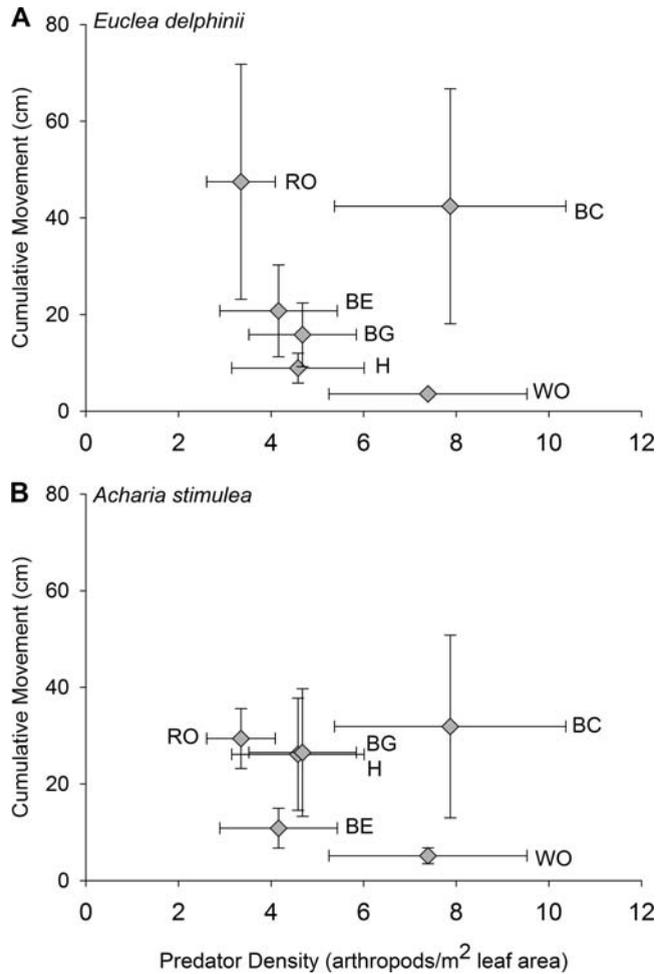


Fig. 3. Scatterplot depicting the cumulative movement of (A) *E. delphinii* and (B) *A. stimulea* during the first 3 d of censuses versus mean arthropod predator density recorded on five host plants per plant species. Means and standard errors are depicted with host plant symbols (BC, black cherry; BG, black gum; BE, American Beech; H, pignut hickory; WO, white oak; RO, red oak). Samples sizes for these means are given in Fig. 1. Linear regressions relating predator density and movement were performed for each caterpillar species separately and as a combined data set for both species. Explanatory power of initial models including black cherry, which was an obvious outlier, was low, but improved substantially when black cherry was excluded.

or *A. stimulea* ($r^2 = 0.05$, $F_{1,5} = 0.21$, $P = 0.67$). Similarly, the average density of other insect herbivores on each host plant was unrelated to cumulative movement of either species ($P > 0.50$ for both regressions). However, cumulative movement distance of both caterpillar species varied inversely with the average density of arthropod predators (which included jumping spiders, ants, assassin bugs, and lacewing larvae, all of which are known or likely predators of the early-instar larvae examined in this study) for five of the six host plants (Fig. 3A and B). With only 5 data points, our power to detect relationships is low, yet predator density explained 62 and 58% of the variation in cumulative movement for *E. delphinii* and *A. stimulea*, respectively (*E. delphinii*: $F_{1,3} = 4.83$, $P = 0.11$; *A. stimulea*: $F_{1,3} = 4.83$, $P = 0.13$), and combining the movement data for both species yielded a significant

negative relationship ($F_{1,8} = 5.19$, $P = 0.05$). In the initial analyses including all six host plants, predator density had very little explanatory power (*E. delphinii*: $r^2 = 0.05$, $F_{1,4} = 0.23$, $P = 0.65$; *A. stimulea*: $r^2 = 0.04$, $F_{1,4} = 0.18$, $P = 0.69$), but graphical investigation suggested that for both caterpillar species, black cherry was an obvious outlier. On this host plant, caterpillars had large cumulative movement distances despite high predator densities, so this host was excluded from final analyses.

Binary measures of site fidelity (whether caterpillars moved or not between censuses) for both caterpillar species were very high on white oak (57 and 62% of censused caterpillars did not move between censuses for *E. delphinii* and *A. stimulea*, respectively) and low on black cherry (only 15 and 21% of caterpillars remained at the same site between successive cen-

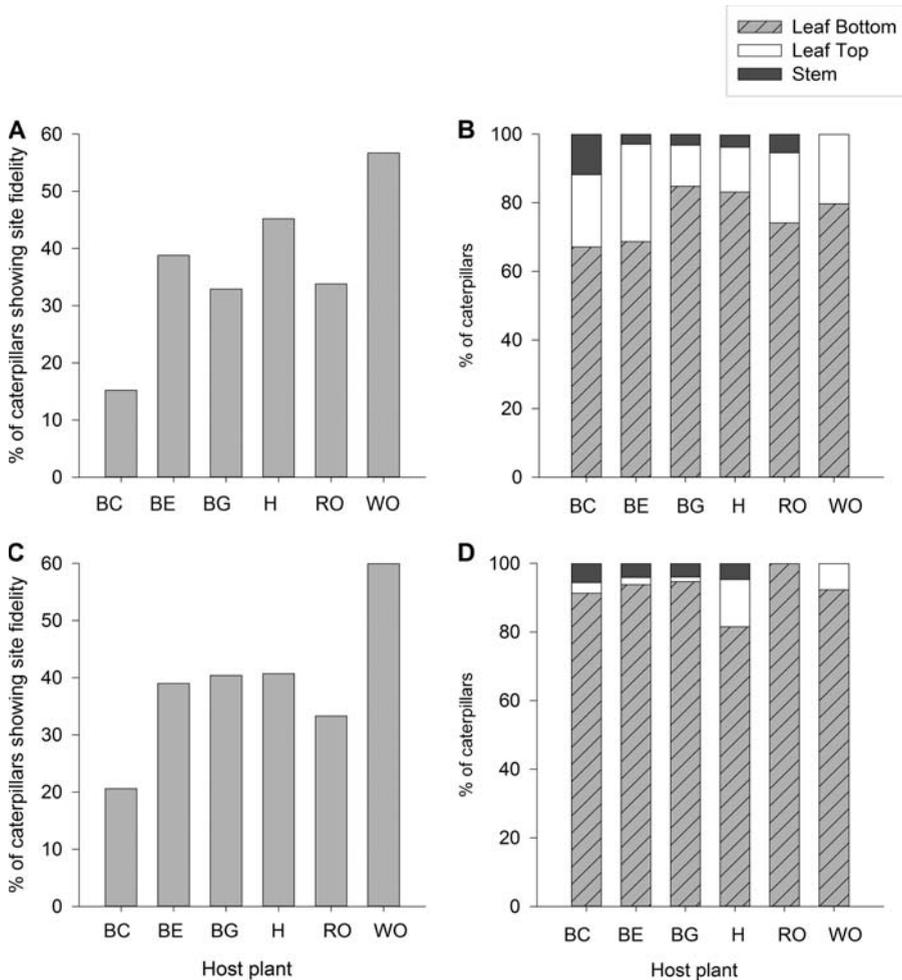


Fig. 4. Host plant effects on site fidelity of *E. delphinii* (A) and *A. stimulea* (C) caterpillars and position on the plant of *E. delphinii* (B) and *A. stimulea* (D) caterpillars. Site fidelity plots (A, C) depict the percentage of caterpillars that were relocated in the subsequent census on the same leaf or an adjacent leaf from the same leaf cluster. These caterpillars were considered to have demonstrated site fidelity whereas caterpillars moving away from the marked leaf (>1 cm distant) were considered to have moved. Movement bouts for each caterpillar species encompass the first four field censuses for *E. delphinii* (425 bouts) and the first three field censuses for *A. stimulea* (294 bouts). The degree of site fidelity differed significantly among host plants for both caterpillar species (*E. delphinii*: $\chi^2 = 31.5$, $df = 5$, $P = 0.0001$; *A. stimulea*: $\chi^2 = 20.44$, $df = 5$, $P = 0.001$), driven primarily by high site fidelity on white oak and very low site fidelity on black cherry. Plant position plots (B, D) depict the positions of relocated caterpillars on each host plant. Caterpillars of both species were initially placed on the bottom leaf surface on all host plants except for pignut hickory, which were initially placed on the top surface. Sample sizes of relocated caterpillars on each host plant range from 63 to 152 for *E. delphinii* and from 65 to 127 for *A. stimulea*. Host plants: BC, Black cherry; BE, American beech; BG, Black gum; H, Pignut hickory; RO, Northern red oak; WO, White oak.

suses for *E. delphinii* and *A. stimulea*, respectively), as indicated by a highly significant host plant effect for both *E. delphinii* ($\chi^2 = 31.5$, $df = 5$, $P = 0.0001$) and *A. stimulea* ($\chi^2 = 20.44$, $df = 5$, $P = 0.001$; Fig. 4A and C). Site fidelity was intermediate and varied little among the other host plant species.

Finally, comparing the positions of caterpillars on plant surfaces demonstrated that both species prefer feeding and resting on the underside of leaves compared with the more exposed top surface; however, *E. delphinii* was more likely to be found on top leaf surfaces than *A. stimulea* for all host plants except

pignut hickory (Fig. 4B and D). Notably, caterpillars were initially placed on the top surface of pignut hickory and most of the recorded instances of occurrence on the top surface occurred early in the experiment, yet $\approx 80\%$ of the individuals of both species were relocated on the bottom leaf surfaces, which suggests that any problems adhering to the bottom surface on hickory were limited to early instars. If we omit pignut hickory from the analysis (because of the starting position bias), we find that caterpillars did not alter their choice of resting positions based on the host plant species ($\chi^2 = 5.09$, $df = 4$, $P = 0.28$). There were

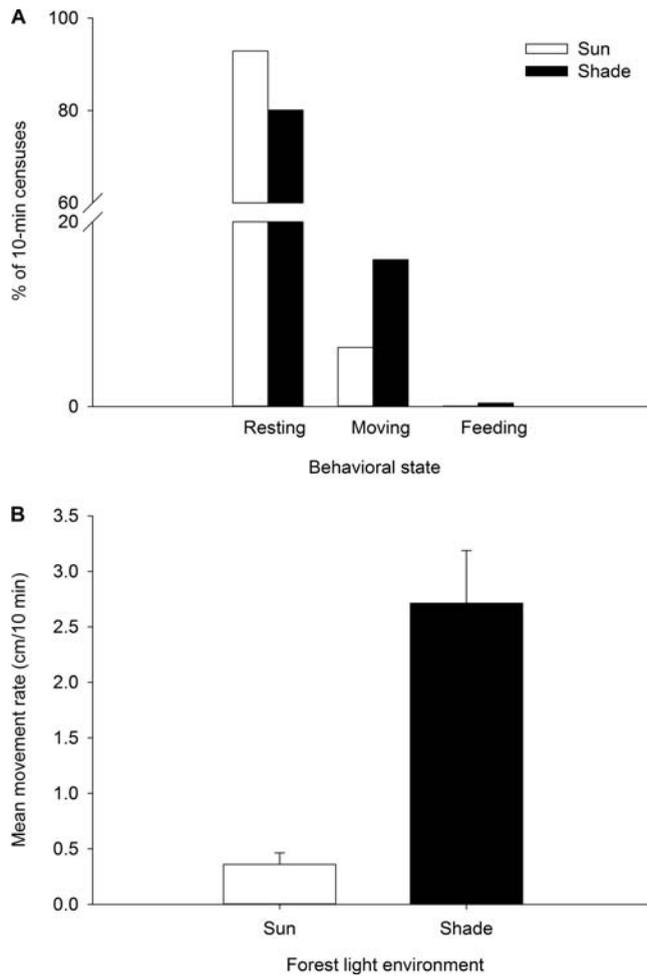


Fig. 5. *E. delphinii* caterpillar activity budget (proportion of censuses in which caterpillars were resting, moving, or feeding) (A) and individual movement rate (mean + SE cm/10-min) (B) on white oak saplings in contrasting forest light environments. White bars: light gap (Sun); black bars: shaded forest understory (Shade).

too few instances of individuals recorded on nonleaf surfaces (stems and twigs) to compare the likelihood of being found on leaf versus nonleaf surfaces (expected values <5 in contingency table). However, we noted that caterpillars of both species were found on stems of black cherry $\approx 12\%$ of the time, which is more than double that for any other host plant. Caterpillars on stems were presumed to be in transit between feeding locations as they were most often found moving.

Field Experiment 2: Effect of Forest Light Environment on Caterpillar Movement. The activity budgets of individual *E. delphinii* caterpillars differed between the light gap and understory (sun and shade, respectively) environments. Caterpillars in the shaded habitat had a greater frequency of moving and feeding than caterpillars in the sun (movement: $U = 14.45$, $df = 1$, $P = 0.0001$; feeding: $U = 8.54$, $df = 1$, $P = 0.0035$; Fig. 5A). Similarly, *E. delphinii* caterpillars in the shade moved 4.7 times greater distances per 10-min census, on average, than caterpillars in the

sun ($U = 18.22$, $df = 1$, $P < 0.0001$; Fig. 5B). In the sun, caterpillars were frequently observed in a posture similar to “stilting” (May 1979) in which they lifted the anterior portion of their body above the leaf surface (Appendix 1), a behavior also reported commonly in grasshoppers (Whitman 1987). This posture was never observed in caterpillars in the shade treatment.

The position of *E. delphinii* caterpillars differed by light environment ($\chi^2 = 419.1$, $P < 0.0001$). Caterpillars were more likely to be found on the top of the leaf in the sun and on the bottom (underside) of the leaf in the shade (Fisher exact test: $P < 0.0001$). Summed over all relocations, site fidelity of caterpillars was also 30% higher in the sun than in the shade ($\chi^2 = 4.27$, $P = 0.039$).

Notably, over the course of only 3 h (11:30 a.m.–2:30 p.m.) on 17 July 2012, we found caterpillars in the shade moved an average of 74 cm and two caterpillars moved >4 m. During this same period, caterpillars in the sun moved an average of 14 cm (81% less than in the shade), but one caterpillar moved almost 2 m. The

distance moved by individual caterpillars per 10-min observation period ranged from 0 to 145 cm in the shade and 0–42 cm in the sun.

Discussion

Our results indicate that both host plant species and light environment differentially affect intraplant movement of generalist slug caterpillars. In the host plant species experiment, we found differences in movement among censuses which may reflect caterpillar ontogenetic changes that occurred as the experiment progressed (i.e., later instars likely needed to move and feed more to meet their nutritional needs); however, because we examined early instar caterpillars, these “census” effects were likely conservative and would likely be greater if we could follow the caterpillars over much longer time spans. Caterpillars feeding on two of the six host plants examined, black cherry and red oak, were considerably more vagile than caterpillars on other hosts, particularly white oak, where caterpillars of both species showed very high site fidelity. For those caterpillars that did move on white oak, however, movement rates and distances were considerable. The light environment experiment showed that caterpillars can move considerable distances even over very short periods (minutes to hours), and that caterpillars were more likely to move and feed rather than rest in shaded microhabitats compared with sunny ones. Furthermore, caterpillars moved at much greater rates in the shade compared with the sun. Together, our experiments suggest that even generalist caterpillars are selective in their choice of feeding or resting positions within the plant canopy.

Host plant effects on movement variables were fairly consistent between the two herbivore species examined, suggesting responses may be generalized. However, the factors promoting differential movement among the set of host tree species examined here appear complex and are likely multifaceted. Although leaf size seemed like a good predictor, due to the fact that caterpillars in later instars could become food-limited on small-leaved plant species before completing a feeding bout, we found no direct relationship between average leaf size and any of our measures of movement. Caterpillars feeding on the host plant with the smallest leaves, black cherry, did move frequently and had the lowest site fidelity, but high movement rates and distances were also recorded for red oak, which had the second largest leaf size. For late-instar *A. stimulea*, it is quite possible that a single leaf of one of the smaller-leaved species, such as black cherry or black gum, could be consumed in a single feeding bout (J.T.L., personal observation), which would presumably prompt the caterpillars to move and which would eliminate the caterpillar’s substrate. However, in our many years of collective observations of tree-feeding slug caterpillars, we have rarely observed caterpillars consuming entire leaves when left to move freely on a host plant; rather, caterpillars tend to disperse their feeding damage among multiple leaves as has been

reported in other studies (Edwards and Wratten 1985, Mauricio and Bowers 1990, Wold and Marquis 1997). Similar experiments with later instar caterpillars (which are more likely to become food-limited than the early instar caterpillars examined in this study) would help to shed light on this issue. We also note that rapidly inducible defenses, which have been hypothesized to affect movement patterns in other systems (e.g., nicotine, Baldwin 1998), are not reported for these woody hosts (Karban and Baldwin 2007) so are unlikely to play an important role in determining host plant-specific movement patterns.

The negative trend relating cumulative movement distance and average predator density for both caterpillar species warrants further study. With the exception of black cherry, which appeared to be an obvious outlier in both experiments, there was a trend of cumulative movement varying inversely with average arthropod predator density. While our power to detect such a pattern was low, the clear negative trend found for both species (and significant relationship when data from the two species were combined), suggests that the presence of arthropod predators on a plant may inhibit caterpillar movement. Theory predicts that the “riskiness” of prey foraging behavior in the presence of predators should increase with declining physiological status or increasing food limitation (Preisser et al. 2005). While food limitation is unlikely to play a role in this system, encounters with potential predators or environmental cues of their proximity could inhibit movement. Planned field studies in which predator densities are manipulated and prey movement quantified are necessary to substantiate this pattern and to determine why caterpillars feeding on black cherry do not appear to demonstrate the same inhibitions. Similarly, the composition of the arthropod predator communities on each host and their use of these caterpillars as prey needs further study.

The consistently high site fidelity exhibited by both caterpillar species on white oak is notable; among the six host plants, white oak is host to the highest diversity and typically has the highest abundance of both other herbivores and predaceous arthropods. Although arthropod community data were not collected as part of the 2008 movement experiment reported here, community data derived from whole-plant censuses of understory trees located at the same study site during the previous summer (2007; 7–14 m² foliage surveyed per host plant) indicated that white oak hosts the highest density of other herbivores and the second highest density of arthropod predators relative to the other five host plants. In contrast, black cherry hosted the second highest herbivore density and the highest predator density, yet both caterpillar species had the lowest site fidelity on this host plant. Movement patterns of both caterpillar species on these two host plants were at opposite extremes, which precludes any simple explanation of caterpillar movement based on the co-occurring arthropod community. One feature that we noted as distinguishing white oak from the other host plants and that may have contributed to the

high levels of site fidelity was the availability of “hiding places” on white oak. Because of high levels of leaf damage and conspicuous numbers of galls and shelter-building caterpillars on white oak (Felt 1917, Lill and Marquis 2007), the foliage of white oak was perhaps the most three dimensional, with numerous pockets, leaf curls, and overlapping leaves that were used frequently as resting and molting sites by experimental caterpillars (J.T.L., personal observation). For this reason, relocating the deployed caterpillars on white oak often took the most time and searchers frequently “missed” caterpillars that were later discovered by additional searchers who carefully examined the same branch. While speculative, it is possible that the abundance and effectiveness of hiding places on white oak may have contributed to the high site fidelity demonstrated by both caterpillar species examined in this study. Experimental studies examining the movement responses of caterpillars exposed to varying shelter densities are needed.

We found that *E. delphinii* caterpillars moved and fed more frequently and moved at greater rates in the shaded forest understory compared with caterpillars in sunny light gaps. Previous research showed that *E. delphinii* caterpillars have up to a six-fold greater risk of being attacked by a parasitoid wasp or tachinid fly in light gaps compared with the understory in the same study sites and microhabitats used here (Stoepler and Lill 2013). Although specific information on host selection cues are lacking for the dominant parasitoid fly in this system, *Austrophorocera* sp. (Tachinidae), tachinid flies are thought to rely primarily on visual cues in host location, including host movement (Stireman 2002). Host movement is also an important cue for short-range host location by many parasitoid wasps (Godfray 1994). Although we cannot directly relate movement to parasitism risk in *E. delphinii*, if movement is associated with an increased risk of parasitism, caterpillars may be selected to move and feed less frequently in these “dangerous” light gap habitats, especially if they are more apparent to visually oriented predators and parasitoids in the sun (Bernays 1997, Rowland et al. 2008).

In addition to these tritrophic interactions, caterpillar behavior and movement differences in sun and shade are influenced by the ectothermic requirement to thermoregulate. Caterpillar movement is often decreased in sunny, hot environments (Casey 1976), and some caterpillars, particularly those with dark coloration, frequently bask in the sun to increase body temperature (Casey 1993). Notably, experimental caterpillars in the sun tended to remain on the top of the leaf in direct sunlight, suggesting that most individuals did not attempt to relocate to the underside of the leaf or a shaded section of the saplings in the light gaps. In contrast, most caterpillars in the host plant species experiment, which was conducted in the shaded understory environment, were relocated on leaf undersides. However, we note that the starting positions and the time scales differed in the two experiments, limiting our ability to make direct comparisons in caterpillar position between the experiments.

While there is clearly still much work to be done to substantiate the underlying mechanisms for these differential movement responses to host plant and light environment, the fitness consequences of caterpillar movement deserve additional consideration. Movement of any kind, and particularly the acts of feeding and defecating, have been shown previously to be extremely risky behaviors for caterpillars due to the visual and chemical signals they produce, which are major cues for natural enemies (Bernays 1997, Weiss 2006). Many caterpillars feed and move primarily at night when detection probabilities and predator foraging activities are often minimized (Heinrich 1979). Increased detection and encounter rates with natural enemies should select for caterpillars that minimize movements, that constrain movements, or both, under particularly risky ecological conditions (e.g., time of day, light environment, or perceived proximity to predator cues). Although theory predicts that herbivore movement should be minimized overall, our research demonstrates that movement patterns vary considerably among different host plant taxa and light environments. Future studies should explicitly consider the identity of the host plant as well as the microhabitat in influencing insect behavior and would be complemented by mechanistic studies examining the relative contributions of plant traits and local arthropod community composition on movement behaviors of a wider array of insect herbivores.

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Appendix 1. Photograph of an *Euclea delphinii* caterpillar in a “stilting-like” posture on a white oak (*Quercus alba*) sapling in a forest light gap. The head (left side) and anterior portion of the body is lifted above the leaf surface, possibly as a mechanism to cool the body by increasing air flow around it. “Slug” caterpillars (Limacodidae), including *E. delphinii*, normally maintain full ventral contact with the leaf surface as they move about. This posture was only observed in caterpillars in the sun (light gaps) and not in the forest understory (shade). A yellow plastic clip used to mark the caterpillar’s position on the sapling is visible in the foreground. Photo by Teresa Stoepler. (Online figure in color.)