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Temporal and Spatial Variations in Microclimate Influence the Larval Foraging Behaviors and Performance of a Conifer-Feeding Sawfly

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ABSTRACT Herbivorous insects are often exposed to broad temporal and spatial variations in microclimate conditions within their host plants and have adapted a variety of behaviors, such as avoidance or basking, to either offset or benefit from such variation. Field experiments were carried out to investigate the influence of daily and intratree variations in microclimate on the behaviors (feeding, resting, dispersal, and hiding) and associated performance of late-instar larvae of the yellowheaded spruce sawfly, *Pikonema alaskensis* (Rohwer) (Hymenoptera: Tenthredinidae) within crowns of 1.25–1.5 m tall black spruce (*Picea mariana* [Miller] Britton Sterns Poggenburg); late instars feed on developing shoots of young spruce and are often exposed to microclimatic extremes with unknown effects on performance. Larvae fed diurnally from just after dawn (0800 h) until dusk (2000 h) and rested throughout the night, with brief periods of dispersal occurring in the morning and evening. Neither larval behavior nor abiotic conditions differed significantly between the upper and lower crowns of trees. Temperature, humidity, and solar insolation all explained >90% of variation in feeding; however, sunrise and sunset were the most likely cues influencing diurnal behavior. Most larvae (94%) fed on the bottom, shaded side of shoots, and field experiments indicated that this behavior is adaptive with respect to microclimate, probably reducing hygrothermal stress. Thus, behavioral adaptations by *P. alaskensis* to daily and within-shoot microclimatic variation may reduce the risk of hygrothermal stress during dispersal or feeding, while still allowing larvae to feed on the preferred and highly nutritious upper crown foliage of young spruce.

KEY WORDS *Pikonema alaskensis*, intracrown, diel activity, diurnal, thermoregulation

The distribution and abundance of herbivorous juvenile insects is often shaped by complex tradeoffs among the sometimes competing imperatives to find and assimilate nutritious foliage, avoid natural enemies, and maintain body temperature within limits that promote rapid larval growth and development. Maintenance of body temperature may be a particular challenge for insects that, as ectotherms, lack the ability to regulate internal body temperature through metabolic heat production (May 1979). As a result, many insects have adapted morphological and behavioral traits that allow them to offset or harness local variations in microclimatic conditions, with associated consequences for physiological performance and interactions with host plants and natural enemies.

Most studies of insect adaptive responses to local weather have focused on immature lepidopterans, emphasizing the influence of microclimatic variations within host plants, seasons, and days on activities such as feeding, resting, and dispersal. Caterpillars of *Malacosoma americanum* Fabricius (Lepidoptera: Lasio-campidae), for instance, partition their feeding into short, synchronous bouts spanning the daytime to enhance feeding efficiency and limit exposure to predators and parasitoids (Snodgrass 1924, Fitzgerald et al. 1988). Late-instar gypsy moth caterpillars (*Lymantria dispar* Linnaeus) (Lepidoptera: Lymantriidae) usually avoid feeding during the daytime altogether, emerging only at night from sheltered parts of the host to feed on foliage (Leonard 1970, Lance et al. 1986). Other caterpillars actively seek out warm, sunlit positions on their host to raise body temperature above ambient as a means of accelerating growth (i.e., by basking) (Porter 1982, Knapp and Casey 1986, Alonso 1997, Bryant et al. 2000) or inducing a fever response to kill parasites or pathogens (Karban 1998, Roy et al. 2006). Caterpillars of *Battus philenor* (Linnaeus), in contrast, have adapted phenotypic and behavioral responses that prevent overheating in excessively hot climates (Nice and Fordyce 2006). Although larvae of many sawflies (Hymenoptera: Symphyta) occupy foraging niches similar to those of lepidopteran caterpil-

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lars and have comparable economic and ecological significance, there are few detailed studies evaluating how sawfly larvae respond behaviorally to spatial and temporal variations in microclimate.

We investigated the influence of microclimatic variation on the foraging behaviors of late-instar larvae of the yellowheaded spruce sawfly, *Pikonema alaskensis* (Rohwer) (Hymenoptera: Tenthredinidae), in young, open-grown black spruce (*Picea mariana* [Miller] Britton Sterns Poggenburger) (Pinaceae). *P. alaskensis* adults eclose in the spring and oviposit their eggs in the newly burst current-year buds by inserting eggs individually into the base of needles (Katovich et al. 1995). Larvae feed for five (male) or six (female) instars (Houseweart and Kulman 1976) on developing foliage, but may feed on older age classes if new foliage becomes scarce (Wilson 1971, Johns and Quiring 2010). After completing development, larvae drop to the ground and spin a cocoon in the upper layer of the soil for overwintering (Pointing 1957). Populations of *P. alaskensis* periodically erupt to cause extensive damage in intensively managed stands of juvenile spruce in northeastern North America (Haack and Mattson 1993, Katovich et al. 1995, Lavigne 1996). Although all varieties of native and non-native spruce are attacked by *P. alaskensis*, black spruce is the predominant host in eastern Canada and has been the main host involved in recent applied and ecological research on this insect in that region (e.g., Lavigne 1996; Johns et al. 2006a,b, 2009; Johns and Quiring 2010).

In attacked black spruce stands, defoliation associated with larval feeding tends to be concentrated in the upper crown of trees (Johns et al. 2009) and can lead to significant growth loss, top-kill, and/or whole-tree mortality after only a few years of defoliation (Kulman 1971, Lavigne 1996). Although oviposition and early instar larval feeding occurs mainly in the mid to lower crown of black spruce (Johns et al. 2006b, 2009), many late-instar larvae disperse acropetally (sensu Quiring 1993), from the lower to the upper crown, before completing larval development (Johns et al. 2009). In a recent study, we found that early instars feeding in the lower crown had higher survival than those forced to feed in the upper crown, whereas late instars that were transferred from the lower to upper crown, mimicking the acropetal dispersal behavior, had both higher survival and more female-biased sex ratios than those transferred in other ways within the crown (Johns et al. 2010). These performance benefits were attributed to intratree variations in foliage nutritional quality, although there may be other advantages to feeding in the upper crown for late instars. Similar to many caterpillars (Porter 1982, Stamp and Bowers 1990), late-instar *P. alaskensis* larvae could enhance physiological performance through raising their body temperature while feeding in the upper crown of their host, either because temperatures are warmer there than in the lower crown or because they are able to bask (i.e., feed in direct sunlight to raise body temperature above ambient). Alternatively, dispersal to the upper crown could incur costs associated with prolonged exposure

to adverse environmental conditions, such as extreme microclimatic conditions or natural enemies (Boone 2006).

Field and manipulative studies were carried out to: (1) elucidate how *P. alaskensis* larvae respond behaviorally to temporal (daily) and spatial (intratree and intrashoot) variations in microclimate; (2) determine whether larvae benefit (via thermoregulation) or suffer (because of hygrothermal stress) from feeding in the upper crown; and (3) determine if observed behavioral responses are adaptive with respect to microclimate. To address these objectives, we studied the diel activity patterns and behaviors of fourth- and fifth-instar *P. alaskensis* larvae feeding in the upper and lower crowns of small, open-grown black spruce. Manipulative field studies were also carried out to test the hypothesis that acropetal dispersal allows late-instar *P. alaskensis* larvae to thermoregulate through basking. From this hypothesis, we predicted that (1) larvae would feed in exposed, sunlit positions to bask during the daytime, (2) ambient temperature would be higher at feeding sites in the upper compared with lower crown, and (3) larvae would elevate body temperature above ambient, as is characteristic of basking, while feeding in the upper crown and/or during the daytime. To determine whether observed behaviors were adaptive, we conducted field studies assessing the performance of larvae feeding on branches or positions within shoots that were either shaded or exposed.

Materials and Methods

Diel Activity Patterns. Studies to assess the daily activity patterns and positioning of larvae on shoots were carried out in 2004 in an intensively managed black spruce stand ≈ 50 km south of Grand Falls-Windsor, Newfoundland (N 48° 40'11.3", W 55° 30'27.5"). Trees were 1.25–1.5 m in height, 7–8 yr old (with one whorl produced per year), and widely spaced so that all branches on trees were exposed to sunlight during the daytime. Small, open-grown trees were used for ease of sampling and because outbreaks of *P. alaskensis* rarely occur in older spruce stands after the trees have reached crown closure (Katovich et al. 1995). Oviposition and acropetal dispersal occur most frequently within the top five whorls of the tree (Johns et al. 2009); thus, we expect that the range of microclimatic conditions provided by trees in the current study should be similar to those experienced by larvae in larger trees. The forest floor between trees was dominated by *Kalmia* sp. Except for a few larvae of *Pikonema dimmockii* (Cress.) (Hymenoptera: Tenthredinidae), which were removed and transported to a nonstudy tree when found, no other herbivore was observed on study trees.

On 28 July, we selected five trees and marked two south-facing branches in the upper (whorl 2) and lower (whorl 5) crown. On this date, larvae were approximately fourth to fifth instar (mean instar ± 1 SE, 4.32 ± 0.24 , where egg = 0 and sixth instar = 6). Based on initial larval counts, larval densities were

<1–2 larvae per branch per tree. We augmented the larval densities on the trees by collecting larvae from an adjacent stand and haphazardly scattering 30 individual late-instar larvae onto branches from the upper to lower crown of each study tree. Sampling was carried out on the same trees on a sunny (2 August) and a partly cloudy (7 August) day. Based on preliminary observations, we found that larvae were inactive during the night time; thus, hourly observations of larval behavior began before dawn (0600 h) until several hours after sunset (2300 h), when all larval activity had ceased. To evaluate larval behavior, observers approached each study tree slowly and waited 1 min for larvae to settle, then haphazardly selected three larvae on branches in the upper and lower crown for assessment. Most larvae exhibited no response to observers, although a few performed a characteristic “snap-bending” defensive behavior before quickly resuming normal activity. Each larva was assessed for 30 s using a magnifying glass before classifying the primary behavior as either: (1) feeding – larval mouthparts were in contact with a needle and slight head and/or mandible movement was observed; (2) resting – larval mouthparts were not in contact with the needle; or (3) searching – larvae were observed walking along shoots and/or lifting the anterior end of the body in an attempt to climb onto nearby shoots. During these observations we also recorded whether larvae were feeding in exposed (i.e., on top of shoot, in direct sunlight) or shaded positions on shoots. Larvae were classified as shaded if their body was either fully shaded or partially shaded with most of its body wrapped and shaded beneath the shoot. While acropetally dispersing through the crown, late-instar larvae could become more exposed to environmental conditions. Thus, to determine if larvae also partition their dispersal activity to certain times of the day, we counted the number of larvae that were present every hour on the leader of each study tree.

Weather conditions were measured hourly using a data logger (CR10 Measurement and Control Module). To measure relative humidity, a probe (model 207 Temperature and Relative Humidity Probe) was tied to the top of a 1.5 m post (approximately aligned with whorl 1 of trees) located among the study trees. Solar insolation was measured in whorls 2 and 5 using a pyrometer (LI200S Single-ended voltage silicon). Air temperature was measured hourly \approx 1–2 cm below the tip of a south-facing branch in whorls 2 and 5 on two adjacent trees using two thermocouples (10TCRT Thermister). Before dawn and after dusk, a flashlight with a red filter, which based on preliminary observations had no effect on larval behavior, was used to illuminate branches when observing larvae.

Relationships between the mean percentage of individuals involved in each of the three activities described above, and the measured abiotic parameters, were evaluated using correlation analyses (PROC CORR; SAS Institute 1999). To determine the influence of sampling date, time, and crown level on the percentage of larvae involved in each larval activity for each study day, we carried out mixed-model analyses

of variance (ANOVAs) with the random effect of tree removed as a blocking factor (Zar 1984). Preliminary analyses indicated that larval behavior differed among sampling dates ($P < 0.01$); thus, each sampling day was analyzed separately. Percent data were arcsine square-root transformed to correct problems with normality and heterogeneous variance (Zar 1984).

Ambient Versus Larval Body Temperature. To determine whether larval body temperature and ambient temperature differ between the upper and lower crown, and throughout the day, field measurements were taken on 7 August 2004 in the same stand described above; the average temperature was $23.9 \pm 1.3^\circ\text{C}$. To sample larval body temperature without killing larvae, we established a relationship between surface body temperature and internal body temperature before the field study (Bardoloi and Hazarika 1994) for 20 larvae feeding on three black spruce trees. Surface body temperature was measured by placing a syringe thermocouple firmly onto the back of an individual larva for 5 s. Larvae rarely dropped from the tree despite this treatment and generally settled down to continue normal activity within 30–60 s. After each measurement, larvae were left for 5 min to settle. The internal body temperature was then measured by rapidly inserting the syringe through the integument behind the larva's head capsule into the body cavity. On 7 August 2004, the leader and south-facing branches in whorls 2 and 5 of five trees adjacent to those used in the study described above were marked. The surface body temperature for one larva in each whorl was measured at 0700, 0900, 1200, and 1800 h. Ambient temperature was also measured after each sample by holding the thermocouple for 5 s just beyond the tip of the shoot where the sampled larva was found feeding.

To determine the relationship between internal and surface body temperature, we used correlations on log-transformed temperature data (Zar 1984). Linear regressions (PROC REG; SAS Institute 1999) were carried out to assess the relationship between ambient temperature and larval surface body temperature.

Effects of Exposure Versus Shading on Larval Survival. To evaluate the effect of exposure at the branch level on larval survival, a manipulative experiment was carried out in 2004 over four mostly clear, sunny days with peak temperatures of 26–31°C. Starting on 2 August, in an open region next to the stand used in diel activity studies, 10 open wooden trays (50 × 50 cm) were constructed to create five shaded and five exposed replicates; these were organized in a randomized block pattern. Shading structures were suspended 50 cm above the trays and covered in black landscaping tarp that draped halfway down the side of the structure. This setup ensured continuous shading of branches throughout the day while also allowing air to flow across the trays. Upper crown branches were collected from undefoliated black spruce in a nearby stand and inserted into a plastic bag filled with water, which was sealed around the base of the branch with a twist tie. Branches were supported upright in each tray using wire, which was wrapped around the base

of the branch and to the side of the tray. Tanglefoot was spread around the perimeter of the tray and on the wire to prevent larvae from leaving the branch during the experiment. For this experiment, late instars were collected from an adjacent stand and placed in groups of three on each study branch. To determine daily survival, larvae were counted at noon every 24 h over four consecutive days. Daily temperatures were assessed based on averages provided from two thermocouples suspended in sunlit positions near the middle of the experimental setup. Temperatures were recorded every day at noon, which was expected to provide a general estimate of the peak temperature for each day.

To evaluate whether feeding in exposed versus shaded positions on shoots (i.e., on the top or bottom of the shoot) reduces larval performance, additional experiments were carried out between 17 June through 7 July (2010) and 21 June through 9 July (2011) in an intensively managed black spruce stand near Fredericton, New Brunswick. Ten (2010) and 20 (2011) open-growing black spruce trees ≈ 1.5 –2 m tall were selected and three whorl 2 branches were randomly assigned a treatment of either: (1) control; (2) exposed (i.e., top of shoot); or (3) shaded (i.e., bottom of shoot). To force larvae to feed in exposed positions, a small section of white cotton batten ($\approx 15 \times 20$ cm) was stitched to the bottom surface of the terminal 15–25 cm of the branch with needle and thread so the shoots were spread flat against the surface of the material. The same protocol was used for the shaded treatment, except that the cotton batten was stitched to the upper surface of the branch. Control branches were left untouched. Fourth- and fifth-instar *P. alaskensis* larvae were collected from several ornamental trees in the Fredericton area and placed in groups of four on each treatment branch, then enclosed in a mesh-cloth sleeve cage (30×50 cm). Before securing sleeve cages to the branch, a handful of sifted peat was added to the bottom of cages to facilitate eventual cocoon formation. Once all larvae had completed development, sleeve cages were removed and the cocoons were counted to determine survival. Prepupae were removed from each cocoon and weighed to provide an estimate of growth during the treatment period.

The effect of year and treatment on larval survival was assessed by fitting the data to generalized linear models (PROC GENMOD, dist = bin, link = logit; SAS Institute 1999). Differences among treatments in prepupal weight, measured only in 2011, were assessed using a one-way ANOVA (PROC ANOVA; SAS Institute 1999).

Results

Diel Activity Patterns. Larval activity on both sampling days was cyclical and characterized by continuous resting throughout the night followed by feeding throughout the day, and brief periods of dispersal by a small proportion of larvae during the morning and afternoon. Activity patterns were similar on both days,

even though the second sampling day had higher temperatures in the early morning and lower solar insolation throughout the day associated with sporadic cloud cover (compare Figs. 1 and 2). On both days, larvae rested throughout the night from ≈ 2200 to 0800 h (Figs. 1 and 2). Although larvae were not examined between 2300 and 0500 h, a few larvae that were marked the previous night and examined early in the morning (at 0600 h) on each of the two sampling days had not moved or eaten any foliage during the night. Larvae in the upper crown generally started feeding earlier than those in the lower crown on both days and ceased feeding later on the second day, resulting in a significant time \times whorl interaction (Table 1). Initiation of feeding appeared to be stimulated by sunlight, which tended to light the upper crown earlier than the lower crown at sunrise and that continued to light the upper crown as shading increased in the lower crown at sunset. Resting by larvae was negatively correlated with temperature ($P < 0.01$; $r = 0.96$), whereas feeding was positively correlated with temperature ($P < 0.01$; $r = 0.97$). Most searching and/or dispersal activity occurred early in the day between 0700 and 1000 h and to a lesser extent later in the evening between 1700 and 2000 h. On the first sampling day, it was mainly the larvae found in the upper crown that were observed dispersing (Fig. 1), resulting in a significant effect of whorl (Table 1), whereas on the second day, larvae from both whorls were similarly active (Table 1; Fig. 2). The initiation and cessation of feeding corresponded closely to sunrise and sunset (Fig. 1b vs. 1d, Fig. 2b vs. 2d). Of all the larvae observed, 94% were observed feeding between the needles on the bottom, shaded side of shoots (Fig. 3), or feeding on needles on the upper side of shoots while wrapping the majority of their body around and below the shoot so that only their head and anterior part of their body was exposed to direct sunlight. Dispersal occurred before and after the hottest time of the day (mid-day) (compare Figs. 1c and 2c vs. 1e and 2e), and was not correlated with any abiotic factor ($P \geq 0.57$; $r \leq 0.14$).

The number of larvae on the leader increased throughout both sampling days (Fig. 4). The highest rate of increase occurred during the latter part of the two periods when larvae were dispersing most (compare with Fig. 1b and 2b). No changes in larval density on the leader were observed after 1800 or before 0700 h for either sampling day.

Ambient Versus Larval Body Temperature. Because there were no temperature differences between the upper and lower crown (PROC ANOVA; SAS Institute 1999; $F_{2,27} = 0.61$, $P = 0.55$), crown-level data were pooled for subsequent linear regressions. Surface body temperature explained 87% of variation in internal body temperature and was thus determined to be a suitable method for evaluating larval body temperature (regression: $y = 1.03x + 0.79$; $F_{1,18} = 55.90$; $P < 0.01$). Ambient temperature increased throughout the day and explained $\approx 97\%$ of the variation in larval body temperature (Regression: $y = 0.98x + 0.15$; $F_{1,58} = 1,670.72$; $P < 0.01$).

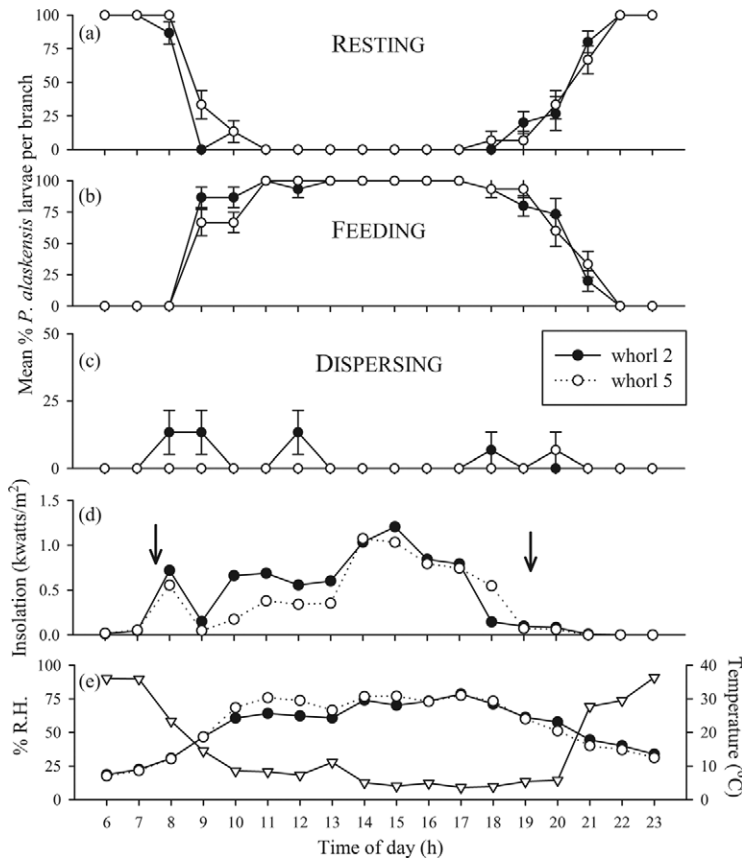


Fig. 1. Mean (\pm SE) percentage of late-instar *P. alaskensis* larvae on whorl 2 (upper crown) and whorl 5 (lower crown) of juvenile black spruce (6–8 whorls total) that were (a) resting, (b) feeding, or (c) dispersing on 2 August 2004. Also represented are: diel measurements of solar insolation (diffuse and direct combined) (d); and temperature and relative humidity (open triangles). Arrows in (d) signify sunrise and sunset, determined based on when the sun crested or sank beneath the horizon of the field site.

Effects of Exposure Versus Shading on Larval Survival. Survival of larvae did not differ significantly between groups feeding on shaded or exposed branches ($F_{1,8} = 0.91$; $P = 0.37$), or between days ($F_{3,24} = 2.82$; $P = 0.06$). During our daily observations, larvae from both treatments were generally found to be feeding on the bottom of shoots.

Larval survival was similar between experiments carried out in 2010 and 2011 ($\chi^2 = 1.14$; $P = 0.29$), and there was no year \times treatment interaction ($\chi^2 = 0.65$; $P = 0.42$). Survival was nearly twice as high for larvae allowed to feed freely on the branch (i.e., control) or in the shade compared with those forced to feed while exposed on top of the shoot ($\chi^2 = 15.24$; $P < 0.01$) (Fig. 5). Prepupal weight, assessed only in 2011, did not vary significantly among treatments ($F_{2,51} = 0.38$; $P = 0.68$).

Discussion

Acropetal dispersal and subsequent feeding in the upper crown of black spruce probably confers minimal thermoregulatory benefits to *P. alaskensis* larvae. Larvae were never observed to “bask” in the sunlight,

and larval body temperature generally conformed to that of ambient temperature among crown levels and at different times of the day. Indeed, ambient temperature was almost the same in the upper and lower crown throughout the day, probably because of the small size of trees (<1–1.5 m), resulting in similar body temperatures between larvae feeding in the upper and lower crown. In contrast, daily and intrashoot variations in microclimate had large effects on larval behavior, and natural selection appears to have generally favored behavioral adaptations that minimize exposure to adverse microclimatic conditions. Although feeding occurred almost continuously throughout the day, the majority of larvae generally stayed in shaded locations on shoots, either feeding on needles beneath the shoot (Fig. 3), or wrapping most of their body around the bottom of shoots when accessing sun-exposed needles. Our field experiments indicated that this behavior is adaptive, as larvae forced to feed in exposed positions on shoots survived half as well as those feeding in the shade or with access to all parts of shoots (Fig. 5). Larvae dispersed only in the morning and afternoon, probably to avoid the hottest pe-

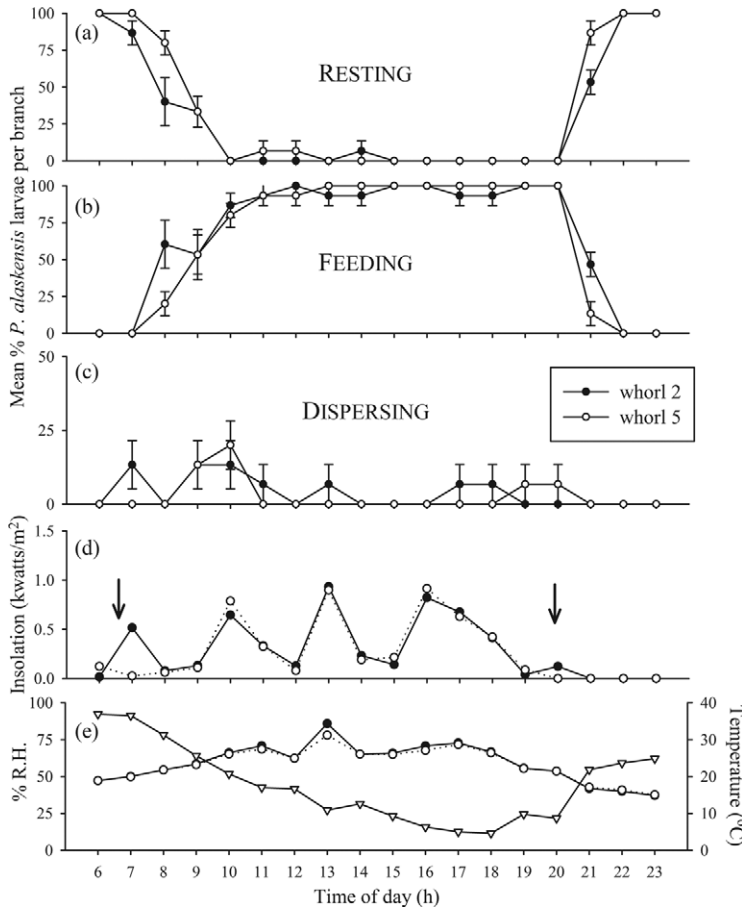


Fig. 2. Mean (± 1 SE) percentage of late-instar *P. alaskensis* larvae on whorl 2 (upper crown) and whorl 5 (lower crown) of juvenile black spruce (6–8 whorls total) that were (a) resting, (b) feeding, or (c) dispersing on 7 August, 2004. Also represented are: diel measurements of solar insolation (diffuse and direct combined) (d); and temperature and relative humidity (open triangles). Arrows in (d) signify sunrise and sunset, determined based on when the sun crested or sank beneath the horizon of the field site.

riods of the mid-day, and rested continuously throughout the night. To our knowledge, our study is the first to investigate the influence of both temporal and spa-

tial heterogeneity in microclimatic conditions on the behavior and associated performance of an immature sawfly.

Cyclical patterns of insect activity may be regulated proximately by a number of abiotic factors, although these factors are generally interrelated, and their in-

Table 1. Summary of mixed-model ANOVA assessing the influence of crown level (CL) (whorls 2 vs 5) and time of day (0600–2300 h) on the percentage of late-instar *P. alaskensis* larvae resting, feeding, or dispersing in black spruce during 2 and 7 Aug. 2004 in central Newfoundland

Activity	Source	2 Aug.		7 Aug.	
		$F_{1-17,143}$	<i>P</i>	$F_{1-17,143}$	<i>P</i>
Resting	Time	121.11	<0.01	78.31	<0.01
	CL	0.01	0.92	3.03	0.08
	Time \times CL	0.94	0.53	1.96	0.02
Feeding	Time	138.13	<0.01	140.29	<0.01
	CL	1.56	0.21	10.12	<0.01
	Time \times CL	2.10	<0.01	2.99	<0.01
Dispersing	Time	1.70	0.05	2.78	<0.01
	CL	5.54	0.02	0.68	0.41
	Time \times CL	1.95	0.02	0.84	0.65

Study days were 1 wk apart and represented different ranges of temperature, relative humidity, and solar insolation.



Fig. 3. A *P. alaskensis* larva feeding on the shaded rather than exposed side of a developing shoot in black spruce.

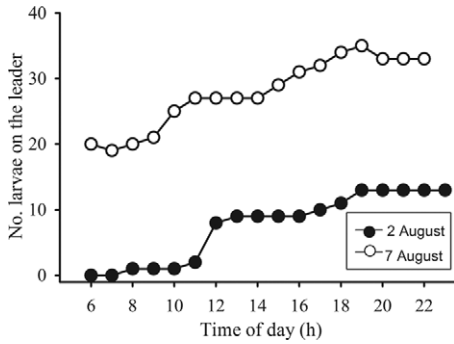


Fig. 4. Number of late-instar *P. alaskensis* larvae on the leader of juvenile black spruce trees from 0600 to 2200 h on 2 and 7 August 2004 ($n =$ five trees per day).

dependent influence difficult to determine. Such was the case in our study, where all abiotic factors were highly related to one another as well as to patterns of resting and feeding. Nonetheless, in separating our diel activity data into the two study days (Figs. 1 and 2), the relative influence of each abiotic factor became more apparent. Activity patterns on both days were nearly identical, yet both temperature and humidity differed dramatically between days. For instance, nighttime temperatures on the second day varied much less than those on the first day, ranging between 15–32°C, and changed only gradually from the morning to afternoon compared with those on day 1 (compare Figs. 2e and 1e). Similarly, humidity declined rapidly on the first day, but more gradually on the second, yet feeding began and ended abruptly at nearly the same time both days. Moreover, on each day, larval feeding often began first in the upper crown (Figs. 1b and 2b), which we observed was the first part of the crown to be illuminated as the sun crested over the horizon. Sunlight is clearly an important factor for other life stages, as evidenced in past studies showing that adults of *P. alaskensis* require direct sunlight to activate their pheromone complex (Bartelt et al. 1982, Bartelt and Jones 1983) and prefer to lay eggs in open-grown, sunlit trees (Morse and Kulman 1984,

Katovich et al. 1995). Our study suggests a similarly important influence on the cyclical alternation of feeding and resting activities of *P. alaskensis* larvae.

In contrast to many immature lepidopterans, larval *P. alaskensis* appear to passively allow their internal body temperature to fluctuate with ambient. In general, basking does not appear to be a common thermoregulatory strategy used by sawflies, although thermoregulation through gregarious feeding has been reported in several species of sawfly (Evans 1934, Seymour 1974, Géri and Goussard 1989, Anstey 2002). Larvae of the balsam fir sawfly, for instance, are able to raise their body temperature by as much as 2°C above ambient by feeding in tight, gregarious clusters on mature balsam fir needles (Anstey 2002). Larvae of *Perga dorsalis* (Hymenoptera: Pergidae), a species belonging to a third and relatively unstudied sawfly family, maintain their body temperature by feeding gregariously, but may also limit their body temperature by as much as 8°C below ambient by defecating a diluted liquid on themselves and one another, causing the group to cool as the liquid evaporates (Seymour 1974). For the closely related *Perga affinis*, individuals that feed in large groups attain higher body temperature and faster growth than those feeding in smaller groups or individually (Fletcher 2009). Although *P. alaskensis* often feed at extremely high densities after dispersal to the upper crown (Johns et al. 2009), there does not seem to be any particular effort to feed in close proximity with conspecifics at lower densities. In general, we found no evidence of either basking or gregarious behavior that could potentially confer thermoregulatory benefits to *P. alaskensis* larvae.

Hiding (or avoidance) is a common and fairly simple adaptation used by many herbivorous insects to avoid adverse environmental conditions, both biotic and abiotic. For some caterpillars, such as gypsy moth, hiding occurs during the day and involves rather laborious daily dispersal from foliage at the branch tips to bark crevices or other shelters at the base of the branches or tree (Leonard 1970, Weseloh 1987). Similarly, larvae of *Yponomeuta mahalebella* (Lepidoptera: Yponomeutidae) disperse to the leaf litter at the base of their host shrub in the early morning to avoid the heat of the day, then disperse acropetally back to the branch tips each evening to feed (Alonso and Herrera 1996, Alonso 1997). Larvae of *P. alaskensis* also disperse acropetally through the crown of their host, but usually only once in their development, between the fourth and sixth instar (Johns et al. 2009). We found no evidence to suggest that larvae ever intentionally return to lower branches or to the base of the tree after dispersing acropetally. Hiding by *P. alaskensis* was fairly straightforward and involved simply feeding in the shade provided by the shoot. This hiding was essentially continuous, except during brief periods of the morning and evening when some larvae occasionally dispersed (Figs. 1c, 2c, and 4). It is often unclear whether such hiding behaviors reflect an adaptation to avoid natural enemies or extreme microclimatic conditions, or a combination of both. Our evidence strongly indicates that microclimate is im-

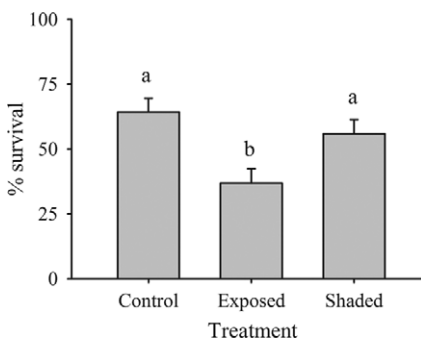


Fig. 5. Mean (± 1 SE) survival of *P. alaskensis* larvae that had fed with access to all shoots (control), to foliage only on the top surface of shoots (exposed) or to foliage only on the bottom surface of shoots (shaded) ($n = 30$ per treatment).

portant, although some of our observations also suggest possible benefits associated with predator or parasitoid avoidance. Larvae that were protected from natural enemies by sleeve cages accrued nearly twice the survival when allowed to feed in the shade compared with those forced to feed in exposed positions on the branch (Fig. 5). The effectiveness of this strategy can explain the results of our field experiment, where larvae were placed on shaded or exposed branches; there was little difference in survival between treatments over the 4 d of observation, most likely because larvae on exposed branches shaded themselves beneath the shoots as they fed. We also observed in our diel activity study that most larvae fed on the shaded, lower side of shoots in the lower crown, even when overtopping branches provided shade to the top of the shoots. These observations may suggest that avoidance of natural enemies is an additional agent of selection promoting the hiding behavior of *P. alaskensis*.

There are few species of sawfly for which diel activity patterns have been described in detail, although for those that have been studied the feeding strategies are quite varied. Several sawflies that either mine or feed on the edge of leaves have been reported to feed more or less continuously, pausing only during molting or when shifting positions on the leaf (Heitland and Pschorn-Walcher 1993). Other deciduous-feeding sawfly larvae feed in short, discontinuous bouts throughout the day and night (Neilson 1958, Flowers and Costa 2003), or in a crepuscular fashion with periods of increased feeding around dawn and dusk (Heitland and Pschorn-Walcher 1993). Fewer examples are available describing sawfly larvae that feed continuously through the day or night. Many Australian sawflies from the family Pergidae feed predominantly at night and rest in tight gregarious clusters during the day (Carne 1962, Schmidt et al. 2002). Fairly strict diurnal feeding such as was observed for *P. alaskensis* may also occur in other sawflies, but we could find no other examples in the literature. *P. alaskensis* differs from most other conifer-feeding insects in its preference for developing foliage (Géri et al. 1993, Haack and Mattson 1993) and in its relatively close evolutionary relationship to deciduous-feeding tenthrinids (Price 2003). Determining whether *P. alaskensis* possesses similar diel activity patterns to conifer-feeding diprionid sawflies or whether it has retained patterns used by its close tenthrinid ancestors will require further study in a wider range of sawfly tree systems.

Feeding by instar larvae on exposed, developing shoots in small trees and shrubs comes with a mix of benefits and costs, which presumably must be balanced with adaptations that promote a net overall gain in performance and associated fitness. For late-instar *P. alaskensis*, feeding on developing upper-crown foliage of open-growing, juvenile spruce is an important adaptation, more advantageous than the alternative strategies of feeding on mature foliage (Johns and Quiring 2010), in the lower crown (Johns et al. 2010), or in shaded stands of spruce (Morse and Kulman 1984). Our study indicates that the benefits derived

from these behaviors may be accompanied by certain costs, in particular increased exposure to adverse microclimates and perhaps natural enemies. We have reported a range of behavioral adaptations employed by *P. alaskensis* to offset the costs of both temporal (diel) and spatial (intra-shoot) variations in microclimatic conditions within their host, and have ruled out possible thermoregulatory benefits that could be gained from feeding in upper crown levels. Further studies in other similar systems would help clarify whether the adaptations reported here reflect a general trend in sawflies that feed in evergreen conifers.

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