

Temporal variations in abiotic conditions exert little influence on diurnal activity of late-instar spruce budworm larvae on balsam fir

S.E. Holmes, E.G. Kettela, P.C. Nigam, S.B. Heard, R.C. Johns¹

Abstract—Spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), larvae can cause extensive defoliation in balsam fir (*Abies balsamea* [Linnaeus] Miller) and exhibit high temporal and spatial variability in individual behaviour. We gathered field data to determine the influence of daily and hourly variation in abiotic conditions on daytime activity patterns of late-instar budworm larvae on balsam fir. In both years of our study, less than 10% of larvae were observed feeding during the daytime. Most larvae observed were either resting, spinning silk, or roaming, although the proportion of individuals engaged in each activity varied between years, with more larvae in the first year roaming (48%) and in the second year either resting (38%) or spinning silk (42%). Daily and hourly variation in abiotic conditions had a limited influence on activity patterns. Our results indicate that in nature, mid- to late-instar budworm larvae maintain fairly consistent activity patterns across a wide range of abiotic conditions. We suggest that site-specific conditions such as variation in host-plant quality and/or budworm population density may be more important than weather in determining the relative frequencies of different larval activities in space and time.

Résumé—Les larves de la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), peuvent causer une sérieuse défoliation chez le sapin baumier et font montre d'une importante variation temporelle et spatiale dans leur comportement individuel. Nous avons accumulé des données de terrain afin de déterminer l'influence de la variation journalière et horaire des conditions abiotiques sur les patrons d'activité journalière des stades avancés des tordeuses sur le sapin. Durant les deux années de notre étude, moins de 10% des larves ont été vues en train de se nourrir durant la journée. La plupart des larves se reposaient, tissaient de la soie ou erraient, bien que la proportion des individus occupés à chacune de ces activités ait varié d'une année à l'autre; la première année, il y avait plus de larves à errer (48%) et la seconde année à se reposer (38%) ou à tisser de la soie (42%). La variation journalière et horaire des conditions abiotiques avait une influence limitée sur les patrons d'activité. Nos résultats indiquent qu'en nature les larves de tordeuses des stades moyens à avancés maintiennent des patrons d'activité assez constants sur une gamme étendue de conditions abiotiques. Nous croyons que les conditions spécifiques au site, telles que la variation de la qualité de la plante-hôte et(ou) la densité de la population de tordeuses, peuvent être plus importantes que les conditions climatiques pour déterminer les fréquences relatives des différentes activités larvaires dans l'espace et le temps.

Received 13 April 2011. Accepted 9 June 2011.

S.E. Holmes, E.G. Kettela, Natural Resources Canada, Canadian Forest Service – Atlantic Forestry Centre, Fredericton, New Brunswick E3G 5P7, Canada

P.C. Nigam, Natural Resources Canada, Canadian Forest Service – Atlantic Forestry Centre, Fredericton, New Brunswick E3G 5P7, Canada; and Research Scientist (retired), Spruce Budworm Behavior and Control, Canadian Forest Service – Atlantic Forestry Centre, New Brunswick, Canada

S.B. Heard, Department of Biology, University of New Brunswick, Fredericton, New Brunswick E3B 5A3, Canada

R.C. Johns,¹ Natural Resources Canada, Canadian Forest Service – Atlantic Forestry Centre, P.O. Box 4000, Fredericton, New Brunswick E3G 5P7, Canada; and Population Ecology Group, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick E3B 5A3, Canada

¹Corresponding author (e-mail: rjohns@nrca.gc.ca).

doi:10.4039/tce.2012.36

Introduction

Many insects can enhance their performance through partitioning activities, such as feeding, resting, and dispersal, relative to spatial and temporal variation in local abiotic conditions. Advantages of such partitioning may reflect the direct influence of abiotic conditions, in particular temperature and humidity, as these parameters often mediate rates of physiological processes and thus impact insect survival and developmental rate (Berridge *et al.* 1983; Bardoloi and Hazarika 1994). Insects may also accrue indirect benefits from linking activity patterns to abiotic variation because abiotic cues can help balance rates of food intake and digestion (van Frankenhuzen and Espinasse 2010), limit exposure to natural enemies (Fitzgerald *et al.* 1988), and help to synchronise social behaviours (Thornhill and Alcock 1983; Quiring 1994). Aside from weather, intrinsic, hormonally mediated influences such as molting, circadian rhythm, and hunger may affect the timing, frequency, and duration of activities (Wellington and Cameron 1947; Nigam 1995). A better understanding of the factors influencing insect activities could help to increase efficiency of pest-control programmes, especially those employing control products that must be ingested to kill the target insect (*e.g.*, *Bacillus thuringiensis* Berliner strain *kurstaki* (Btk) and tebufenozide). Deploying such products during peak periods of feeding would be expected to increase the uptake of insecticide, and could thus significantly enhance the efficiency and efficacy of control agents.

We investigated how variation in abiotic conditions, in particular weather, influences activity patterns of larvae of spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), the major defoliator of balsam fir (*Abies balsamea* [Linnaeus] Miller) and spruces (*Picea* Dietrich spp.) in eastern Canada. In western New Brunswick, where this study was carried out, second-instar budworm larvae emerge in early to mid-May and mine mature needles or swelling buds. At all instars, larvae use silk to link adjacent needles and shoots, forming protective silk shelters in which to feed and rest. Because both shoots and larvae grow continuously throughout the season, larvae continuously repair and expand their shelters. If resources within a shelter become depleted during late instars, the occupant may roam to neighbouring

shoots to acquire fresh needles (foraged needles are generally clipped at the base and dragged on a silken thread back to the feeding shelter for consumption). In a recent laboratory study, van Frankenhuzen and Espinasse (2010) reported that mid- to late-instar larvae feed discontinuously throughout the day. Overall, less than 10% of activity time was allocated to feeding (active ingestion), while resting and silk spinning comprised the majority of their daily activity time budget (together 28–52%) (van Frankenhuzen and Espinasse 2010). Although several studies have investigated how temperature, and sometimes humidity, influence adult activity patterns (Sanders 1975) and juvenile developmental rate (Reichenbach and Stairs 1984; Régnière 1987) of spruce budworm, no field studies have asked how variation in local abiotic conditions influences budworm larval activity. We describe results from a 2-year field study carried out to determine the influence of daily and hourly variations in temperature, humidity, and solar insolation on diurnal activity patterns of late-instar larvae of spruce budworm on mature balsam fir.

Methods

Experimental setup

We used video recording to observe the association between larvae activity and abiotic conditions. We recorded for 24 hours a day for 29 days (May 31–June 28) in 1987 and for 12 days (June 15–26) in 1991. We analysed data only for well-lit daylight hours (05:00–20:00), because review of the videos suggested that timer-controlled flashlights used to illuminate larvae at night might influence their activity; to our knowledge, nocturnal activity patterns of budworm larvae have not been studied. Furthermore, we retained data only for days for which both activity and weather data were available from 05:00 to 20:00 hours (1987, 10; 1991, 11).

Our observations were made in natural stands of mixed balsam fir and red spruce (*Picea rubens* Sargent) (Pinaceae) ~10 km south of Upper Blackville, New Brunswick (46°33'N, 65°55'W) (1987) and about 36 km west of Miramichi, New Brunswick, near the Fraser Burchill Road (47°08'N, 65°59'W) (1991). Tree density was ~1000–1100/ha and most trees had a height of 6.6–11.0 m. Budworm populations in the region

were in the declining phase of outbreak and were generally present at low densities in the study sites (Speight 1987). In a relatively open section of each stand, scaffolding was erected adjacent to groups of balsam fir and five (1987) or eight (1991) video surveillance cameras (Panasonic WV-1554, Panasonic Canada, Mississauga, Ontario) were set up to record larval activities on one to two mid-crown branches per tree. We positioned each camera slightly above and 10–20 cm away from a branch and monitored a specific microhabitat for as long as at least one larva was present within the field of view. At a daily check, if a camera no longer had a larva in its field of view we shifted it to an adjacent branch occupied by a larva. Cameras were connected to a central control system that regulated recording intervals, with a sequential switcher (Panasonic WJ-527) automatically initiating each camera in sequence for an interval of 3 (1987) or 4 (1991) continuous minutes of video recording. Incoming video was recorded using a time-lapse video cassette recorder (Panasonic NV-8050) in the 12-hour mode, which permitted 12 hours of continuous recording on a 2-hour T120 VHS tape; we replaced tapes every 12 hours.

We reviewed video tapes and one of several observers scored the primary activity of each larva within each 3–4-minute video clip (*i.e.*, one ‘observation’) as follows: (1) feeding – cutting, moving, and chewing needles, (2) resting – immobile or motionless, (3) spinning – spinning silk in or around the microhabitat in the course of building or maintaining a feeding/resting shelter, (4) roaming – wandering or movement not clearly associated with either feeding or spinning. Video tapes and associated observations were spot checked periodically to ensure consistency of scoring among the various observers.

Working in stands adjacent to the study sites, we assessed larval instar every 2 days for the duration of video recording. We randomly collected 50 larvae on each sampling date, and scored developmental stages (second to sixth larval instars = 2–6, prepupa = 6.5, pupa = 7) following McGugan (1954). From the beginning to the end of each video recording period, larvae ranged from mean instar 4.6–5.9 (1987) and 5.6–6.6 (1991).

To assess local climates, we installed a 13 m tall tower with a 1 m mast extension in the midst of each study stand. We measured insolation (direct and diffuse combined) with a silicon pyranometer

(LI-200SZC, Li-Cor, Inc., Lincoln, Nebraska) attached to a mounting arm with a levelling fixture near the middle of the tower, about mid-canopy level. We measured air temperature and relative humidity using a probe (model 207, Campbell Scientific, Inc., Logan, Utah) housed within a radiation shield located below the pyranometer. We also recorded temperature near each microhabitat videotaped using thermocouples (copper constantan) placed beneath the observed shoots. Air and microhabitat temperatures were highly correlated (Pearson’s $r = 0.95$, $P < 0.001$, $y = 1.07x - 3.64$), and for simplicity we used only microhabitat temperatures in subsequent analyses. All instruments were connected to a battery-operated Campbell Scientific 21x micrologger (Campbell Scientific Canada Corp., Edmonton, Alberta), which was housed inside a weather-proof enclosure bolted to the weather tower. Weather data were recorded at 1-minute intervals and saved onto the internal memory of the micrologger until it could be downloaded for storage and backup. We used these fine-scale data to estimate mean insolation, temperature, and humidity for each day (pooling across hours) and for each hour (pooling across days). Not surprisingly, temperature and relative humidity were strongly (negatively) correlated, especially across hours within days. We report only activity patterns with temperature but caution that effects of temperature and humidity cannot be separated in our data.

Statistical analyses

For each study year, we fit generalised linear models (GLM) (proc GENMOD, dist = bin, link = logit; SAS Institute 1999) to test the influence of day and hour on each activity. We treated day and hour as continuous, interval-scale variables, and initially fit models including a quadratic term in day or hour. We were particularly interested in testing for quadratic fits with hour, as activities might well peak at midday (quadratic, concave down) or at dawn and dusk (quadratic, concave up). When the quadratic term was not significant (at $\alpha = 0.05$), we report the linear analysis instead. In several cases, GLM diagnostics such as scaled deviance indicated over-dispersion or under-dispersion of data relative to the modelled error structure, and where over-dispersion or under-dispersion was strong

(deviance/df > 3.0 or < 0.33) we do not report any fit. More stringent values for these deviance cutoffs, such as described in Atkinson (2001), would reduce the number of fitted relationships we show, but not alter any of our major conclusions. We used the same procedure to test the influence of mean daily and hourly temperature, and solar insolation on each activity, again beginning with a model including a quadratic term in temperature or insolation but reporting the linear fit instead when the quadratic term was nonsignificant.

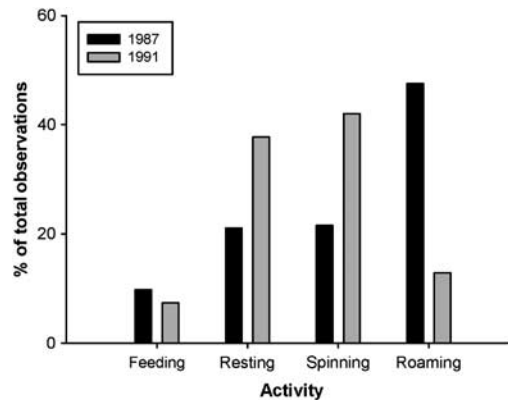
Results

Of the total 1847 and 2969 observations in 1987 and 1991, respectively, only 43% and 68% of larvae were visible in video footage for activity identification. In both years, <10% of visible larvae were observed feeding during the daytime (Fig. 1). Most larvae in 1987 were observed roaming (~50%) with less than half as many either resting or spinning silk (Fig. 1). Comparatively few larvae in 1991 were observed roaming and were generally observed to be either resting or spinning silk (Fig. 1).

Activity patterns often differed significantly among days, although effects were rarely consistent between years (Fig. 2, Table 1). Feeding increased linearly throughout 1987 but did not change significantly in 1991 (Fig. 4, Table 1). Resting in 1991 only increased positively with day, whereas roaming in both years decreased with day (Fig. 4, Table 1). Relationships could not be fitted for silk spinning in either year (Table 1). Daily variations in activities were generally not associated with corresponding variations in abiotic conditions, except in 1991 when spinning and roaming were negatively related with temperature (Fig. 4G, 4H, Table 1) and resting was positively related to solar insolation (Fig. 4N, Table 1). As temperature, humidity, and insolation are all interrelated (Pearson's correlations: range of $r = 0.51-0.98$, $P < 0.05$), it is not possible to determine the independent influence of each factor on activities.

In both years, feeding, resting, and silk spinning—but not roaming—varied significantly among the hours of the day (Fig. 3, Table 2). Although feeding was negatively related to temperature only in 1991 (Fig. 5E, Table 2), resting and silk spinning were positively related to

Fig. 1. Overall mean percentages of late-instar budworm larvae feeding, resting, spinning silk, or roaming on mid-crown branches of mature balsam fir in 1987 and 1991.



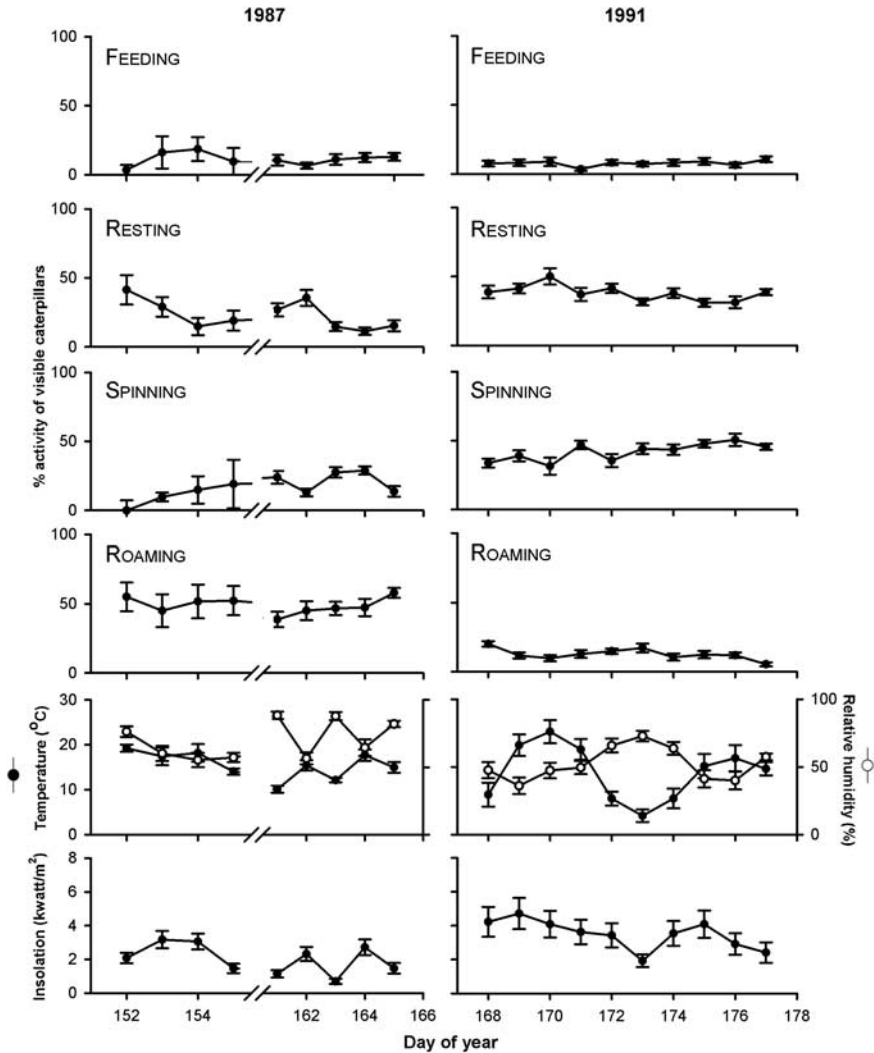
temperature in both years (Fig. 5B, 5F, Table 2). Roaming generally decreased with increasing temperature, although the relationship was only significant in 1991 (Fig. 5H, Table 2). Only resting in 1987 was significantly related to solar insolation (Fig. 5J, Table 2).

Discussion

Less than 10% of budworm larvae were observed feeding during this study; most were observed to be either resting, spinning silk, or roaming (Fig. 1). Resting, of course, is not necessarily unproductive as budworms, similar to other herbivores that feed on low-quality foliage, may require additional time after consuming foliage for digestion and other post-ingestion processes (here included in “resting”). Indeed, van Frankenhuzen and Espinasse (2010) found that *in vitro* lengths of budworm resting bouts were correlated with lengths of the preceding feeding periods, likely because larger meals required more processing time. Our results for feeding activity are consistent with those of van Frankenhuzen and Espinasse (2010), who reported that budworm larvae allocate less than 10% of their time during the day to feeding.

Activity patterns for silk spinning, roaming, and resting differed between the 2 years of our study. In 1991, roaming was fairly infrequent, while nearly 40% of larvae were observed either resting or spinning silk. In 1987, however, nearly half of all larvae observed were roaming with a comparatively small percentage resting and spinning

Fig. 2. Daily mean percentages (± 1 SE) of late-instar budworm larvae feeding, resting, spinning, or roaming on developing shoots of mature balsam fir in 1987 and 1991; and mean (± 1 SE) relative humidity, solar insolation (diffuse and direct combined), and temperature measurements for the same days. Days 156–160 in 1987 are omitted due to unavailability of either abiotic or activity data for those days.



silk (Fig. 1). Slight differences in larval age between the two study years are unlikely to explain these differences as activity patterns appear to be similar from fourth to sixth instar (van Frankenhuzen and Espinasse 2010). It is more likely that the higher proportion of larvae roaming in 1987 was due to lower site quality, possibly caused by reduced foliage availability coupled with higher larval densities (Blais 1952). In 1987, budworms were still abundant in the region and trees in the area had sustained

heavy defoliation over the preceding 3 years (Speight 1987). By 1991, populations in the region had declined such that there were few obvious signs of larvae and almost no recent defoliation. The lower frequency of “visible” larvae in 1987 (43% versus 68% in 1991) may support this hypothesis as highly active larvae would have been more likely to move out of the limited field of view of cameras.

Past laboratory studies have reported that gradients in temperature and humidity can modify

Table 1. Results from GENMOD analyses assessing relationships between daily mean % of late-instar budworm larvae feeding, resting, spinning silk, or roaming and day, temperature, and SI.

Year	Activity	χ^2 -values (df = 1) ¹		
		Day	Temperature	SI
1987	Feeding	11.3***	<i>0.68</i> ²	<i>0.66</i>
	Resting	No fit	No fit	No fit
	Spinning	No fit	No fit	No fit
	Roaming	<i>8.26</i> */ <i>8.69</i> **	No fit	No fit
1991	Feeding	2.78	<i>0.02</i>	<i>0.13</i>
	Resting	<i>5.21</i> */ <i>5.13</i> *	0.04	<i>7.58</i> **
	Spinning	No fit	<i>26.7</i> ***/ <i>27.1</i> ***	No fit
	Roaming	<i>11.4</i> ***	<i>9.54</i> **	No fit

¹ Where two values are shown, the first is for a linear term and the second for a quadratic. Where a single term is shown, the quadratic term was not significant.

² Italicised χ^2 -values indicate negative parameter estimates (for quadratic term, negative is convex up).

*.***.*** tests significant at $P < 0.05$, $P < 0.01$, $P < 0.001$.

“No fit”, deviance/df > 3.0 or < 0.33 for both linear and quadratic fits.

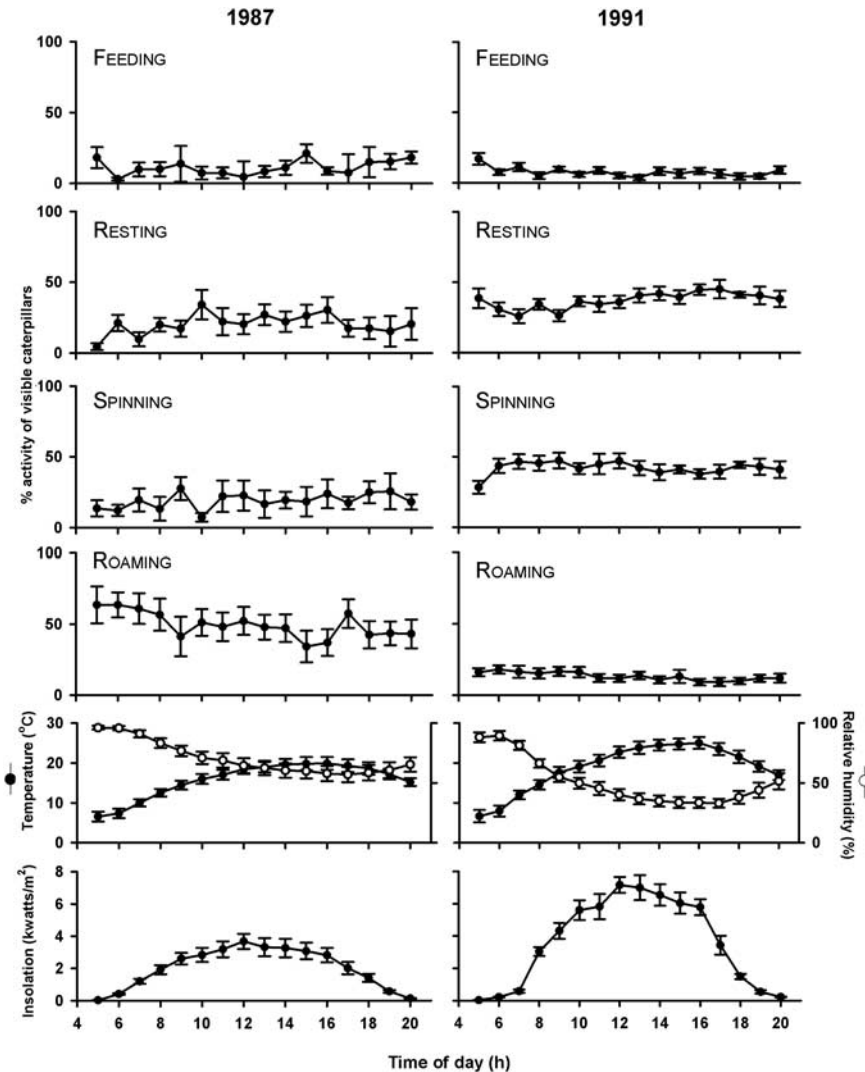
SI, solar insolation.

budworm larval activity (Wellington 1950a, 1950b), however, we did not detect these effects on budworm in field conditions. The occurrence of feeding by larvae was generally not influenced by daily or hourly variations in abiotic conditions, except in 1991 where there was a slight decreasing trend relative to increasing temperature (Fig. 5e). We emphasise that this does not imply feeding is unaffected by temperature; Retnakaran (1983) demonstrated previously an almost fivefold increase in larval feeding rate between 12°C and 27°C, presumably because warmer temperatures facilitate more rapid consumption and digestion of foliage. Instead, our results indicate that the frequency of feeding by mid- to late-instar budworm is fairly stable across a range of weather conditions and that variations in abiotic conditions have a limited impact on the relative frequency of different activities. Even where relationships were significant, such as those between daily silk spinning or roaming and temperature (Table 1), we could see only slight changes in activity in response to quite dramatic variations in temperature and insolation (Figs. 4G, 4H). Similarly, hourly variations in weather, although significantly related to several activities, yielded relatively subtle changes in larval activity (Fig. 5), especially when compared with the large variations in larval activity reported in a number of

other Lepidoptera (*e.g.*, Edwards 1964; Leonard 1970; Fitzgerald *et al.* 1988).

Interestingly, larvae maintained similar activity patterns on most days, and during mornings and evenings, even when temperatures averaged below 10°C; below 10°C (and above 30°C) larval growth slows significantly in both field and laboratory colonies (Reichenbach and Stairs 1984; Régnière 1987). It is possible that the silken tunnels in which larvae spend much of their time buffer ambient climatic conditions, allowing larvae to continue activities despite low temperatures outside the shelter. For other Lepidoptera species that develop primarily in silken shelters, the internal enclosure temperatures can be as high as 2–4°C above ambient (Fitzgerald *et al.* 1988; Ruf and Fieldler 2002). Budworm may also possess adaptations similar to those of other Lepidoptera that allow for continued locomotion and feeding during low temperatures. A large number of Lepidoptera species feed predominantly at night to avoid natural enemies (Raubenheimer and Browne 2000; Shiojiri *et al.* 2006) and some, such as the tent caterpillar (*Malacosoma americanum* (Fabricius)), are able to continue nighttime activities even at temperatures $\leq 7^\circ\text{C}$ (Joos 1992). Although we were not able to analyse nocturnal activity, budworm could also be feeding at night, accruing benefits from maintaining normal activity, even when temperatures are less favourable for growth.

Fig. 3. Hourly mean percentages (± 1 SE) of late-instar budworm larvae feeding, resting, spinning silk, or roaming on mid-crown branches of mature balsam fir in 1987 and 1991; and mean (± 1 SE) relative humidity, solar insolation (diffuse and direct combined), and temperature for the same hours.



Such behaviour could help larvae avoid exposure to predators and parasitoids that favour warm, daytime conditions.

Understanding budworm activity patterns has important implications for the integrated pest management of this intermittent pest as the two main insecticides used to protect trees, Btk and to a lesser extent tebufenozide (Mimic[®], Valent BioSciences Corporation, Libertyville, Illinois, U.S.A.), must be ingested to be effective. As such, conditions that influence budworm activity are likely to influence the uptake and associated

efficacy of control agents. Although ours and past studies (*e.g.*, van Frankenhuzen and Espinasse 2010) show that budworm clearly partition their day to accommodate several essential activities, we found only weak dependence of feeding behaviour on environment and it is not yet clear the extent to which activities besides feeding influence Btk efficacy. Cleaning and repairing the silken shelter occurs more frequently than feeding and may provide an alternative route for Btk to enter the gut as larvae use their mouthparts for both these activities. Budworm on branches sprayed with Btk

Fig. 4. Relationships between mean daily temperature or solar insolation and the % of larvae feeding (A, E, I, M), resting (B, F, J, N), spinning silk (C, G, K, O), and roaming (D, H, L, P) in 1987 and 1991. Bold symbols represent relationships that were significant (see Table 1).

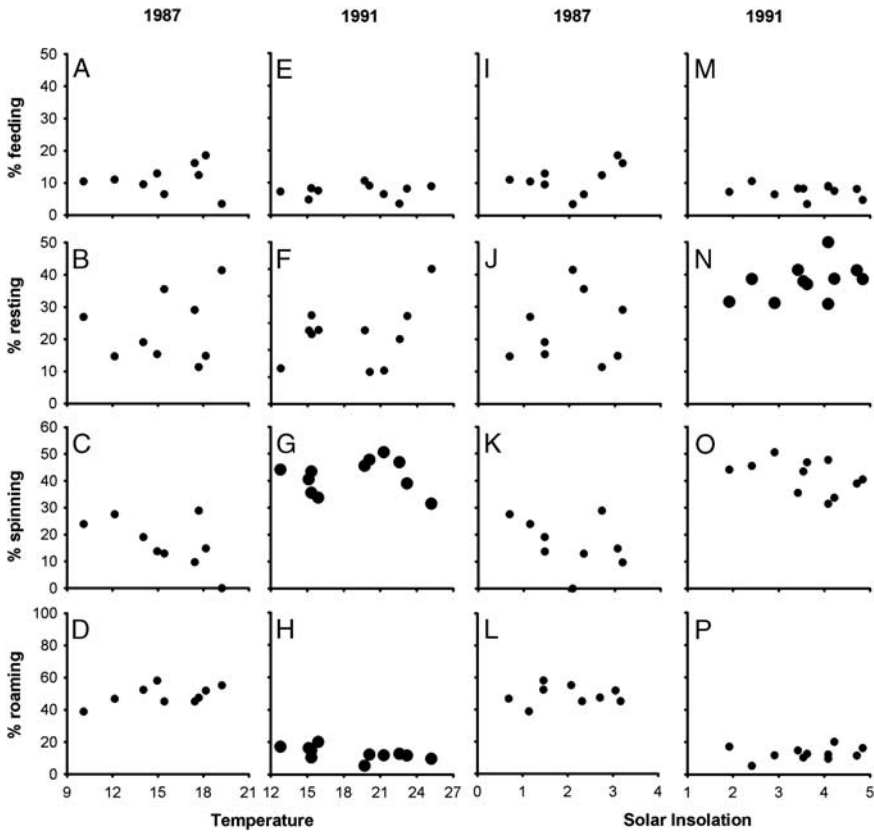


Table 2. Results from GENMOD analyses assessing relationships between hourly mean % of late-instar budworm larvae feeding, resting, spinning silk, or roaming and time of day (hour), temperature, and SI.

Year	Activity	χ^2 -values (df = 1) ¹		
		Hour	Temperature	SI
1987	Feeding	4.95***	1.05	0.88 ²
	Resting	9.36**/8.17**	8.83**	7.66**
	Spinning	5.22*	4.63*	0.60
	Roaming	0.3	0.23	0.02
1991	Feeding	4.58*	6.34*	2.46
	Resting	15.8***	14.7***	3.66
	Spinning	4.35*/3.96*	8.13**/7.02**	1.72
	Roaming	No fit	4.40*	0.35

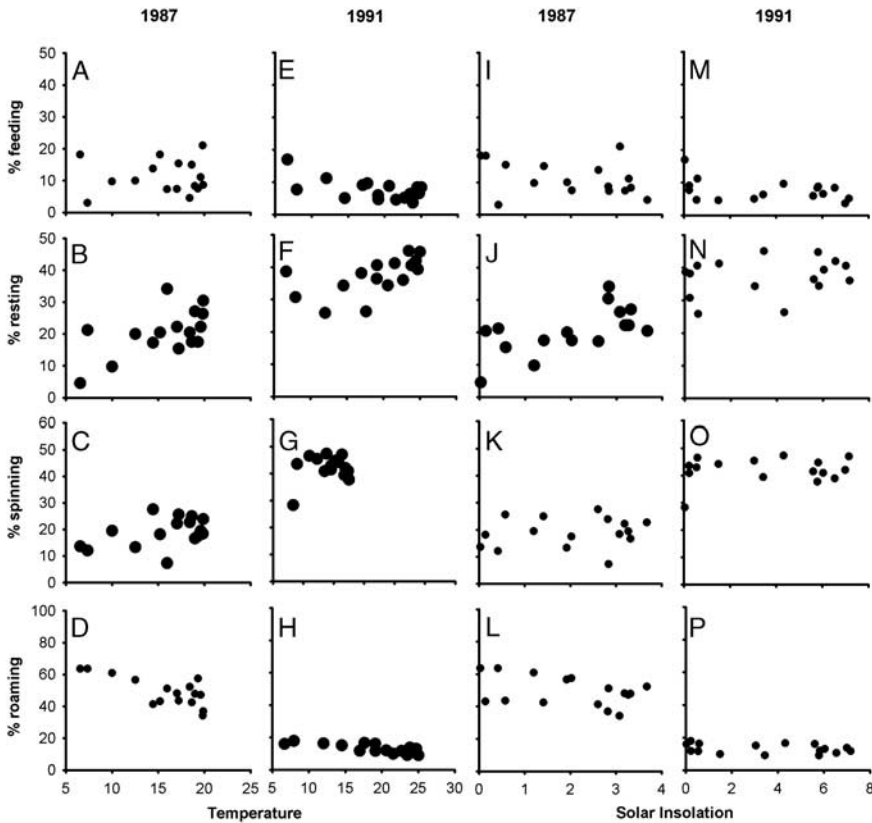
¹ Where two values are shown, the first is for a linear term and the second for a quadratic. Where a single term is shown, the quadratic term was not significant.

² Italicised χ^2 -values indicate negative parameter estimates (for quadratic term, negative is convex up).

*** ** * tests significant at $P < 0.05$, $P < 0.01$, $P < 0.001$.

SI, solar insolation.

Fig. 5. Relationships between mean hourly temperature or solar insolation and the % of larvae feeding (A, E, I, M), resting (B, F, J, N), spinning silk (C, G, K, O), and roaming (D, H, L, P) in 1987 and 1991. Bold symbols represent relationships that were significant (see Table 2).



have been observed collecting spray droplets in their mouths while cleaning their shelter, although whether this behaviour led to greater mortality was not tested (P.C. Nigam, unpublished data). Extensive roaming may further increase exposure to control agents, particularly if particles are accidentally transferred into the feeding shelter to be ingested incidentally later during feeding and shelter maintenance. Further investigation may shed light on the importance of each activity for determining Btk ingestion and whether or not factors influencing the proportion of time allocated to each behaviour have a corresponding influence on product efficacy.

Although climate has a dramatic influence on several aspects of budworm biology and ecology, including adult mating activity (Sanders 1975), host-plant selection (Lysyk 1989), larval diapause break (Bean 1961; Régnière 1987), and developmental rate (Reichenbach and Stairs 1984; Régnière 1987), the present study detected only minor effects

on activity patterns of late-instar larvae, particularly compared with effects documented for other Lepidoptera (*e.g.*, Edwards 1964; Leonard 1970; Fitzgerald *et al.* 1988). We postulate that other factors, such as population density and host-plant quality, are more important mediators of activity in spruce budworm, as has been reported for other outbreaking Lepidoptera (*e.g.*, Lance *et al.* 1986).

Acknowledgements

We thank G. Burgess, J. Fidge, J. Fullerton, G. Henderson, M. Mersereau, P. Neilson, G. Speight, B. Sturgeon, B. Tang, and J. Tyre for technical assistance and G. Broderson, D. Carleton, E. Eveleigh, L. Flaherty, S. Fraser, D. Quiring, M. Rhains, A. Smith, J. Sweeney, G. Thurston, K. van Rooyen, and R. Webster for constructive criticism of the manuscript. Also thanks to D. Quiring for thoughtful discussions on statistical

analyses and presentation of results. Financial support was provided by the Canadian Forest Service with substantial logistical support from Forest Protection Limited. We also thank the staff of Instructor Aids Limited (Dartmouth, Nova Scotia) who customised cameras to suit the study objectives and who were instrumental in designing and setting up the video array at field sites.

References

- Atkinson, A.C. 2001. Regression diagnostics for binomial data from the forward search. *The Statistician*, **50**: 63–78.
- Bardoloi, S. and Hazarika, L.K. 1994. Body temperature and thermoregulation of *Antheraea assama* larvae. *Entomologia Experimentalis et Applicata*, **72**: 207–217.
- Bean, J.L. 1961. Predicting emergence of second-instar spruce budworm larvae from hibernation under field conditions in Minnesota. *Annals of the Entomological Society of America*, **54**: 175–177.
- Berridge, M.J., Treherne, J.E., and Wigglesworth, V.B. 1983. *Advances in insect physiology*, vol. 17. Academic Press, New York.
- Blais, J.R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana*, Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). *Canadian Journal of Zoology*, **30**: 1–29.
- Edwards, D.K. 1964. Activity rhythms of lepidopterous defoliators. II. *Halisidota argentata* Pack. (Arctiidae), and *Nephytia phantasmaria* Stkr. (Geometridae). *Canadian Journal of Zoology*, **42**: 939–958.
- Fitzgerald, T.D., Casey, T.M., and Joos, B. 1988. Daily foraging schedule of field colonies of the eastern tent caterpillar *Malacosoma americanum*. *Oecologia*, **76**: 574–578.
- Joos, B. 1992. Adaptations for locomotion at low body temperatures in eastern tent caterpillars, *Malacosoma americanum*. *Physiological Zoology*, **65**: 1148–1161.
- Lance, D.R., Elkinton, J.S., and Schwalbe, C.P. 1986. Feeding rhythms of gypsy moth larvae: effect of food quality during outbreaks. *Ecology*, **67**: 1650–1654.
- Leonard, D.E. 1970. Feeding rhythm in larvae of the gypsy moth. *Journal of Economic Entomology*, **63**: 1454–1457.
- Lysyk, T.J. 1989. Stochastic model of eastern spruce budworm (Lepidoptera: Tortricidae) phenology on white spruce and balsam fir. *Journal of Economic Entomology*, **82**: 1161–1168.
- McGugan, B.M. 1954. Needle-mining habits and larval instars of the spruce budworm. *The Canadian Entomologist*, **86**: 439–454.
- Nigam, P.C. 1995. Response of spruce budworm, *Choristoneura fumiferana*, larvae to insecticides. *In Forest insect pests in Canada. Edited by J.A. Armstrong and W.G.H. Ives. Natural Resources Canada, Ottawa. pp. 107–112.*
- Quiring, D.T. 1994. Diel activity pattern of a nocturnal moth, *Zeiraphera canadensis*, in nature. *Entomologia Experimentalis et Applicata*, **73**: 111–120.
- Raubenheimer, D. and Browne, L.B. 2000. Developmental changes in the patterns of feeding in fourth- and fifth-instar *Helicoverpa armigera* caterpillars. *Physiological Entomology*, **25**: 390–399.
- Régnière, J. 1987. Temperature-dependent development of eggs and larvae of *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) and simulation of its seasonal history. *The Canadian Entomologist*, **119**: 717–728.
- Reichenbach, N.G. and Stairs, G.R. 1984. Response of the western spruce budworm (Lepidoptera: Tortricidae) to temperature and humidity: developmental rates and survivorship. *Environmental Entomology*, **13**: 611–618.
- Retnakaran, A. 1983. Spectrophotometric determination of larval ingestion rates in the spruce budworm (Lepidoptera: Tortricidae). *The Canadian Entomologist*, **115**: 31–40.
- Ruf, C. and Fieldler, K. 2002. Tent-based thermoregulation in social caterpillars of *Eriogaster lanestris* (Lepidoptera: Lasiocampidae): behavioral mechanisms and physical features of the tent. *Journal of Thermal Biology*, **27**: 493–501.
- Sanders, C.J. 1975. Factors affecting adult emergence and mating behavior of the eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *The Canadian Entomologist*, **107**: 967–977.
- SAS Institute. 1999. The SAS system version 8 for Windows. SAS Institute, Cary, North Carolina.
- Shiojiri, K., Ozawa, R., and Takabayashi, J. 2006. Plant volatiles, rather than light, determine the nocturnal behavior of a caterpillar. *PLoS Biology*, **4**: 1044–1047.
- Speight, G.C. 1987. The effects of weather on spruce budworm activity. B.Sc.F. Honours thesis, University of New Brunswick, Fredericton, New Brunswick, Canada.
- Thornhill, R. and Alcock, J. 1983. *The evolution of insect mating systems*. Harvard University Press, Cambridge.
- van Frankenhuzen, K. and Espinasse, S. 2010. Observations on the feeding behaviour of late-instar larvae of *Choristoneura fumiferana*. *The Canadian Entomologist*, **142**: 388–392.
- Wellington, W.G. 1950a. Effects of radiation on the temperatures of insects and habitats. *Scientific Agriculture*, **30**: 209–234.
- Wellington, W.G. 1950b. Variations in silk spinning and locomotor activities of larvae of the spruce budworm, *Choristoneura fumiferana* (Clem.), at different rates of evaporation. *Transactions of the Royal Society of Canada*, **44**: 89–101.
- Wellington, W.G. and Cameron, J.M. 1947. Investigations on meteorological and other physical factors. Bi-monthly Progress Report, Forest Insect Investigation, Agriculture Canada, **3**: 2.