THE INFLUENCE OF PARASITISM BY *APANTELES FUMIFERANAE* VIER. (HYMENOPTERA: BRACONIDAE) ON SPRING DISPERSAL AND CHANGES IN THE DISTRIBUTION OF LARVAE OF THE SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE)

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Abstract

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Most emerging 2nd-instar larvae of spruce budworm, *Choristoneura fumiferana* (Clem.), tested in the laboratory were photopositive and there was no difference in response between healthy larvae and larvae parasitized by *Apanteles fumiferanae* Vier. However, in the field, parasitized individuals were under-represented among larvae dispersing on silk threads between tree crowns. There is evidence that this was due to the relatively late emergence of parasitized larvae. These parasitized larvae therefore encountered fewer crawling larvae at the tips of branches, and consequently their propensity for dispersing was reduced.

The vertical distribution of dispersing, parasitized larvae caught on sticky traps more closely resembled that of established larvae than it did the vertical distribution of the overwintering population. This indicates that there was some differential redistribution of parasitized and nonparasitized individuals. Despite these differences, the estimate of parasitism by *A. fumiferanae* based on mid-crown branch samples is justified because it is most consistent and most closely reflects the overall frequency of parasitism.

Résumé

La plupart des larves émergeantes de la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clem.), testées en laboratoire étaient photopositives, et nous n'avons trouvé aucune différence de réponse entre les larves saines et celles parasitées par *Apanteles fumiferanae* Vier. Toutefois, sur le terrain, les individus parasités étaient sous-représentés parmi les larves se dispersant sur un fil de soie entre les couronnes des arbres. Certaines données suggèrent que ceci serait causé par l'émergence relativement tardive des larves parasitées. Ces mêmes larves rencontreraient moins de larves rampant à l'extrémité des branches, ce qui les porterait moins à se disperser.

La distribution verticale du taux de parasitisme dans les larves en dispersion capturées sur des pièges collants se rapproche davantage de celle dans les larves établies que de celle dans les larves en hibernation, ce qui indique une redistribution différentielle, dans la couronne, des individus parasités et non-parasités. En dépit de ces différences, un estimé du taux de parasitisme par *A. fumiferanae* obtenu à partir d'un échantillon prélevé à la mi-couronne est justifié puisque c'est là que ce taux est le plus consistant et qu'il reflète le plus étroitement le taux global.

Introduction

A sample of 2nd-instar larvae of the spruce budworm, *Choristoneura fumiferana* (Clem.), consisting of mid-crown foliage taken prior to spring emergence, is often used to estimate the density and spatial distribution of overwintering larvae (Miller 1958). The same sample can be used to estimate the rate of parasitism by *Apanteles fumiferanae* Vier., which attacks early-instar spruce budworm larvae during the summer and overwinters inside the host. After emerging from their hibernacula, budworm larvae are photopositive (Wellington 1948) and tend to move to the tips of branches, where they may disperse within and between crowns on silk threads. There is some evidence that the distribution of larvae in the crown changes during that period (unpublished data); however, the vertical

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distribution of dispersing larvae caught between tree crowns generally reflects the distribution of overwintering larvae and it is therefore not likely that observed changes in the distribution of larvae between the overwintering and feeding stages is due to inter-crown dispersal (Régnière and Fletcher 1983).

There does not appear to be much budworm mortality caused directly by inter-crown dispersal (Régnière and Fletcher 1983; Jennings *et al.* 1983) but it is not clear if this is equally true for parasitized and nonparasitized larvae. Lewis (1960) noted apparent increases in the proportion of parasitism by *A. fumiferanae* between emergence and establishment in feeding sites by host budworm larvae. Because all parasitism occurs in the previous summer, Lewis suggested that such an increase could be due to differences in the behavior of parasitized and healthy larvae. Lewis presented preliminary data suggesting that parasitized spruce budworm larvae did not exhibit a typical photopositive response. If parasitism by *A. fumiferanae* affects spruce budworm behavior, the result may be differential mortality, as well as redistribution, during the spring emergence period. This may, in turn, lead to errors in interpretation of parasitism rates obtained before and after emergence.

To test Lewis' hypothesis, and to determine the suitability of mid-crown samples to assess parasitism of the spruce budworm by *A. fumiferanae*, we compared the light responses of healthy and parasitized, newly emerged budworm. We also compared the frequency, and vertical distribution, of parasitism in spruce budworm larvae collected from (1) foliage prior to emergence, (2) sticky traps during inter-crown dispersal, and (3) foliage after establishment in feeding sites.

Materials and Methods

Parasitized and nonparasitized spruce budworm larvae were obtained by allowing 1st-instar larvae to spin hibernacula on balsam fir twigs bearing staminate flower scars and then exposing these to adult *A. fumiferanae* in the laboratory. The larvae were held for 2 weeks at 20°C, 2 weeks at 15°C, and were then stored 6 months at 2°C to fulfill the overwintering requirements of budworm larvae (Grisdale 1970). The twigs with larvae were then placed at room temperature in clear plastic containers designed to keep relative humidity near 100%. Emerging larvae were removed daily and tested immediately for their reactions to a point light source, using Wellington's (1948) method. Two 25-W, frosted lightbulbs were mounted at both ends of the hypotenuse (72.5 cm) of a right-angle, isosceles triangle made of heavy black cardboard. Budworm larvae were placed at the apex of the triangle (i.e. equidistant from either light source). Their response was classified as positive (larvae crawling directly between the two lightbulbs), negative, or neutral (larvae crawling away, off the cardboard, not crawling, or wandering aimlessly). The insects were then dissected and any larvae of *A. fumiferanae* were identified (Brown 1946) and recorded.

Field data were collected in 1984 in a mixed-wood stand located at Black Sturgeon Lake, in northern Ontario (49°20′N, 88°53′W). The current stand originated in the mid-1950s following a spruce budworm outbreak and subsequent harvesting. Codominant conifers are approximately 15 m high. Fifty percent of the stand consists of conifers, of which 80–90% are balsam fir (*Abies balsamea* [L.]) and 10–20% white spruce (*Picea glauca* [Moench] Voss) and black spruce (*P. mariana* [Mill.] B.S.P.).

To determine the frequency and vertical distribution of parasitism by *A. fumiferanae* in larvae dispersing between crowns, we dissected larvae caught on sticky traps suspended at four crown levels, between trees, according to the method of Régnière and Fletcher (1983). The traps were 2.5 m apart (12, 9.5, 7, and 5.5 m above the ground) and at least 1 m from the nearest foliage. Traps were coated with petroleum jelly to ease the removal of the budworm larvae. The larvae were washed in ethyl acetate before dissection, to remove the petroleum jelly.

Table 1. Reactions to light of emerging 2nd-instar larvae of *C. fumiferana* parasitized by *A. fumiferanae*. The numbers in parentheses are the percentage of total showing different responses

Parasitism	Response		Total
	Photopositive	Photonegative, neutral	
Nonparasitized	160 (81%)	38 (19%)	198
Parasitized	69 (77%)	21 (23%)	90
Total	229 (80%)	59 (20%)	288

Branch samples were taken from 10 balsam fir and 10 white spruce at four crown levels. A first sample, consisting of whole branches, was taken in mid-April, before budworm emergence. The budworm overwintering in this sample were recovered by the method of Miller (1958); the branches were cut into manageable sections, wrapped in paper-towelling, and suspended in individual cubicles in a well-lit room at 20°C, and 14L:10D photoperiod. The branches were sprayed with water regularly, and larvae were removed as they crawled on the outside of the wrapping. These larvae were then either dissected or reared individually (Thomas 1984) on artificial diet (McMorran 1965) to determine the rate of parasitism. Preliminary tests had shown that dissection and rearing yielded comparable estimates of parasitism.

Branch samples were taken during the spring dispersal period and larvae established in feeding sites were dissected. A final sample, consisting of 45-cm branch tips, was taken after most larvae had become established in feeding sites (reproductive or vegetative buds). The foliage from this sample was examined and the budworm larvae were removed. These larvae were all reared, as described above, to determine parasitism.

Results and Discussion

The reactions to light of 288 newly emerged 2nd-instar spruce budworm larvae were recorded (Table 1). As Wellington (1948) described, budworm of this age class have a strong photopositive orientation. The percentage of larvae exhibiting the various responses did not change significantly in larvae parasitized by *A. fumiferanae* ($G^2=0.64$, df$=1$, $P>0.05$). Thus, the hypothesis of Lewis (1960) that parasitized spruce budworm larvae have abnormal reactions to light is not supported. These results are not surprising as the probable role of the photopositive response is to orient larvae towards the tips of branches, where most of the new growth, and thus feeding sites, are found. Interference with that behavior might endanger the host larva and the parasite itself.

The frequency of parasitism by *A. fumiferanae* in dispersing budworm larvae was much lower than in overwintering larvae ($G^2=108.57$, df$=1$, $P<0.01$) (Table 2). Yet there was no difference in the frequency of parasitism between overwintering and feeding larval populations ($G^2=2.87$, df$=1$, $P>0.05$). This reduced frequency of parasitized individuals among larvae dispersing between crowns may be due to an alteration in behavior of parasitized larvae, although not in the way envisaged by Lewis (1960).

Miller (1958) noted that parasitized larvae tended to emerge from hibernation later than nonparasitized larvae. Renault (1972) made the same observation. We found a similar tendency in our sample of overwintering larvae in which the frequency of parasitism increased over the period that larvae were recovered from the wrapped foliage (Fig. 1). However, the time at which a larva was recovered from a wrapped branch was not necessarily the same time that it emerged from overwintering, because larvae may stay on the foliage inside the wrapper for some time after emerging from hibernacula.

Our inter-crown trapping data indicate that parasitized larvae tended to disperse between crowns later than did nonparasitized larvae (Fig. 2). Unpublished laboratory data of Régnière indicate that the bulk of dispersal of 2nd-instar budworm larvae on silk threads

Table 2. Frequency of parasitism by *A. fumiferanae* in *C. fumiferana* before emergence from hibernacula, trapped during inter-crown dispersal, and after establishment in feeding sites, at four crown levels. Black Sturgeon Lake, Ontario, 1984

Crown level	% parasitism ± SE (sample size)		
	Overwintering	Dispersing	Feeding
1 (top)	38.2±1.9 (638)	10.6±1.7 (319)	13.9±5.8 (36)
2	27.8±1.7 (669)	16.0±2.2 (281)	23.2±6.4 (43)
3	22.4±1.5 (759)	17.5±1.8 (439)	26.0±5.0 (77)
4 (bottom)	14.0±1.7 (422)	8.3±1.3 (469)	7.1±6.9 (14)
Overall	26.5±0.9 (2488)	12.9±0.9 (1508)	21.2±3.1 (170)

occurs at emergence or shortly thereafter. Thus our field data suggest that parasitized larvae tend to emerge from hibernacula later than nonparasitized larvae.

Although such a change in the time of emergence may not seriously compromise the survival of these late-emerging, parasitized larvae, it may have an important influence on their propensity to disperse. Wellington and Henson (1947) noted that dropping on a silk thread was promoted by crowding of larvae at the tips of branches. The unpublished data of Régnière also indicate that the propensity to disperse is density-dependent in 2nd-instar larvae of spruce budworm. We suggest that the observed reduction in frequency of parasitism in dispersing larvae is caused by the relatively late emergence of parasitized larvae, at a time when much of the population has already become established in feeding sites, and crowding of larvae crawling at the branch tips is less pronounced. The frequency of parasitism in spruce budworm larvae collected in the same plot, in feeding sites during and after the period of inter-crown larval dispersal, suggested an increase in the frequency of parasitism (Fig. 3). This would be expected if parasitized larvae did, indeed, emerge

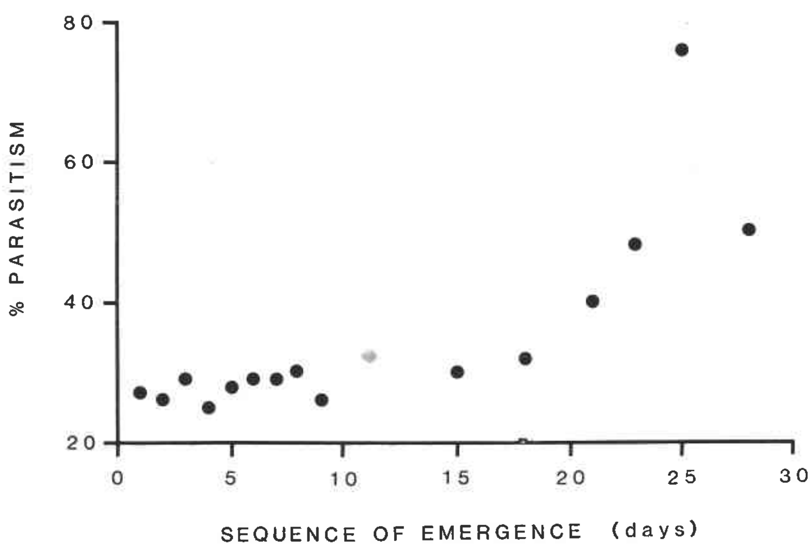

FIG. 1. Change in the frequency of parasitism by *A. fumiferanae* in spruce budworm larvae during the period when larvae emerged from branch-bundles in the laboratory.

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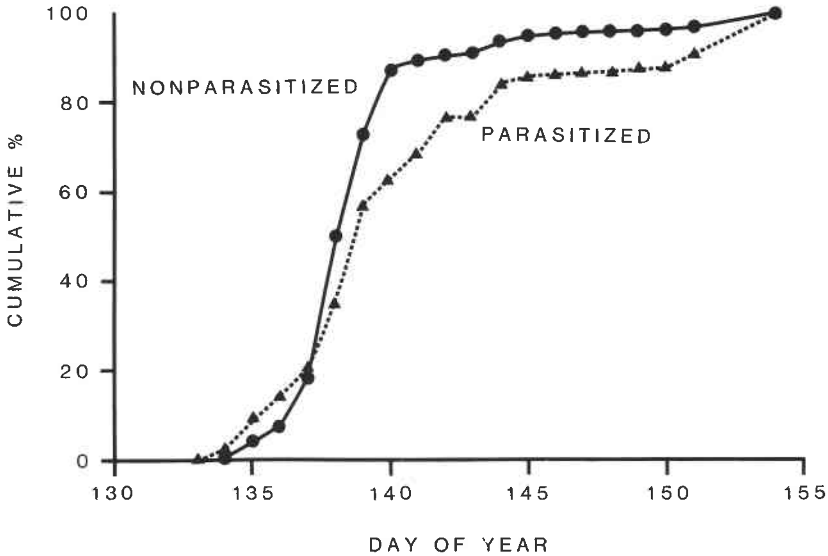

FIG. 2. Cumulative percentage catch of spruce budworm larvae on sticky traps set between tree crowns. Solid line: healthy larvae (n = 1314). Dotted line: larvae parasitized by *A. fumiferanae* (n = 194). Black Sturgeon Lake, 1984.

later than nonparasitized larvae. However, this tendency was not significant ($F = 4.52$, df = 1,2, $P > 0.15$).

The vertical distribution of parasitism differed considerably between the samples of overwintering, dispersing, and feeding larvae (Table 2). The distribution of parasitism in larvae caught dispersing between crowns reflected more closely that found in feeding larvae ($G^2 = 9.76$, df = 3, $P < 0.05$) than that in overwintering larvae ($G^2 = 44.97$, df = 3, $P < 0.001$). It is possible that parasitized larvae tend to redistribute by crawling towards the lower portion of the crown. However, it seems more likely that nonparasitized larvae redistribute towards the upper crown, and that some may redisperse between trees after

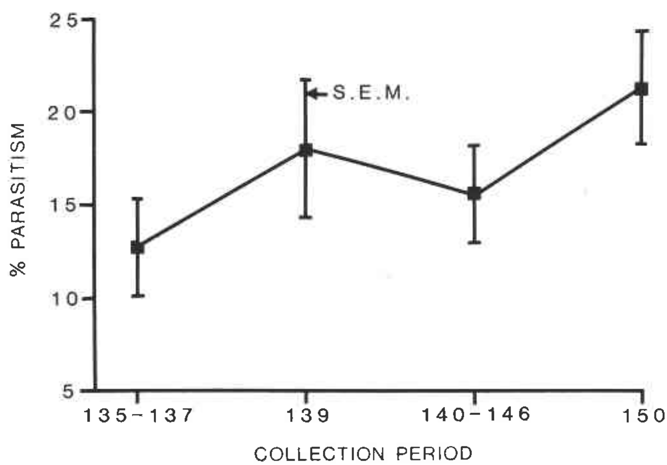

FIG. 3. Percentage parasitism by *A. fumiferanae* in feeding larvae of the spruce budworm during the spring emergence period. Black Sturgeon Lake, 1984. Collection period is in Julian dates.

getting to the upper crown, so that the relative frequency of parasitized larvae dispersing from there is reduced.

From the sampling point of view, however, it seems that the mid-crown remains an appropriate sample location from which to obtain estimates of the frequency of parasitism by *A. fumiferanae* on spruce budworm because it reflects overall frequency, and does not vary much as a result of differential mobility between parasitized and nonparasitized larvae.

These results emphasize the necessity of considering the behavior of insects in the design and interpretation of field studies. Differences in the distribution of parasitized and healthy individuals may lead to large sampling biases and introduce inconsistent estimates of parasitism (e.g. Ryan 1985). There are methodological problems in the estimation of budworm density between emergence in the spring and establishment of larvae in feeding sites. These problems are due largely to extensive larval movement at this time, and the possibility that this movement may be further influenced by parasitism complicates the estimation of parasitism during that period. But the measurement of the frequency of parasitism by *A. fumiferanae* based on mid-crown branch samples taken either before spring emergence or after the larvae are settled in their feeding sites is adequate because these estimates appear to be most consistent and closely reflect the overall frequency of parasitism.

Acknowledgments

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