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Life history of *Iridopsis ephyraria*, (Lepidoptera: Geometridae), a defoliator of eastern hemlock in eastern Canada

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Abstract: The pale-winged gray moth, *Iridopsis ephyraria* (Walker) (Lepidoptera: Geometridae), is an indigenous, widespread species in eastern North America, with no prior record of outbreak. It has recently caused high levels of defoliation of eastern hemlock, *Tsuga canadensis* (L.) Carr. in southwestern Nova Scotia, Canada. We carried out lab rearings and field collections to describe the life history of *I. ephyraria*. Distinctive green eggs were laid singly in bark crevices on the tree bole of mature hemlock trees. Egg densities from bark samples were highest in the upper crown of trees. Larvae emerged in late June and passed through five instars, determined by distinct head capsule widths. Larval mortality rates varied between 35.9 – 68.5%. Natural enemies of field-collected larvae included a fungus (*Entomophaga* sp.), unknown predators, and parasitism by *Pimpla pedalis* (Cresson) (Hymenoptera: Ichneumonidae) later in the outbreak. Both early- and late-instar larvae completed development when caged on eastern hemlock, red maple, *Acer rubrum* (L.), sweet fern, *Comptonia peregrina* (L.) Coult., balsam fir, *Abies balsamea* (L.) Mill., and red oak, *Quercus rubra* (L.), but not on white pine, *Pinus strobus* (L.). Pupation occurred in mid July, at a depth of <10 cm in the soil. Pupal mortality was 94%. Adults were active from late July until early August.

Résumé : L'arpenteuse à taches (*Iridopsis ephyraria* [Walker]) (Lépidoptères : Géométridés) est une espèce indigène largement répandue dans l'est de l'Amérique du Nord. Aucune infestation n'avait été signalée jusqu'à tout récemment, mais au cours des dernières années, l'*I. ephyraria* a gravement défolié la pruche du Canada (*Tsuga canadensis* [L.] Carr.) dans le sud-ouest de la Nouvelle-Écosse, au Canada. Nous avons réalisé des élevages en laboratoire et procédé à des cueillettes sur le terrain dans le but de décrire le cycle vital du ravageur. Les femelles déposent individuellement leurs œufs, d'un vert distinctif, parmi les anfractuosités de l'écorce, sur le fût de pruches matures. Les plus fortes densités d'œufs ont été observées dans les échantillons d'écorce provenant de la portion supérieure de la cime. Les œufs ont éclos à la fin de juin. La détermination des stades larvaires, au nombre de cinq, est fondée sur la mesure de la largeur de la capsule céphalique. Les taux de mortalité larvaire ont oscillé entre 35,9 et 68,5 %. Les ennemis naturels obtenus des chenilles récoltées sur le terrain incluaient un champignon (*Entomophaga* sp.), des prédateurs inconnus et, plus tard au cours de l'infestation, le parasitoïde *Pimpla pedalis* (Cresson) (Hyménoptères : Ichneumonidés). Lors des élevages en cage, tant les chenilles des premiers stades que du dernier stade ont bouclé leur développement sur la pruche du Canada, l'érable rouge (*Acer rubrum* [L.]), la comptonie voyageuse (*Comptonia peregrina* [L.] Coult., le sapin baumier (*Abies balsamea* [L.] Mill.) et le chêne rouge (*Quercus rubra* [L.]), mais pas sur le pin blanc (*Pinus strobus* [L.]). La nymphose est survenue au milieu de juillet, à plus de 10 cm dans le sol. La mortalité nymphale s'élevait à 94 %. Les adultes ont émergé entre la fin de juillet et le début d'août.

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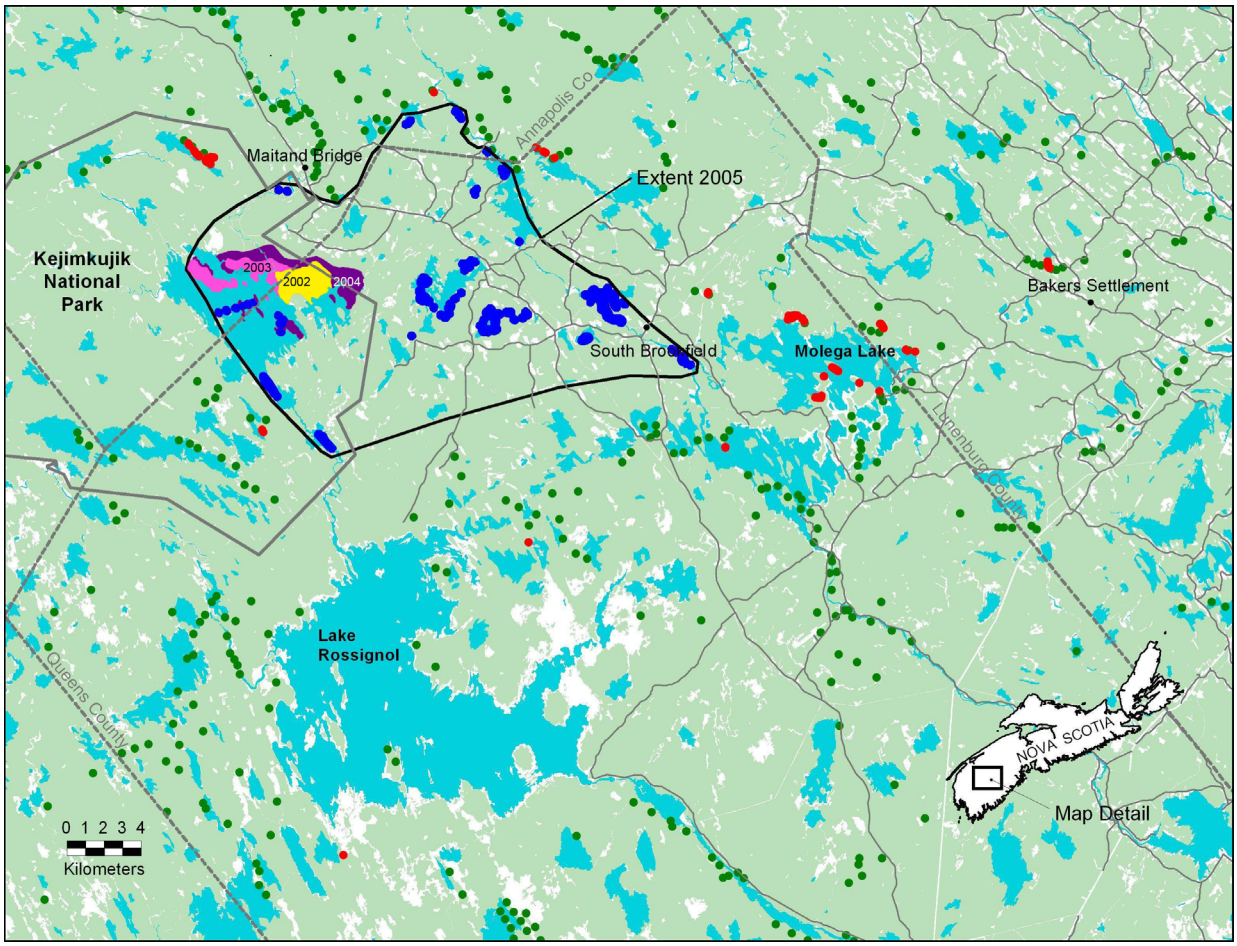
INTRODUCTION

The pale-winged gray moth, *Iridopsis ephyraria* (Walker) (Lepidoptera: Geometridae), recently caused high levels of defoliation of eastern hemlock, *Tsuga canadensis* (L.) Carr. (Pinaceae), in southwestern Nova Scotia resulting in mortality of up to 40% of mature hemlock in some stands (J. Kershaw, University of New Brunswick, unpublished data). In 2002, severe defoliation began in a few isolated hemlock stands, and has since spread across the region (Fig. 1). There is no record in the refereed literature of a previous pale-winged gray moth outbreak. In addition, aside from systematic articles (e.g., Rindge 1966; McGuffin 1977), and two government reports (Landry et al. 2002; Anonymous 2005), there is very little biological knowledge about this species. *Iridopsis ephyraria*, (formerly referred to as *Anacamptodes ephyraria*), is widely distributed from Alberta to Nova Scotia, and as far south as Texas (Ferguson 1954; Rindge 1966; McGuffin 1977). Larvae of *I. ephyraria* have been described both as green (Ferguson 1985), and alternatively, brown to black with a herringbone pattern along their dorsum (McGuffin 1977). Adults have been well described in Rindge (1966) and McGuffin (1977), but immature stages have not been formally studied in the field. Similarly, although the months when larvae, pupae and adults were present has been reported previously (Landry et al. 2002), seasonal occurrence of different life stages had not been described in detail, nor the number of larval instars determined.

Iridopsis ephyraria larvae have been collected on a wide variety of coniferous and deciduous trees and shrubs (Schaffner & Griswold 1934; Ferguson 1954; Prentice 1963; McGuffin 1977; Landry et al. 2002) but it is not known

Fig. 1. Distribution of hemlock defoliation by *I. ephyraria* detected during aerial surveys in 2002 (yellow), 2003 (pink), 2004 (purple). Defoliated sites in 2005 are indicated by dark blue circles with the extent of the outbreak outlined in black; in 2006 by red circles with undefoliated sites indicated by green circles.



whether the caterpillars feed extensively or can complete development on all reported species. This study is intended to fill the gaps in the current descriptive knowledge to permit accurate field diagnosis of all *I. ephyraria* life stages and to improve understanding of the ecology of this occasional pest. We describe all juvenile life stages and their seasonal phenology. Performance of larvae on a variety of potential hosts is quantified and mortality of larvae and pupae is documented. We also present a successful method to rear pale-winged gray moth eggs.

MATERIALS AND METHODS

Description of hemlock stands

This study was carried out in hemlock-dominated (>60% of the upper canopy) stands in southwestern Nova Scotia, Canada, in and around Kejimkujik National Park, on trees whose diameter at breast height ranged from 30.7 – 49.1 cm. The study area is part of the southwest Nova Scotia ecoregion in the Atlantic Maritime ecozone (Environment Canada 2005). Common canopy species, in addition to eastern hemlock, included red maple, *Acer rubrum* (L.) (Aceraceae); sugar maple, *Acer saccharum* (L.) (Aceraceae); red spruce, *Picea rubens* (Sarg.) (Pinaceae); yellow birch, *Betula alleghaniensis* (Britt.) (Betulaceae); and white pine, *Pinus strobus* (L.) (Pinaceae). Immature trees in the understory included balsam fir, *Abies balsamea* (L.) Mill. (Pinaceae); red oak, *Quercus rubra* (L.) (Fagaceae); American beech, *Fagus grandifolia* (Ehrh.) (Fagaceae); yellow birch; striped maple, *Acer pennsylvanicum* (L.) (Aceraceae); trembling aspen, *Populus tremuloides* (Michx.) (Salicaceae); and red maple. Sweet fern, *Comptonia peregrina* (L.) Coult. (Myricaceae); bracken fern, *Pteridium aquilinum* (L.) Kuhn. (Hypolepidaceae); and mosses were also present in the understory.

Life Stages of *I. ephyraria*

Eggs

Dissection of gravid females and observations of mated females in the laboratory and in the field suggested that *I. ephyraria* lays green eggs in deep bark crevices on the main bole of hemlock trees. Based on this information, eggs were obtained from both foam oviposition traps (Hébert et al. 2003) and bark samples from a private woodlot in South Brookfield, Nova Scotia, (N 44°23'45.6", W 65°00'17.1") in August 2005. To estimate egg densities on tree boles, squares of hemlock bark were cut to the depth of the phloem (<2.5 cm), removed and transported to the laboratory for processing. No other green eggs resembling those of *I. ephyraria* were found in the study area.

Bark samples were washed for eggs using the following procedure: 11 mL of Triton X-100 was added to 5.0 L of water at 25 °C in a large bucket, and lightly agitated and stirred every 10 minutes with bark samples, for 1 h. The liquid portion was poured through a #18 mesh sieve placed atop a #60 mesh sieve to filter out particles too large or too small to be eggs. Bark pieces were rinsed again above the sieve to remove any remaining eggs. Material collected by the #60 sieve was poured onto dampened filter paper placed in a 15 cm Büchner funnel. The funnel was mounted on a 2 L vacuum flask to drain off excess water, using a vacuum pump drawing at 1.5 - 2.0 L/min. The filter paper was then placed under a microscope to count the number of eggs removed from 100 cm^2 of bark surface.

Eggs were also obtained from foam oviposition traps, in a manner similar to that used for hemlock looper, *Lambdina fiscellaria fiscellaria* (Guenée) (Lepidoptera: Geometridae) (Hébert et al. 2003). Foam oviposition traps consisted of white polyurethane foam cut into 30 cm x 17 cm x 2.5 cm blocks. One foam trap was stapled to the bole of each of 30 hemlock, located 10 m apart along a linear transect, just prior to pupation in late July. Foam traps were removed from the tree bole following the end of adult activity (the end of August) and examined under a microscope for eggs.

In 2005, foam oviposition traps containing eggs were held outdoors throughout the winter to obtain emerging first-instar larvae the following spring. In each foam trap, the position of viable-looking (i.e., green and rounded) eggs was marked with a permanent marker. Foam traps were dipped in tap water, and permitted to air dry at 20 °C for two days. Once dry, foam traps were placed in a nylon mesh bag outdoors in an area sheltered from snow, in Fredericton, N.B. In early May, eggs were brought into the lab and removed from the foam traps. One hundred forty-three viable-looking eggs were placed in groups of five eggs, (except 2 groups with six eggs, one with four eggs and one with two eggs), on damp filter paper, in 29 small plastic cups (240 mL, Solo). Eggs were lightly misted daily with water, enough to slightly dampen the filter paper, until hatch occurred.

To determine where eggs were laid on the bole of hemlock trees, four mature hemlock trees, 18.6 ± 1.8 m in height, were felled in South Brookfield. Strips of bark ranging from 90 cm^2 to 945 cm^2 were taken every 2.4 m along the length of the bole of each tree, beginning 1.3 m from the ground, and were washed for eggs. As the diameter of the tree bole is expected to decline sharply near the tree apex, no egg samples were taken <1.5 m from the top of the tree. Egg densities were log-

transformed to normalize the data, and sample heights were represented as a proportion of the tree height.

Larvae

Larval colouration was described and instars differentiated by head capsule widths. To collect first-instar larvae, a 5.1-cm wide band of adhesive tape (PheroTech Inc.), sticky on both sides, was placed around the lower bole of mature hemlock trees just after egg hatch, in 2005. The bands ensnared first instars from the lower bole of the tree as they climbed up towards foliage in the crown. Adhesive bands were placed around 30 haphazardly selected mature hemlock trees 1.5 m from the ground, near the group campground site in Kejimkujik National Park (N 44°24'00.4"; W 65°13'58.5") prior to egg hatch. One week following egg hatch, first-instar larval corpses were removed from the adhesive bands with forceps. In 2006, first instars that emerged from overwintered eggs laid in oviposition traps were examined.

One hundred second-instar larvae were obtained from the field by beating hemlock tree foliage with a wooden dowel and collecting larvae on a 1 m^2 beating sheet (Lucarotti et al. 1998). Individual larvae were placed in 13 cm x 7 cm x 7 cm transparent plastic cups with a fine nylon mesh bottom that were placed upside down on a Styrofoam cup base. Cups were placed in a field insectary that provided shelter from rain, but also allowed airflow with the outdoors, due to mesh walls on all sides. A small branch of freshly cut hemlock foliage in water was placed in each cup. Hemlock foliage was replaced with fresh foliage every 4 – 7 days, as needed. Head capsule widths were measured weekly (± 1 day) from 12 June until pupation (approximately 21 July). In addition, groups of 40 larvae were collected weekly from the field using beating sheets, beginning 12 June, from the same site. Head capsule widths of collected larvae were measured to verify that insectary larvae were similar to those in the field and to determine the number of instars.

Larval mortality was estimated in 2006 during the declining phase of the current outbreak. One lower-crown hemlock branch, located approximately 1.5 m above the ground, was selected and tagged on each of 10 trees at three sites. All trees were mature and located at the edge of stands. The number of larvae per branch was counted on 23 June, when most larvae were second instars, and 6 July, just prior to pupation. First-instar larvae were too small to accurately count on hemlock foliage. It was assumed that immigration and emigration from the branch were approximately equal. The percent mortality of insectary-reared larvae was compared to field mortality rates to see if the absence of parasitism or predation after the second instar (in the field insectary) increased survival.

In 2004 and 2005, groups of 100+ larvae were collected every 14 days from high population density sites in Kejimkujik National Park using a beating sheet. Larvae were reared on freshly cut hemlock foliage in groups of 10 - 30 larvae, in large mesh cages (40 cm x 25 cm x 15 cm) within the field insectary and observed daily for parasitoid emergence and fungal infection, until the end of pupation. In 2006, 30 groups of five second-instar larvae were collected from hemlock and isolated in nylon mesh sleeve cages on hemlock branches at the same site. These were monitored until late in the third instar for fungal infection, easily identified by the drooping posture of dead cadavers, or parasitoid emergence. Field-collected third and fourth instars were reared similarly until pupation. Any parasitoids that emerged were captured and identified to species. Fungal identification was carried out by examination of the host cadaver and examining fungal conidia and smears of the cadavers with phase contrast microscopy (Humber 1998).

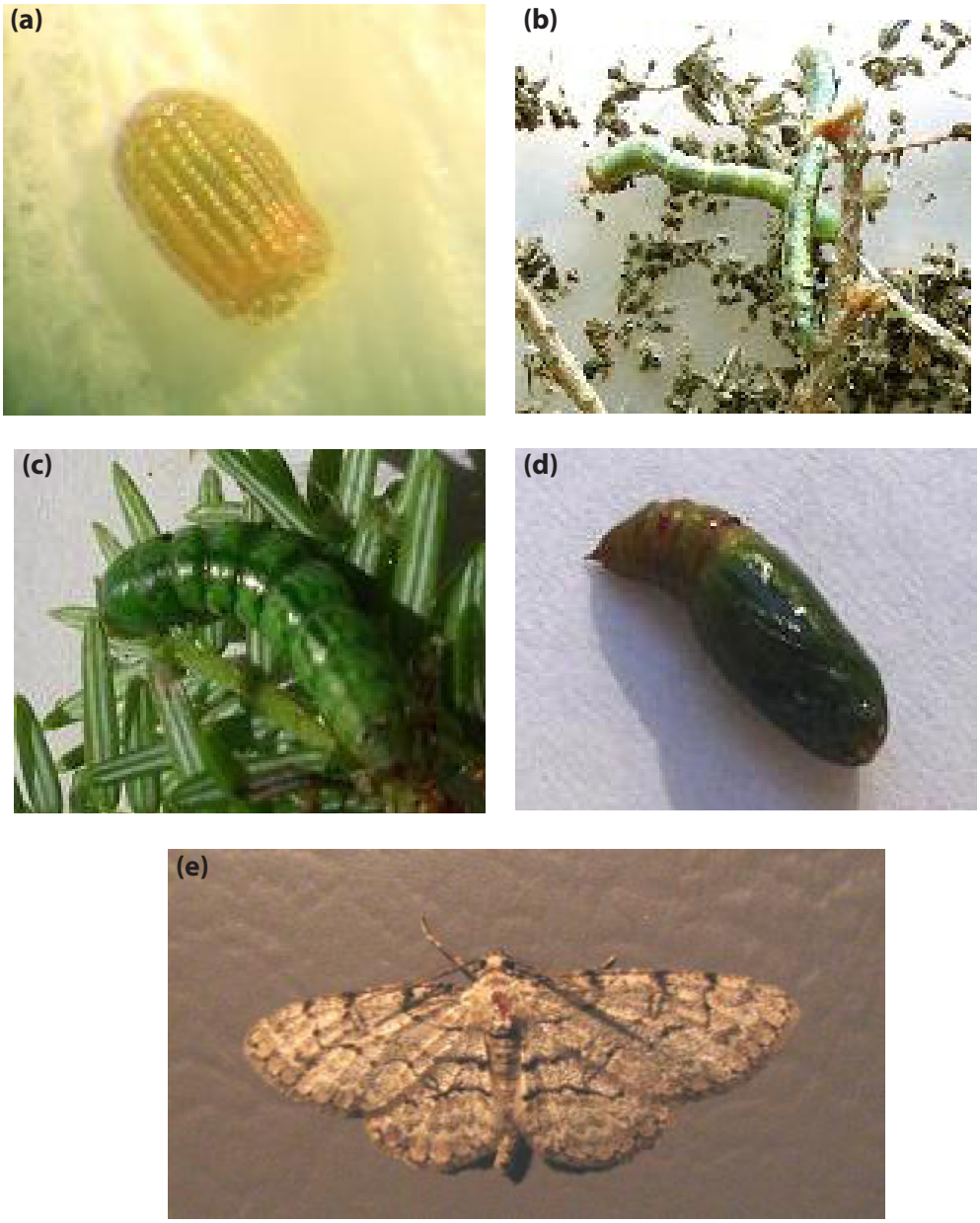
In early June, 2005, early instar *I. ephyraria* were observed feeding on red maple, white pine, sweet fern, balsam fir and red oak. To determine the suitability of these potential alternate host plants, five second-instar larvae collected from hemlock were placed on each of 10 branches of each host (one branch per tree) and enclosed within nylon mesh sleeve cages in the field. When the majority of larvae were in the late third instar (after 10 days), cages were opened; surviving larvae were counted and removed. Five new late third- or early fourth-instar larvae, collected from hemlock foliage, were then placed on the study branches and enclosed in sleeve cages until pupation (6 days). Survival was determined for early instars (i.e., second until late third/fourth instar), and for late instars (i.e., third/fourth instar until pupation). The influence of host plant and instar stage on survival was evaluated using a two-way ANOVA (Zar 1984).

Pupae - Adults

Descriptions of pupation and pupae were based on visual observations of *I. ephyraria* individuals developing in the field insectary in 2005. As pupation began, caterpillars were observed continuously and morphological changes occurring during metamorphosis recorded.

To determine the rate of pupal mortality in the soil, soil samples were collected to estimate the number of prepupae entering the ground, and emergence traps were monitored to measure the number of adults emerging from an adjacent area of soil. In 2005, one low-hanging

Fig. 2. Life stages of *I. ephyraria*: (a) egg, a few weeks after oviposition; (b) late-instar larvae; (c) prepupa; (d) pupa; and (e) adult moth.



branch on each of 10 trees at five sites in Kejimkujik National Park was selected and tagged. As soon as all larvae had dropped from branches, a 30-cm diameter circle of soil underneath the branch was dug to a depth of 11 cm, and carefully sifted for pupae. To estimate the number of emerging adults, one circular 30-cm diameter emergence trap was placed adjacent to the soil-sifted area beneath each branch, and the number of emerging moths counted and removed daily. Voucher specimens of adults have been deposited at the Canadian Forest Service, Atlantic Forestry Centre in Fredericton, New Brunswick.

RESULTS

Eggs

Iridopsis ephyraria eggs were easily identifiable as bright

green with a reddish, flattened end, with regular rows of small, rounded swellings along their length, and were approximately 0.5 mm wide and 0.8 mm long (Fig. 2a). In the bark samples, eggs were regularly observed wedged into deep crevices, or underneath flaking pieces of lichen. Except for two cases where eggs were laid in pairs, eggs were laid singly on all bark samples and foam traps (N = 200).

Following overwintering, 87.3% of eggs (N = 182) in foam traps retained their original oval shape and were not deflated or desiccated. Larvae emerged from 70.8 ± 0.1% (N = 29 cups) of the 143 successfully transferred viable-looking eggs. Using this rearing method, the total survival rate from egg lay to larval emergence was 61.8%. No parasitoids or fungi were detected, and all egg mortality appeared to be due to desiccation.

Although there was considerable variation, egg density increased linearly from the bottom to the top of tree boles (Fig. 3). The majority of eggs were laid on the bole within the live crown (108.94 ± 26.99 eggs/1000 cm²) rather than on the lower tree bole (17.43 ± 5.04 eggs/1000 cm²).

Fig. 3. Relationship between the log-transformed density of *I. ephyraria* eggs from bark samples and the vertical height up the bole of four mature hemlock trees, expressed as the proportion of the total height.

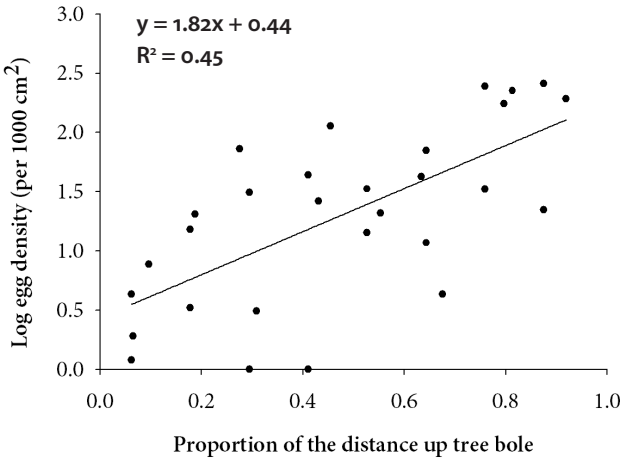
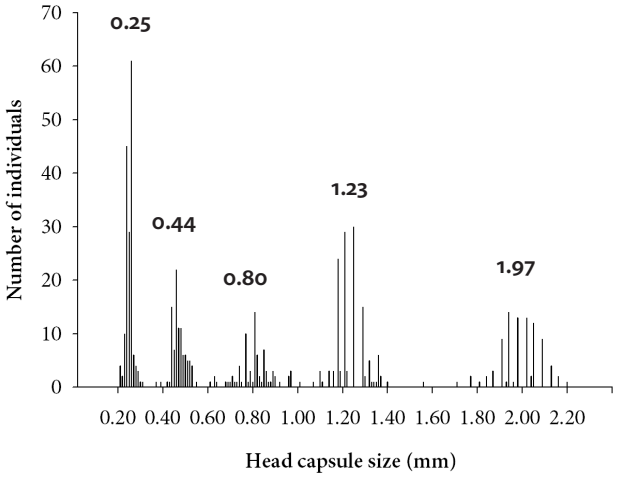


Fig. 4. Frequency distribution of head capsule widths of *I. ephyraria* larvae from field collections, insectary rearings and first-instar larvae that emerged from overwintered eggs in the lab. Means of the widths for each instar are indicated above the bars (SE < 0.01 for all means), N = 125, 96, 76, 104, 118 for first-, second-, third-, fourth-, fifth-instar larvae, respectively.



Larvae

The distribution of head capsule widths suggests that *I. ephyraria* passes through five instars, each with a non-overlapping range of head capsule widths (Fig. 4). The ranges for first, second, third, fourth, and fifth instars were 0.20 – 0.29 mm, 0.37 – 0.54 mm, 0.61 – 0.97 mm, 1.01 – 1.40 mm, and 1.68 – 2.20 mm, respectively. Only one head capsule width (1.55 mm) was not included in these five size ranges (Fig. 4).

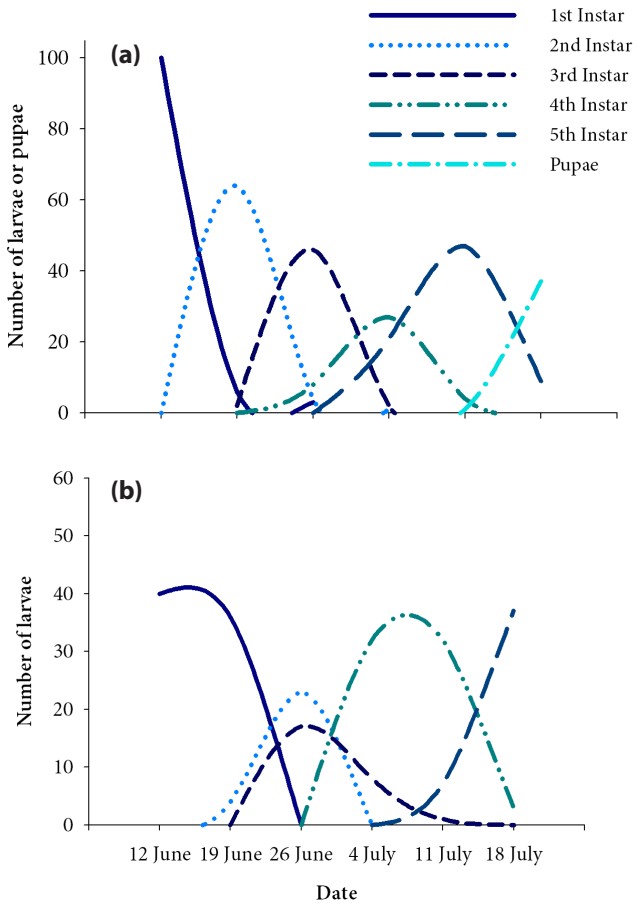
Larvae were easily distinguished by a rust-coloured head capsule with two prominent dorsal lobes. Larval bodies varied in colour from dark olive to a brilliant emerald green (Fig. 2b). First and second instars were often paler than older instars. The dorsal herringbone pattern reported by McGuffin (1977) was present in only a few larvae, and then only very faintly.

Larvae developed approximately one week faster in the insectary (Fig. 5a) than in the field (Fig. 5b). Most instars were only present for 7 – 10 days, except for the fourth instar, which occurred for more than 2 weeks (Fig. 5b). There was substantial overlap in the timing of larval instars for individuals that developed in the insectary and in the field on almost all sample dates. At the end of larval development, larvae ceased to feed and became shortened, fattened, bright in colour, and glabrous (Fig. 2c). Prepupae subsequently dropped to the soil, burying themselves just under the surface to a maximum depth of <10 cm.

Larval mortality varied significantly between the three study sites in 2006 ($F_{2,29} = 5.63$; $P < 0.01$), and ranged between 35.9 ± 7.6% and 68.9 ± 7.1%. Larval mortality in the insectary in 2005 was 53%, which falls within this range.

A fungus in the genus *Entomophaga*, likely *E. aulicae*, was observed on late instar larvae in the insectary and

Fig. 5. The temporal distribution of *I. ephyraria* instars during summer 2005. The spline function of SigmaPlot (2001, Version 7.0) was used to estimate densities between the six sample dates. Distributions of the number of larvae in each instar are shown for: a) insectary-reared larvae, (N = 108, 69, 50, 39, 77, 38 for first-, second-, third-, fourth-, fifth-instar larvae and pupae, respectively); and b) field-collected larvae (N = 76, 27, 26, 67, 44 for first-, second-, third-, fourth-, fifth-instar larvae, respectively).



in the field during 2004, 2005 and 2006. Larvae killed by the fungus appeared gray and rigid. No parasitoids emerged from larvae during any of the three years of study. In the field, predation of larvae by large arachnids, ants (Hymenoptera: Formicidae) and wasps (various Hymenoptera) early in the season, and by red squirrels (*Tamiasciurus hudsonicus* (Erxleben)) and birds later in the season was occasionally observed.

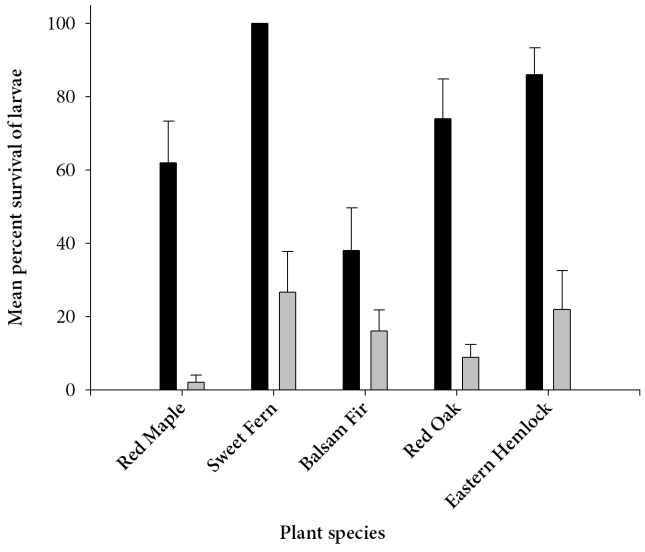
As no larvae survived on white pine, this species was removed from subsequent analyses. Survival of early instars (71.4 ± 5.0%) was significantly greater than that of late instars (15.3 ± 3.4%) ($F_{1,87} = 109.4$; $P < 0.001$). Survival varied significantly among plant species ($F_{4,86} = 5.45$; $P < 0.002$). Early instar survival was high on all the potential hosts examined except balsam fir, where survival only averaged 38% (Fig. 6). In contrast, late instars had the highest survival on sweet fern and eastern hemlock (Fig. 6), resulting in an interaction between host plant and instar stage ($F_{4,86} = 2.76$; $P = 0.033$).

Pupae - Adults

The transformation to pupa took <1 hr. Initially, pupae retained a greenish hue (Fig. 2d) before fading to reddish-brown. Pupal length ranged between 8.1 – 12.8 mm, with an average of 10.8 ± 0.2 mm (N = 44). Based on field observations and emergence traps, the duration of pupation in the soil was approximately 1–2 weeks.

The average mortality of pupae was 94.2 ± 2.9% and did not differ between sites ($F_{4,39} = 1.23$; $P = 0.31$). No parasitoids emerged from pupae in 2004 or 2005 but adult *Pimpla pedalis* (Cresson) (Hymenoptera: Ichneumonidae) emerged singly from approximately 6.2% (N = 73) of field-collected pupae in 2006.

Fig. 6. Mean (± SE) percent survival of early- (black bars) and late-instar (gray bars) larvae of *I. ephyraria* on six potential alternate host species in South Brookfield in 2006.



Adults emerged between 27 July and 16 August 2005, about 2 weeks after the beginning of pupation (Fig. 5a). Casual field observations suggested that peak moth abundance occurred between 7 and 13 August 2005.

DISCUSSION

Pale-winged gray moth eggs were laid singly in deep bark crevices of hemlock, and females appear to oviposit preferentially in the upper bole. These behaviours may minimize egg predation (Warrington & Whittaker 1985) or mortality from fungal pathogens (Hajek 2001). Larvae emerging from eggs in the upper bole might also benefit from closer proximity to sun leaves (Fortin & Mauffette 2002; Ide 2006).

Given the large number of eggs collected from foam traps and bark samples, both sampling techniques may provide good estimates of *I. ephyraria* egg densities. Foam traps have already been successfully used to sample hemlock looper eggs (Hébert et al. 2003).

Although the descriptions of larval instars in the present study differed from those in previous reports, where body colour was substantially darker and a dorsal herringbone pattern was more apparent (McGuffin 1977; Landry et al. 2002), it is possible that these differences reflect a local phenotype. Head capsules of first and second instars had not been measured previously. Mean larval head capsule measurements reported in this paper are consistent with the ranges for fourth and fifth instars and the single measurement value for the third instar presented in McGuffin (1977), although our fourth instar ranges are broader. The broader range of head capsule widths of fourth instars observed in the present study might be due to feeding on different hosts (Bernays 1986), or localized differences in morphology. Pupae were morphologically similar to those described by McGuffin (1977).

Larvae developed one week more quickly in the field insectary than in the National Park, most likely due to warmer ambient temperatures (Stamp & Bowers 1990) and a plentiful diet (Tammaru et al. 2004).

The fungal pathogen was present at all sites and appeared to kill a large number of larvae. Several years prior to this outbreak, *E. aulicae* infected the white-marked tussock moth, *Orgyia leucostigma leucostigma* (J.E. Smith) (Lepidoptera: Lymantriidae) in the same area of Nova Scotia (van Frankenhuyzen et al. 2002), and *L. fiscellaria fiscellaria* in New Brunswick (Lucarotti et al. 1998). Widespread infections in white-marked tussock moth larvae in Nova Scotia may have established a reservoir of *E. aulicae* in regional soils (Hajek 2001).

In contrast to high levels of parasitism in other caterpillars (Auerbach 1991; Hawkins et al. 1997; Barbosa et al. 2001; Tanhuanpaa et al. 2001), parasitoids were not detected in this system until 2006, when parasitism rates were still very low. Low parasitism rates have been observed for other insects feeding on *Tsuga*, supporting the hypothesis that this host plant may influence parasitoid behaviour or performance (Lill et al. 2002). Larval survival in the field was similar to that in the field insectary, suggesting that predation rates were also relatively low during this study.

Larvae survived well on all hosts studied except balsam fir and white pine, supporting reports that *I. ephyraria* has a wide host range (Prentice 1963; McGuffin 1977). The generalist diet of *I. ephyraria* is consistent with that of other geometrid larvae (Carroll 1956; Cuming 1961). Feeding on alternate hosts might allow *I. ephyraria* larvae to maximize a wider variety of nutrients, minimize hemlock toxins, and ensure adequate nitrogen uptake (e.g., Barbosa & Greenblatt 1979; Stockhoff 1993). The majority of larvae observed in the field remained on hemlock foliage for the duration of their larval period, and it is not known if larvae switch hosts or whether individual larvae could specialize on certain hosts. Eastern hemlock has more canopy nitrogen and a lower nitrogen mineralization rate than other conifers (Ollinger et al. 2002), making it more nutritious for caterpillars (White 1984), potentially leading to the observed lower survival rates on balsam fir and white pine. It should be noted that larvae for this study were obtained from hemlock foliage and might have been pre-adapted to feed on hemlock through previous experience (Jermy et al. 1968; deBoer & Hanson 1984).

Pupal mortality in the soil was very high but cannot be explained by pupal parasitism. Pupal mortality might be due to predation by insects (Frank 1967) or small mammals (Port & Thompson 1980; Valenti et al. 1998; Tanhuanpaa et al. 1999), as previously reported for other moths pupating in the soil.

Although outbreaks of *I. ephyraria* have not been previously reported, it has similar habits to a frequently outbreaking geometrid, the hemlock looper. The hemlock looper also overwinters as an egg, is univoltine (Raske et al. 1995), eats current-year as well as old foliage, is capable of generalist feeding, has a patchy feeding distribution (Carroll 1956), and is a wasteful feeder, not consuming the entire needle (Carroll 1956; Raske et al. 1995). As a result, it might be possible to effectively use some of the ecological knowledge and management tools already developed for the hemlock looper, such as foam oviposition traps (Hébert et al. 2003), to manage this congeneric. Despite these similarities, the hemlock looper differs from *I. ephyraria* in several respects, such as the hemlock looper's tendency to lay eggs in clusters (Carroll 1956) and to defoliate more hosts at moderate densities (Rose & Lindquist 1977). Consequently, a complete understanding

of the life history of the pale-winged gray moth and of the factors influencing its dynamics is indispensable for the establishment of a successful pest management program.

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