Aerial dispersal and host plant selection by neonate *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae)

ROBERT G. MOORE 1 and LAWRENCE M. HANKS 2  
1United States Army Center for Health Promotion and Preventive Medicine, North, Attention: MCHB-AN Entomological Sciences Division, Maryland and 2Department of Entomology, University of Illinois at Urbana–Champaign, U.S.A.

Abstract. 1. Neonate evergreen bagworms, *Thyridopteryx ephemeraeformis* (Haworth) (Lepidoptera: Psychidae), disperse by dropping on a strand of silk, termed *silking*, and ballooning on the wind. Larvae construct silken bags with fragments of plant foliage. This species is highly polyphagous, feeding on more than 125 species of woody plants of 45 families. The larvae commonly infests juniper (*Juniperus* spp.) and arborvitae (*Thuja* spp.), but rarely feed on deciduous hosts such as maples. The hypothesis is proposed that polyphagy in *T. ephemeraeformis* is maintained by variation among larvae in dispersal behaviour, and time constraints on the opportunity to disperse, but patterns of host species preference result from a predisposition for larvae to settle on arborvitae and juniper but disperse from other hosts.

2. Consistent with that hypothesis, laboratory experiments revealed: (a) starved larvae varied in their tendency to disperse from paper leaf models; (b) starved larvae readily silked only during their first day; (c) larvae became increasingly sedentary the longer they were exposed to plant foliage; (d) when provided with several opportunities to silk, larvae became sedentary after exposure to arborvitae foliage, but repeatedly silked after exposure to maple (*Acer* species) foliage or paper; and (e) larvae were less inclined to silk from foliage of arborvitae than from maple.

3. Field experiments supported the hypothesis by demonstrating that: (a) neonates tended to disperse from maple leaves while larvae older than 1 day tended to settle and remain; and (b) neonates were less likely to disperse from arborvitae and juniper trees than from maples.

Key words. Bagworm, ballooning, caterpillar, host plant location, plant–insect interaction
Barbosa, 1976), but dispersal behaviour can be modified by a variety of intrinsic and extrinsic factors (Leonard, 1970; Lance & Barbosa, 1981; Carrière, 1992; Diss et al., 1996; Rhaïnds et al., 1997, 2002). Neonates may be more likely to silk and balloon if they encounter hosts of low quality (Ramachandran, 1987; Rhaïnds et al., 2002), non-preferred or unsuitable host species (van der Linde, 1971; Capinera & Barbosa, 1976; Lance & Barbosa, 1981; Futuyma et al., 1984; Ramachandran, 1987), or when food is not available (Leonard, 1970; van der Linde, 1971; Capinera & Barbosa, 1976). Dispersal behaviour also may show diel periodicity (Mitchell, 1979; Zlotina et al., 1999; Rhaïnds et al., 2002) and may be influenced by weather, particularly wind speed, air temperature, and precipitation (Mitchell, 1979; McManus & Mason, 1983; Cox & Potter, 1986).

Passive aerial dispersal is risky for phytophagous insects because they can not control flight direction or the plant species to which they are carried, and consequently is associated with high mortality rates (e.g. Hanks & Denno, 1998; Zalucki et al., 2002). In fact, most aerially dispersing caterpillars travel only short distances and many perish on the ground (Mitchell, 1979; Weseloh, 1985, 1997; Cox & Potter, 1986; Ghent, 1999; Rhaïnds et al., 2002). Of course, the odds of encountering a suitable host are improved greatly if larvae are polyphagous (see Young, 1997). In that case, the greatest proportion of ballooning neonates presumably would be intercepted by the host species that presents the largest target: those that are most abundant, tallest, and having the broadest canopies (Ghent, 1999). Ballooning caterpillars may achieve some degree of host selection by rejecting hosts and re-dispersing (Lance & Barbosa, 1981; Lance, 1983; Barbosa et al., 1989; Ward et al., 1990; Rhaïnds et al., 2002; Zalucki et al., 2002), but this ability is temporally constrained, however, because small larvae succumb quickly to starvation and desiccation (Capinera & Barbosa, 1976; Stockoff, 1991; Reavey, 1993).

In this article, new information on aerial dispersal by neonate caterpillars of the evergreen bagworm, *Thyridopteryx ephemeraeformis* (Haworth) (Lepidoptera: Psychidae) is presented, and the relationship between dispersal behaviour and host species preference is evaluated. This species is native to North America and is univoltine. Larvae construct a silken bag that they ornament with fragments of bark and foliage, but during this process do not consume plant materials (for general information on biology and behaviour, see Haseman, 1912; Jones, 1927; Jones & Parks, 1928; Kaufmann, 1968; Leonhardt et al., 1983; Cox & Potter, 1986; Neal, 1986). Larvae never leave their bag, with only their head and thorax protruding, and enlarge it as they grow. Vermiform adult females fill their bags with as many as 1000 eggs. Eggs overwinter in the maternal bag and neonates (~2 mm long) usually hatch in early June in the area of the study (Champaign County, Illinois; Morden & Waldbauer, 1971).

Neonate *T. ephemeraeformis* usually balloon in the morning (Cox & Potter, 1986) and may silk immediately upon emerging from the mother’s bag (Cox & Potter, 1986; Ghent, 1999), as is true for other psychid species (Gromyszek et al., 1960). Silking behaviour is not influenced by the order in which larvae emerge from the mother’s bag, and is only weakly influenced by maternal effects such as the maternal host (Ward et al., 1990; Moore, 2001).

*Thyridopteryx ephemeraeformis* is a highly polyphagous species (see Howard & Chittenden, 1908; Haseman, 1912; Neck, 1977; Johnson & Lyon, 1988), feeding on more than 125 species of woody plants of 45 families (Davis, 1964). Despite its polyphagous nature, high-density populations usually arise on the evergreen shrubs juniper or red cedar (*Juniperus* spp.) and arborvitae (*Thuja* spp.) of the Cupressaceae, but rarely on maples (*Acer* spp., *Aceraceae*) and other deciduous trees (*Jones & Parks, 1928; Johnson & Lyon, 1988*). In the area of the studies (Champaign Co., Illinois), infestations most commonly arise on *Juniperus virginiana* L., *J. communis* L., and *Thuja occidentalis* L., including low-growing cultivars (Ghent, 1999; L.M. Hanks, pers. obs.). These species do not seem the most likely to intercept ballooning larvae, being neither the most abundant of potential hosts in urban habitats (maples are dominant) nor the largest (sycamores, *Platanus* spp., can be much taller and broader; L.M. Hanks, pers. obs.).

Moreover, this pattern of dispersion apparently is not attributable to variation in larval performance because *T. ephemeraeformis* can complete development on non-preferred hosts, and even unnatural hosts such as sedges (*Carex* spp.; Howard & Chittenden, 1908; Haseman, 1912; Jones & Parks, 1928; Neal & Santamour, 1990; Ward et al., 1990, 1991).

The hypothesis is proposed that polyphagy in *T. ephemeraeformis* is maintained by inherent variation among larvae in the tendency to disperse, and time constraints on dispersal, but that patterns in host species preference result from a tendency in larvae to aerially disperse from non-preferred hosts, but to settle on arborvitae and juniper. This hypothesis was evaluated with experiments that tested the following predictions: (a) neonates vary in their inherent tendency to disperse; (b) the tendency to disperse declines with larval age; (c) the tendency to disperse declines with exposure to host foliage (and the opportunity to construct a bag); and (d) larvae will tend to disperse from non-preferred hosts but remain on preferred hosts. The research contributes much-needed information on the behaviour and ecology of first-instar caterpillars, rarely studied because of their small size (see Zalucki et al., 2002), and on the association between aerial dispersal and host plant preference (see Ward et al., 1990).

Materials and methods

Sources of larvae

*Thyridopteryx ephemeraeformis* bags that contained eggs were collected from junipers and arborvitae in late fall and early winter from areas in Champaign County, Illinois, including The Hoot Owl Christmas Tree Farm, the campus of the University of Illinois at Urbana–Champaign, Mt...
Olive cemetery in Mayview, and the 4Es Tree Farm in Macon County, Illinois. Bags were stored in a 4°C refrigerator to suspend egg development, and emergence was encouraged by bringing eggs to room temperature. Neonates usually emerged within 4 weeks. It was not possible to discriminate between sexes of neonate T. ephemeraeformis and therefore sexual differences in dispersal behaviour could not be directly assessed.

Tree species

In the experiments, T. ephemeraeformis larvae were presented with juniper (J. virginiana or J. communis) and arbor vitae (T. occidentalis) that are the common hosts (hence referred to as preferred hosts), as well as maples which are rarely infested (non-preferred hosts), including silver, sugar, and Norway maples (Acer saccharinum L., A. saccharum Marshall, and A. platanoides L.; Aceraceae). Maples are recorded hosts of T. ephemeraeformis (see Jones & Parks, 1928; Davis, 1964; Johnson & Lyon, 1988), and larvae can complete development on them (Baerg, 1928; Barrows, 1974). In one study, tree of heaven [Ailanthus altissima (Miller), Simaroubaceae] was included, which is not a host of T. ephemeraeformis (see Davis, 1964; L. M. Hanks, pers. obs.).

Bioassay design

Neonate T. ephemeraeformis continually produced a strand of silk while walking that anchored them to the substrate (gypsy moth larvae show the same behaviour; McManus & Mason, 1983). It was considered that silking, dropping from the substrate on a silk line, constituted a dispersal behaviour and predisposed neonates to ballooning and aerial dispersal; larvae that were more inclined to silk would be more likely to disperse from the host (see Reavey, 1993).

To study dispersal behaviour, laboratory bioassays were conducted in which larvae were transferred either to paper or to foliage of host plants and the percentage that silked during a specific time interval (dispersal rate) was recorded. Placing neonate caterpillars on paper leaf models provides an assessment of the innate tendency and ability to disperse while controlling for the influence of the substrate (see Capinera & Barbosa, 1976; Ramachandran, 1987). The apparatus for the filter paper bioassays consisted of 10 pieces of filter paper (halved disks, 11 cm in diameter; no. 1 qualitative, Whatman International Ltd, Kent, U.K.) attached 3 cm apart to a glass rod with binder clips, positioned at an angle of ~20° above horizontal and 10 cm above the bench top. Bioassays were conducted on a bench adjacent to north facing windows, under ambient room conditions. Air vents were blocked to eliminate breezes that might influence dispersal (wind speed was undetectable with a hot wire anemometer). With a fine paintbrush, one neonate was transferred to the centre of each paper. This handling did not appear to harm the larvae in any way. Larvae could walk to the edge and silk within seconds, and the few that fell without silking were eliminated from data sets (accounting for minor discrepancies in sample sizes for some experiments). Bioassays were conducted between 09.00 and 16.00 hours during April to July of 1999–2001.

Evaluating phenotypic variation in dispersal behaviour

Prediction A, that neonate T. ephemeraeformis vary in their tendency to silk, was tested with laboratory experiment 1 over a 5-day period. Five bags from an infested stand of juniper were collected and held individually in plastic Petri dishes to rear neonates. Neonates of unknown age were tested with the filter paper bioassay, recording how long they took to silk during a 0.5-h period (n = 10 siblings per trial, 12 trials). The study revealed that most larvae that silked did so within 0.25 h (see Results), and this time limit was adopted in measuring dispersal rate in subsequent bioassays.

Evaluating the influence of larval age on dispersal behaviour

Two laboratory experiments and a field experiment were conducted to test prediction B, that the tendency to silk would decline with larval age. In laboratory experiment 2, dispersal rate was measured for the same individual larvae every 24 h for 6 days (after which larvae began to die). Five newly emerged neonates were collected from each of 10 bags and cohorts were caged individually in cardboard cups without food. Dispersal rate in 0.25-h filter paper bioassays was analysed by repeated-measures ANOVA with time a fixed effect and maternal bag a random effect. Because larvae readily silked only during the first day (see Results), later experiments were conducted with neonates that had emerged that morning. Because larvae could construct bags from fibres and wax of cardboard cups, potentially influencing silking behaviour, neonates were subsequently reared in plastic Petri dishes.

In laboratory experiment 3, changes in silking behaviour over the course of the first day were evaluated, predicting a uniformly strong inclination to disperse. At ~08.30 hours, two bags were isolated in Petri dishes and five neonates from each bag that had emerged during a 0.17-h period were collected. The dispersal rate for each neonate was immediately measured with the filter paper bioassay, neonates were transferred to individual Petri dishes, and re-tested at 2-h intervals for 6 h. Dispersal rate was analysed by repeated-measures ANOVA with time a fixed effect and maternal bag a random effect.

Field experiment 1 was based on the observation in laboratory experiment 2 that silking behaviour declined after 24 h, and tested prediction B on host trees, predicting that newly emerged larvae would disperse from non-preferred hosts more readily than older larvae. Larvae were reared from five bags in Petri dishes without food. Neonates (<2 h old) or 1-day-old larvae were transferred...
to different leaves of four Norway maples trees in two trials, on 1 July (n = 5 larvae per age treatment and tree) and 6 July 2001 (n = 10 larvae). On both days, weather conditions were suitable for aerial dispersal (see Cox & Potter, 1986; Ghent, 1999): skies clear or partly cloudy, maximum temperatures 25–30°C, average wind speed 2–2.7 m s⁻¹, peak gusts 4–9 m s⁻¹ (Illinois State Water Survey, Champaign, Illinois). The number of larvae that dispersed was determined at 2-h intervals for 8 h (dispersal also assessed after 24 h in first trial only). Dispersal rate was tested by ANOVA with neonate age and time as fixed effects and trial and tree as random effects. Although larvae may have been removed by natural enemies, it seemed unlikely that the probability of predation would differ for neonates and 1-day-old larvae.

Evaluating the influence of host species encountered by larvae on dispersal behaviour

To test prediction C, that dispersal behaviour would be influenced by the host species encountered by young larvae (<4h old), three laboratory experiments and a field experiment were conducted. Laboratory experiment 4 was intended to simulate variation in the amount of time larvae are exposed to a single host, and can construct a bag, due to weather conditions that inhibit ballooning (such as rainfall and cool air temperatures). It was predicted that larvae would be most inclined to silk after being exposed to foliage of non-preferred hosts, but would become sedentary on preferred hosts over time. Neonates that had emerged within a 0.25-h period from five bags were individually caged in Petri dishes with fresh foliage cuttings (branchlets with leaflets or single leaves) of either arborvitae, juniper, or sugar maple for periods of 1–7 h in 1-h increments (n = 5 larvae per time period/host treatment). The experiment was replicated twice on different days. Dispersal rate was measured with the filter paper bioassay and tested by ANOVA with hour a covariate, plant species a fixed effect, and tree a random effect. It was also recorded whether larvae had bags. Dispersal rate was tested by ANOVA with hour and tree species as fixed effects.

Laboratory experiment 5 was similar in design to experiment 4 (above), but larvae were provided with multiple opportunities to silk over the course of a day, and thus simulated conditions that favoured ballooning. It was predicted that larvae exposed to foliage of a non-preferred host (maple) would disperse readily and repeatedly, but those exposed to foliage of a preferred host (arborvitae) would be more sedentary. Neonates were caged individually in Petri dishes with filter paper or fresh foliage of either arborvitae, juniper, or sugar maple for periods of 1–7 h in 1-h increments (n = 5 larvae per time period/host treatment), and dispersal rate was measured with the filter paper bioassay after 0, 1, 3, and 5 h. The experiment was replicated on two different days, and data were analysed as in laboratory experiment 4, but as a repeated-measures ANOVA.

Laboratory experiment 6 tested prediction D, that young larvae would be more likely to silk from foliage of non-preferred hosts (sugar maple) and non-hosts (tree of heaven) than from foliage of preferred hosts (arborvitae). Foliage samples were taken from at least five trees per species in urban landscapes and consisted of a single leaf (sugar maple), a compound leaf (tree of heaven), or a branchlet with leaflets (arborvitae), that were ~5 cm long but varied in leaf area across species. To maintain foliage turgor, samples were transported separately in wet plastic bags, then the bases of cuttings were wrapped in damp paper towelling, and samples were used in experiments within 1 h. Ten foliage samples of each species were clipped to aluminium rods, randomising position. Neonates were placed individually on cuttings and dispersal rate was recorded during a 1-h period. The experiment was replicated five times on five different days. Dispersal rate was tested by ANOVA with plant species and hour as fixed effects, and trial a random effect.

Field experiment 2 tested prediction D, that neonates would tend to disperse from foliage of non-preferred hosts (one silver maple, and two sugar and Norway maples) than preferred hosts (five junipers and three arborvitaes). Study trees were at Mt Hope cemetery, Champaign Co., Illinois, and initially were free of bagworms. Five neonates (<2 h old) were placed on separate leaves of each tree at a height of 1–2 m, and dispersal rate was recorded after 2, 4, 6, and 24 h. It was also recorded whether larvae had bags. Dispersal rate was tested by ANOVA with hour and tree species as fixed effects. Data for the three maple species were combined because they did not differ significantly. The experiment was started at 09.00 hours on 27 June 2001, and weather conditions were suitable for ballooning (skies clear, maximum temperature 28.5°C, average wind speed 1 m s⁻¹, peak gust 4.8 m s⁻¹).

Data analysis

ANOVA was used to test differences between treatment means (PROC MIXED; SAS Institute, 2001). Original data were log transformed (linear measurements) or angular transformed (percentages) as necessary to meet ANOVA assumptions. Differences between means were tested with full ANOVA models, but insignificant interactions and random effects were eliminated in a stepwise fashion, starting with highest order interactions, leaving only significant terms (see Milliken & Johnson, 1984). Pre-planned comparisons of means were conducted using t-tests (SAS Institute, 2001). In a few instances the G goodness-of-fit test (Sokal & Rohlf, 1995) was used to test differences between single percentages and values expected from null hypotheses. Untransformed means ± 1 standard error are presented throughout except where stated otherwise.

Results

Evaluating phenotypic variation in dispersal behaviour

As predicted, dispersal behaviour of T. ephemeraeformis larvae varied considerably in laboratory experiment 1. Even

© 2004 The Royal Entomological Society, Ecological Entomology, 29, 327–335
though the paper provided neither food nor substrate with which to construct a bag, some apparently healthy and active larvae wandered, encountering the margin of the paper several times, but avoided silking. Of 109 larvae, 93 (85%) silked from paper within 0.5 h (Fig. 1), and times to dispersal averaged 8.5 ± 5.9 min (mean ± SD). Because the primary sex ratio of *T. ephemeraeformis* approximates 1:1 (Barrows, 1974), it is unlikely that the 16 larvae that did not silk were of a different sex than the 93 larvae that did (G-test, *P* > 0.5). A significant difference between the sexes in silking behaviour also may have resulted in a bimodal frequency distribution which was not evident in Fig. 1.

Evaluating the influence of larval age on dispersal behaviour

Laboratory experiment 2 confirmed the prediction that dispersal behaviour would decline with larval age; most larvae silked from paper when tested on the first day, but by the second day were much less inclined to do so (Fig. 2; overall ANOVA *F*₁₅,₅₈ = 26.4, *P* < 0.0001; day effect was the only significant term).

In laboratory experiment 3, larvae showed a consistent and strong tendency to silk over the course of the day, as predicted. All larvae silked every time they were tested during the 6-h study (overall ANOVA for dispersal rate *P* = 1). The strong tendency to disperse during the first day was consistent with laboratory experiment 2 (above).

Field experiment 1 confirmed the prediction that younger larvae would be more likely to disperse from non-preferred hosts than older larvae. Among neonates (<2 h old at the onset of the experiment), 83.8 ± 8% dispersed before hour 2, and 87.8 ± 5.6% by hour 8, while percentages of older larvae (>24 h) that had dispersed by hours 2 and 8 were 48.1 ± 6.9 and 61.9 ± 10.6% respectively (overall ANOVA *F*₁,₆₃ = 7.33, *P* < 0.0001; age effect *F*₁,₆₃ = 33.8, *P* < 0.0001; other effects not significant). Thus, most larvae that dispersed did so during the first two hours, regardless of their age. Of the few larvae that did not disperse, most had constructed bags with maple foliage by the end of the day (>90% in both age groups). All larvae in the first trial that remained on hosts for 8 h (age groups combined) still were present after 24 h.

Evaluating the influence of host species encountered by larvae on dispersal behaviour

Laboratory experiment 4, in which larvae were exposed to tree foliage for varying periods of time, confirmed the prediction that dispersal rate would decline with exposure time (Fig. 3; overall ANOVA *F*₃,₄₁ = 23.5, *P* < 0.0001; hour covariate *F*₁,₄₁ = 68.8, *P* < 0.0001), but did not show the expected host species effect (*F*₂,₃₁ = 0.91, *P* = 0.42). It was concluded from this study that larvae that do not have an opportunity to disperse will become increasingly sedentary over time regardless of their host species.
In the same experiment, the percentage of larvae that had constructed bags with leaf fragments increased rapidly (Fig. 4a; overall ANOVA $F_{3,41} = 13.8, P < 0.0001$; hour covariate $F_{1,41} = 50.0, P < 0.0001$; host and trial effects not significant). Larvae that had bags showed a sharp decline in dispersal rate with exposure period (solid line in Fig. 4b; ANOVA $F_{3,24} = 3.2, P = 0.027$; hour covariate $F_{1,24} = 9.94, P = 0.0036$; other terms not significant), but larvae that did not have bags showed a consistently stronger tendency to silk (dotted line in Fig. 4b; overall ANOVA $P > 0.05$; sample size not sufficient for analysis after day 4). These findings suggest that larvae vary in their tendency to make bags, and that bag construction is associated with increasing sedentariness over time.

The results of laboratory experiment 5, in which larvae were repeatedly provided with an opportunity to silk, were more consistent with the prediction that dispersal would be strongly influenced by host species. Larvae exposed to foliage of three tree species (see Fig. 3) and (b) the percentage of larvae that had constructed bags with leaf fragments increased rapidly (overall ANOVA $F_{6,23} = 10.2, P < 0.0001$; hour covariate $F_{1,23} = 10.6, P = 0.0046$; host effect $F_{2,23} = 17.5, P < 0.0001$; host $\times$ hour effect $F_{2,23} = 6.7, P = 0.007$; trial effect not significant). These findings suggest that, under conditions that favour ballooning, larvae will repeatedly reject non-preferred or unsuitable hosts and re-disperse, but would tend to remain on preferred hosts.

In the same experiment, sedentary behaviour again was associated with construction of a bag, consistent with laboratory experiment 4. None of the larvae exposed to filter paper produced bags, and all showed uniformly high dispersal rates. High rates of silking in the maple foliage treatment, compared to the arborvitae treatment, also were associated with absence of bags; in the maple treatment, 0, 32.5 $\pm$ 7.5, and 45.0 $\pm$ 5.0% of larvae had bags by hours 1, 3, and 5 respectively, while 47.5 $\pm$ 28 of larvae on arborvitae had begun constructing bags within 1 h and 100% had bags by the third hour. In fact, most of the larvae that silked did not have bags, regardless of host species (78 and 80% of larvae that silked in maple and arborvitae treatments respectively).

Laboratory experiment 6, in which larvae were placed on foliage, confirmed the prediction that larvae would tend to silk from non-hosts and non-preferred hosts, but remain on preferred hosts. Nearly all larvae silked from the non-host tree of heaven during the 1-h trial (Fig. 6), and dispersal rates were high for sugar maple, but significantly lower (<40%) for arborvitae (means significantly different, overall ANOVA $F_{2,14} = 9.4, P = 0.0034$; host species was the only significant term). Of the four larvae remaining on tree of heaven, only one constructed a bag, while 93% or more of foliage (filter paper), readily and repeatedly silked in filter paper bioassays (Fig. 5), even after 5 h, but larvae exposed to arborvitae foliage showed a sharp decline in dispersal rate (overall ANOVA $F_{6,23} = 10.2, P < 0.0001$; hour covariate $F_{1,23} = 10.6, P = 0.0046$; host effect $F_{2,23} = 17.5, P < 0.0001$; host $\times$ hour effect $F_{2,23} = 6.7, P = 0.007$; trial effect not significant). These findings suggest that, under conditions that favour ballooning, larvae will repeatedly reject non-preferred or unsuitable hosts and re-disperse, but would tend to remain on preferred hosts.

![Fig. 4](image.png)

**Fig. 4.** Relationship between (a) the percentage of *Thyridopteryx ephemeraeformis* larvae that had constructed bags when exposed to foliage of three tree species (see Fig. 3) and (b) the percentage of larvae with bags and without bags that silked during filter paper bioassays, and the amount of time that larvae were exposed to foliage of three tree species in Petri dishes (laboratory experiment 4). $n = 30$ larvae per time period. Means $\pm$ SE with different letters are significantly different ($t$-tests; $P < 0.05$).

![Fig. 5](image.png)

**Fig. 5.** Relationship between the percentage of *Thyridopteryx ephemeraeformis* larvae that silked during filter paper bioassays and the amount of time they had been exposed to plant foliage or paper in Petri dishes (the same individuals were tested repeatedly; laboratory experiment 5). $n = 40$ larvae per time period/host treatment. Means $\pm$ SE with different letters are significantly different ($t$-tests; $P < 0.05$).
larvae that remained on foliage of the other host species at least had begun constructing bags by the end of the experiment.

Field experiment 2 further confirmed the predictions that young larvae would be more inclined to disperse from non-preferred maple hosts than preferred hosts. Within 4 h almost all of the neonates dispersed from maple leaves, but very few dispersed from juniper and arborvitae (Fig. 7; overall ANOVA: $F_{6,64} = 16.5$, $P < 0.0001$; species effect: $F_{2,64} = 41.4$, $P < 0.0001$; time effect: $F_{4,64} = 3.96$, $P = 0.0066$). More larvae dispersed from arborvitae and juniper in late afternoon, but after 24 h more than 30% of larvae were still present on these hosts. Regardless of host species, almost all of the neonates that did not disperse (95.4%) were making bags by the second hour.

![Fig. 6](image)

**Fig. 6.** Influence of plant species on percentage of neonate *Thyridopteryx ephemeraeformis* that silked from foliage samples (laboratory experiment 6). $n = 50$ larvae per host species. Means with different letters are significantly different ($t$-tests; $P < 0.05$).

![Fig. 7](image)

**Fig. 7.** Relationship between the accumulated percentage of *Thyridopteryx ephemeraeformis* larvae that dispersed and the time since they had been released on foliage of three tree species (field experiment 2). $n = 15$ larvae for the arborvitae treatment and 25 larvae per juniper and maple treatment. Means $\pm$ SE with different letters are significantly different ($t$-tests; $P < 0.05$).

**Discussion**

Laboratory experiment 1 confirmed prediction A, that larvae vary in their tendency to silk, as is true for aerially dispersing caterpillars of other species (Capinera & Barbosa, 1976; Lance & Barbosa, 1981; Ramachandran, 1987). Some bagworm larvae avoided silkimg from filter paper, a completely unacceptable host, even though they were starved. In nature, such variation in dispersal behaviour would result in larvae settling to feed on a diversity of host species.

Prediction B, that the tendency to disperse would decline with larval age, also was supported. Larvae readily silked from paper during their first day, and would do so repeatedly, but subsequently were much less willing to silk even though they had no food and eventually died (laboratory experiments 2 and 3). These findings suggest that sedentary individuals in laboratory experiment 1 may have been older than those that actively dispersed.

Field experiment 1 demonstrated that larvae would be much more likely to remain on a non-preferred host after their first day of life. A greater tendency to disperse in neonates compared to 1-day-old larvae also has been reported for the tortricid *Choristoneura rosaceana* (Harris) (Carriére, 1992).

Experiments to test prediction C, that the tendency to disperse would decline with exposure to foliage of hosts, yielded some unexpected results. Young larvae confined to foliage for varying periods of time in laboratory experiment 4 showed a declining tendency to silk regardless of host species, even when caged with paper. When larvae were provided several opportunities to silk in laboratory experiment 5, however, they soon became sedentary after exposure to foliage of arborvitae, and showed a strong and consistent tendency to silk after being exposed to maple foliage or paper. These findings suggest that larvae will repeatedly disperse from non-preferred hosts when there is an opportunity to do so, but if ballooning is hindered for even a few hours, larvae will become sedentary on any host.

Experiments also supported prediction D, that larvae would tend to disperse from non-preferred hosts and remain on preferred hosts. Most larvae silked from foliage of the non-preferred host maple in laboratory experiment 6, but tended to remain on arborvitae. Similarly, almost all the larvae dispersed from maple in field experiment 2, but many remained on juniper and arborvitae.

In nearly all of the experiments in which larvae had access to materials with which to make a bag, sedentary behaviour was associated with bag construction. In field experiment 1, the few young larvae that did not disperse from maple had constructed bags. When larvae were caged with foliage in laboratory experiment 4, sedentary individuals tended to be those that had bags. In laboratory experiment 5, a decline in dispersal rate on arborvitae was associated with bag construction. Finally, in field experiment 2, larvae that did not disperse from either preferred or non-preferred hosts constructed bags. Despite the consistent association between sedentary behaviour and bag construction, a small proportion of larvae that had bags nevertheless silked in both
laboratory and field experiments (laboratory experiments 4 and 5, field experiments 1 and 2). In contrast, earlier studies have reported that ~36–75% of aerially dispersing larvae had at least partially constructed bags (Cox & Potter, 1986; Ghent, 1999). Cox and Potter (1986) also report, however, that all neonates silked immediately after emergence, but those not carried away by wind later constructed bags. It therefore seems likely that the proportion of neonates that balloon without bags is determined by weather conditions; under conditions favourable for ballooning, most dispersers will not have bags.

The findings in the work reported here support the hypothesis that polyphagy in *T. ephemeraeformis* is maintained by variation among larvae in the tendency to disperse and the limited time available for dispersal, but that relative preference for plant species is determined by the inclination to disperse. The ability to complete development on a variety of host species is obviously adaptive in an insect that has limited opportunity to move between hosts as a neonate, and subsequently becomes even more sedentary. In fact, there is a strong association between flightlessness and polyphagy in other families of Lepidoptera (reviewed by Barbosa et al., 1989).

This study provides insight into factors responsible for the patchy distribution of *T. ephemeraeformis* in urban habitats. Sedentary behaviour on preferred hosts juniper and arborvitae would result in an accumulation of larvae and high-density populations where regulation by natural enemies is not effective. Larvae are strongly inclined to silk and high-density populations where regulation by natural enemies is not effective. Larvae are strongly inclined to silk from the non-preferred host maple, and neonates emerging on such hosts therefore would be likely to disperse, and via-dispersing larvae are more likely to reject them and re-disperse (see Ward et al., 1990). Nevertheless, larvae of the same age showed variation in their innate tendency to silk, the extreme case being the one larva that constructed a bag with foliage of tree of heaven. As a result, a few neonates emerging on non-preferred hosts may not disperse, and some ballooning larvae inevitably would become stranded on non-preferred hosts at the end of their first day when they become sedentary. These larvae then will construct a bag, take up permanent residence, and may complete development. The interacting influences of the host plant and innate variation in dispersal behaviours of larvae therefore result in higher population densities on juniper and arborvitae, but also assure the persistence of a broad host range.

**Acknowledgements**

We gratefully acknowledge advice provided by J. A. Ellis in rearing bagworms, and her assistance in collecting insects for experiments while the first author was in active military service in Kuwait. We also appreciate helpful comments on the manuscript by M. D. Ginzel, J. F. Tooker, two anonymous reviewers, and editor M. D. E. Fellows. This work was in partial fulfilment of a MS degree for R.G.M. from the University of Illinois at Urbana–Champaign and is based upon work supported by the Cooperative State Research, Education, and Extension Service, U.S. Department of Agriculture, under Agreement nos 99-35316-7850 and 2001-35316-11275.

**References**


Accepted 13 November 2003