Monitoring and Temperature-Based Prediction of the Whitemarked Tussock Moth (Lepidoptera: Lymantriidae) in Blueberry

RUFUS ISAACS[1] AND STEVEN VAN TIMMEREN

Department of Entomology, Michigan State University, East Lansing, MI 48824

ABSTRACT   Larvae of the whitemarked tussock moth, *Orgyia leucostigma* (J.E. Smith) (Lepidoptera: Lymantriidae), defoliate and contaminate blueberries, *Vaccinium corymbosum* L., in eastern North America, but infestations are often not detected until economic damage has been caused. To improve monitoring techniques and understand the phenology of the whitemarked tussock moth in blueberry, we compared four trap types and determined temperature-based phenology of this pest over two growing seasons. Large delta traps captured the greatest number of male moths, and similar moth captures were found with or without monthly lure changing. Traps placed at field perimeters adjacent to woods trapped significantly more moths than those inside fields, whereas position in the canopy (high versus low) did not affect captures. Under laboratory conditions, the lower developmental threshold for larvae was 12.3°C, in close agreement with field studies indicating a 12.8°C threshold. Using the 12.8°C threshold, monitoring of *O. leucostigma* cohorts on caged blueberry plants revealed a spring generation with egg hatch starting at 206 ± 3 growing degree-days (GDD) and a late-summer generation with egg hatch starting at 1,157 ± 52 GDD. Combined use of optimized monitoring methods and the phenology model for *O. leucostigma* is expected to improve integrated management of this pest in blueberry.

KEY WORDS   tussock moth, growing degree-days, developmental rate

Tussock moths feed on a broad range of deciduous and coniferous trees, shrubs, and ornamental plants (Johnson and Lyon 1991), and have a high degree of temporal and spatial variability in their abundance in natural systems. Population outbreaks are produced by the insect's high fecundity combined with the dispersal behavior of young larvae that limits top-down regulation and also leads to establishment of new colonies (Harrison 1997, Maron et al. 2001, van Frankenhuyzen et al. 2002, Yoo 2006). Population crashes are caused by disease epizootics and other natural enemies (Howard 1897, Embree et al. 1984, Cunningham and Kaupp 1995, van Frankenhuyzen et al. 2002). During tussock moth outbreaks, urban and crop areas adjacent to woods may become infested by larvae as they colonize additional habitats (Howard 1896, Dustan 1923). Human interaction with these larvae can cause discomfort due to urticating hairs (Gilmer 1923, Embree et al. 1984) and in people sensitive to the toxins symptoms include irritation of skin and mucous membranes, termed tussockosis (Perlman et al. 1976, Ooi et al. 1991).

The whitemarked tussock moth, *Orgyia leucostigma* (J.E. Smith) (Lepidoptera: Lymantriidae), has wingless female moths that lay 100–300 eggs in a single mass on the cocoon from which they emerge (Wagner 2005). After overwintering within an egg mass, the light brown larvae eclose in the spring and feed gregariously on the undersides of young foliage, subsequently dispersing by ballooning (Wagner 2005). Later instars are conspicuous in their white, yellow, red, and black coloration, and they voraciously consume foliage (Rose and Lindquist 1982) while moving throughout the plant canopy. Once mature, the larvae pupate in cocoons of silk and body hair, emerging as winged males or flightless females a few weeks later (Martineau 1984, Johnson and Lyon 1991).

In recent years, infestations of highbush blueberry, *Vaccinium corymbosum* L., fields in the Great Lakes region of the United States with *O. leucostigma* larvae have caused severe tussockosis in pickers. In addition, *O. leucostigma* larvae have been collected during mechanical harvesting causing significant economic implications for producers. Additionally, feeding by this species can defoliate blueberry plants when larval abundance is high, even causing young plants to be killed from the loss of leaves (R.I., unpublished data).

Insect monitoring is the foundation of an effective pest management program (Binns and Nyrop 1992, Fettig et al. 2005) and can be used to provide blueberry producers with information on insect emergence timing and abundance. The sex pheromone of *O. leucostigma* has been identified (Grant 1977, Grant et al. 2003); yet, there is little information on the

[1] Corresponding author, e-mail: isaacsr@msu.edu.

optimal trap design or placement in blueberry fields for capturing male moths. The utility of a monitoring system is much greater if it can be used to help decide when to make insecticide applications against the most susceptible life stages. However, the phenology of *O. leucostigma* in blueberries has not been reported, and this has left producers and pest management advisors unclear about when best to apply insecticides. Determination of the lower developmental threshold for *O. leucostigma* would enable prediction of important phenological events, including the timing of larval eclosion when insecticides can be applied to control larvae when they are most sensitive. Previous published reports suggest *O. leucostigma* has anywhere from one to three generations per year depending on the climate (Howard 1897, Martineau 1984, Johnson and Lyon 1991, Rose and Lindquist 1994). Wilson (1991) found one generation of *O. leucostigma* per year occurred in a black walnut plantation in southwest Michigan. However, our preliminary observations suggest two generations of this pest in blueberry fields in southwestern Michigan, with spring generation larvae emerging from overwintering egg masses during bloom (May) and second generation larvae emerging during July. Given the flightless female stage, such a bivoltine life history might allow application of insecticides to control first generation larvae as a strategy to minimize the risk of infestation of the crop during harvest and minimize the need for insecticide applications near harvest.

This study was conducted to compare trap designs and placement for monitoring male *O. leucostigma* and to determine whether lure changes are needed to maintain efficiency. We also conducted laboratory and field studies to determine the temperature-driven phenology of this insect in highbush blueberry.

Materials and Methods

Monitoring of Male Moths. Three experiments were conducted in 2005 and 2006 to determine the most effective trapping program for monitoring male *O. leucostigma* moths. These experiments took place in fields of *V. corymbosum* L. 'Jersey', at farms with a history of infestation by this insect. The field used in 2005 was 9.7 ha (24 acres) of blueberry in Ottawa County, MI, whereas the 2006 field site was 3.8 ha (9.3 acres) of blueberry in Van Buren County, MI. Traps were installed on 17 May 2005 and 7 June 2006 and were checked until October in both years. In all studies, sticky inserts were replaced as needed, depending on how many extraneous insects were caught in traps.

To determine optimal trap design for monitoring *O. leucostigma* infestations, four trap designs were compared; a small diamond trap (IPM P2, Trecé Inc., Adair, OK), a large diamond trap (Trecé Pherocon IIC), a wing trap (Trecé Pherocon 1C), and a large plastic delta trap (Scentry Biologicals Inc., Billings, MT). The small diamond and large diamond traps were made of thin waxed cardboard with glue coated on the inside surfaces. Wing traps had a plastic top section and a replaceable waxed cardboard section

containing the glue, whereas large plastic delta traps were made entirely of corrugated plastic with a replaceable cardboard insert coated with glue. All traps were baited with *O. leucostigma* pheromone lures (Trecé Inc) that were replaced every 4 wk through the length of the experiment. Traps were hung in the top third of blueberry bushes at least 10 m into the field with trap designs placed in a random order and at least 10 m apart within each replicate. Six replicates were spaced evenly through one blueberry field with each replicate occupying a row and at least 10 m between replicates. Traps were checked once a week throughout the season, with the total number of adult male moths counted and removed at each visit. Sticky inserts, trap bottoms, and traps were replaced as needed, depending on the condition of the trap and how many extraneous insects were caught on the sticky surfaces.

To determine the effects of trap height and position in the field, large plastic delta traps (Scentry Biologicals, Inc., Billings, MT) were placed either on blueberry bushes at the edge of the field (edge) or at least 10 m inside the field (inside). Traps also were placed either at the top of the bush (high) or halfway between the top of the bush and the ground (low) at both of these locations, in a randomized complete block design with six replicates (blocks) positioned along the wooded border of the same field. Each block was separated by at least 20 m. Moth captures were determined each week, and pheromone lures were changed every 4 wk.

To compare moth captures in traps with or without regularly changed lures, large plastic delta traps were installed along the edges of two blueberry fields. Two traps were placed at least 15 m apart along each border, with one of the traps receiving no lure changes through the season (16 wk) and the lure in the other traps being changed every 4 wk through the season (four changes), with eight replications. Traps were checked weekly throughout the season, and the male moths captured were counted and removed at each visit.

In all trapping experiments, moth captures were $\log(n + 1)$ transformed before analysis to meet the assumptions of normality and homoscedasticity. Moth captures were compared among trap types using a one way analysis of variance (ANOVA) and among trap positions and heights using a two-way ANOVA, followed by Fisher protected least significance test for post hoc comparisons (Statview 5.0.1, Abacus Concepts Inc., Berkeley, CA). In the comparisons of trap designs, data were also subjected to simple linear regression analysis to determine whether trap distance into the fields affected captures. The effect of lure changing regimes on moth captures was compared using *t*-tests.

Temperature-Based Development. To determine the developmental thresholds of *O. leucostigma*, larvae were held in environmental chambers at 10, 16, 18, 22, 25, 28, or 35°C. For each temperature, ten neonate larvae within 12 h of eclosion were each placed into a ventilated 20- by 10- by 30-cm plastic box containing two to three shoots of untreated blueberry foliage with
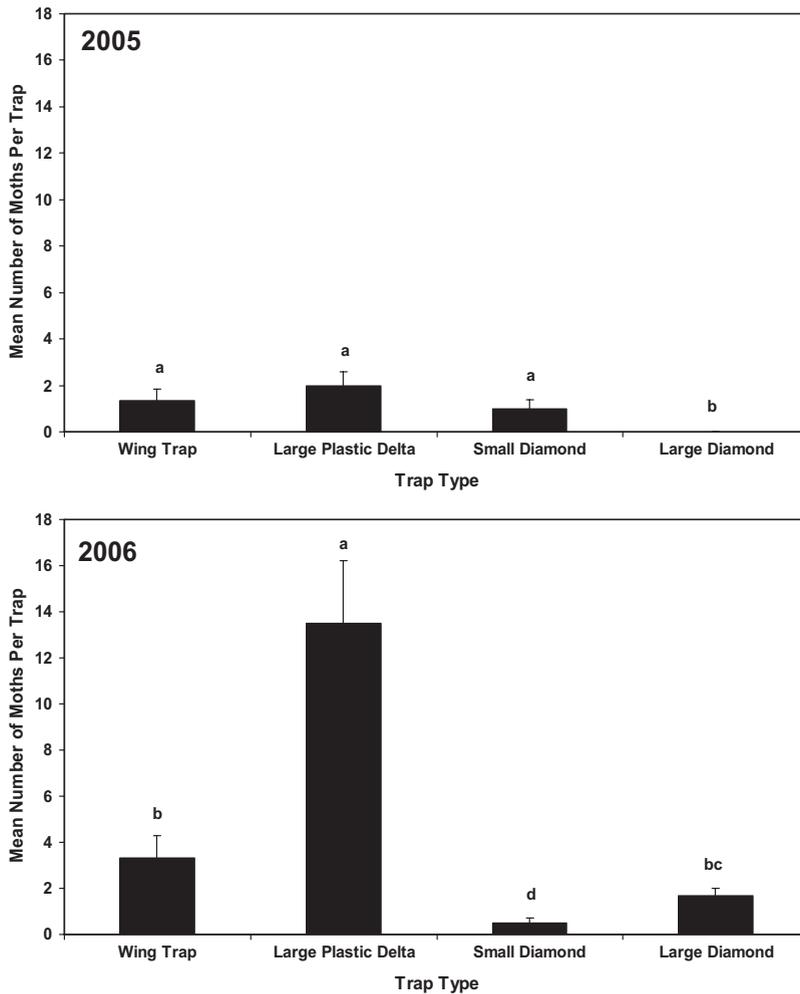
Fig. 1. Mean number of *O. leucostigma* adult males (±SE) caught in traps of four different designs in 2005 and 2006. Mean captures are from the entire season, and bars with the same letter are not significantly different at α = 0.05.

a moist tissue for moisture, under a photoperiod of 16:8 (L:D) h. Containers were checked daily and the foliage was replaced as needed to provide unlimited food. The duration of larval development from first instar to pupation (D) was determined and this was used to calculate the development rate for each insect (1/D). The effect of temperature on larval development was determined using simple linear regression of development rate values against temperature in Statview 5.0.1, without using larvae that died during the experiments, following the methods of Jones et al. (2005).

To determine *O. leucostigma* phenology under field conditions, egg masses were collected from blueberry farms in Ottawa and Van Buren counties, MI, during April 2005 and brought to the Trevor Nichols Research Complex (TNRC) in Fennville, MI. Two egg masses were attached to each of four *V. corymbosum*- 'Bluecrop' bushes, and each bush was enclosed by a 1.83- by 1.83- by 1.83-m mesh cage (BioQuip Products,

Inc., Rancho Dominguez, CA). Tussock moth in cages during 2006 and 2007 came from egg masses laid in the previous year. From early May until late September 2005 and 2006, weekly counts were made in each cage of the number of tussock moth egg masses, larvae, pupae, and adult male and female moths as well as dates when egg hatch occurred. Larval measurements were taken at the same time that weekly counts were conducted by photographing larvae next to a ruler and obtaining exact lengths by using Adobe Photoshop version 5.0 (Adobe Systems, San Jose, CA). A Watchdog temperature sensor (model 125, Spectrum Technologies, Inc., Plainfield, IL) was placed at the base of each blueberry bush in each of the cages to record air temperature every hour. These data were used to calculate growing degree-day (GDD) accumulation in each cage using the Baskerville–Emin method (Baskerville and Emin 1969) with a 1 March start date and with different lower development thresholds (7.2, 10.0, or 12.8 °C). Weekly counts and larval measure-
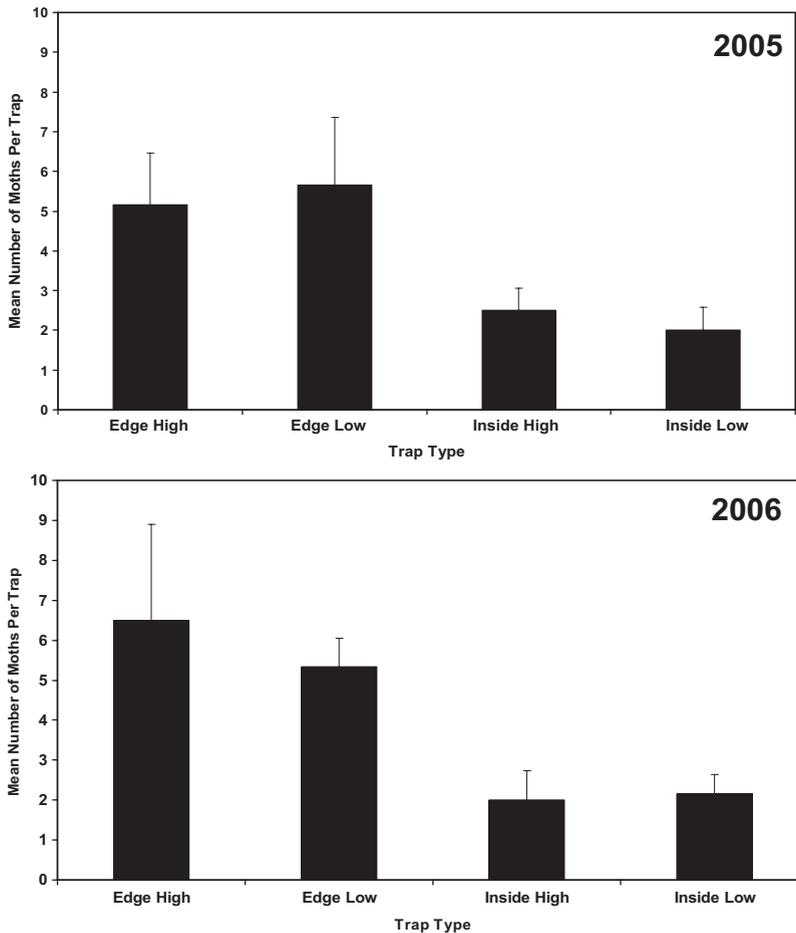
Fig. 2. Number of *O. leucostigma* adult males (mean ± SE) caught in traps positioned either low or high in blueberry bushes at the field edge or on the inside of the field. Mean captures are from the entire season for 2005 and 2006.

ment data from 2007 were not included in this study due to high parasitism rates after the second generation egg hatch. The date of larval eclosion was recorded in each cage in 2005, 2006, and 2007, and the mean ± SE accumulated GDD for each base temperature was determined for those events.

Results

Monitoring Male Moths. There were significant differences in the number of moths captured among trap types in both years (2005: $F = 4.44$; df $= 3, 20$; $P = 0.015$; 2006: $F = 23.93$; df $= 3, 20$; $P < 0.001$), although the population was much lower at the site used in 2005 (Fig. 1). The large plastic delta trap caught the greatest number of moths in 2006, capturing >3 times the number of moths than the next most effective trap. Placement of all the traps at least 10 m from the field border resulted in no relationship between moth capture and distance to the field border in either year (2005: $r^2 = 0.027$; $P = 0.44$; 2006: $r^2 = 0.018$; $P = 0.54$).

The patterns of moth capture with trap placement were consistent across both years, with traps placed at the field edge catching 2–3 times more moths than those placed inside the field, and with no effect of trap height (Fig. 2). In 2005, significantly more moths were trapped at field edges than at the interior ($F = 5.69$; df $= 1, 20$; $P = 0.027$), whereas there was no significant response to trap height ($F = 0.33$; df $= 1, 20$; $P = 0.57$) and no interaction between these factors ($F = 0.08$; df $= 1, 20$; $P = 0.78$). A similar result was observed in 2006 with traps placed at the field edge trapping more moths than those placed inside the fields ($F = 13.69$; df $= 1, 20$; $P = 0.001$), whereas there was no significant response to trap height ($F = 0.07$; df $= 1, 20$; $P = 0.8$) and no interaction between these factors ($F = 0.071$; df $= 1, 20$; $P = 0.79$) (Fig. 2).

Changing lures did not significantly increase the capture of male moths compared with traps that retained the same lure all summer. In 2005, traps with monthly lure changes caught 4.38 ± 0.91 moths, whereas those without changes trapped 4.38 ± 0.73 moths ($t = 0.015$; df $= 14$; $P = 0.88$). In 2006, male moth catches were slightly higher with traps that had lures changed every 4 wk catching 11.75 ± 2.1 moths, whereas traps without lure changes trapped 8.75 ± 1.2
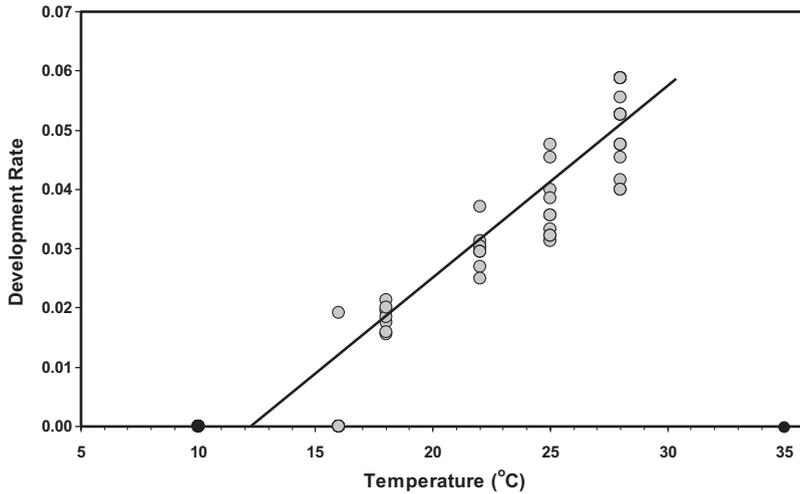
Fig. 3. Developmental rate of *O. leucostigma* larvae (1/duration of development from first instar to pupation) reared on untreated blueberry foliage in environmental chambers at different temperatures. Best-fit correlation analysis was performed on data between 16 and 28°C. Black dots show the lack of development of larvae at 10 and 35°C.

moths, but this difference was not significant ($t = 1.25$; df = 14; $P = 0.23$).

Phenological Development of Tussock Moth. Larval developmental rate increased with temperature in the range between 16 and 28°C, whereas at the extremes of 10 and 35°C, larval development was prevented (Fig. 3). Analysis of the rate of tussock moth development between 16 and 28°C revealed a significant effect of temperature on development ($F = 491.3$; df = 1, 62; $P < 0.0001$). The best fit regression line ($y = -0.037 + 0.003x$, $r^2 = 0.89$) intercepted the x-axis at 12.3°C, indicating this is the lower threshold for development of this insect. Larvae at 10°C were able to complete the first molt but did not progress beyond that. At 16°C, 40% of larvae were able to complete larval development, but only one larva was able to pupate. From 18 to 28°C, almost all larvae completed development and were able to complete pupation. At 35°C, larvae quickly died and none were able to molt.

On the caged blueberry bushes under field conditions, larvae of the first generation of tussock moths were observed for the first time on 10 May 2005, 15 May 2006, and 8 May 2007. In all 3 yr, larvae remained clustered on egg masses for several days before dispersing throughout the blueberry bushes. Second gen-

eration egg hatch was first observed on 8 July 2005, 19 July 2006, and 23 July 2007. The accumulated growing degree-days from 1 March using different base temperatures revealed that the mean first generation egg hatch over the three years of this study was at 460, 313, and 206 GDD for bases 7.2, 10.0, and 12.8°C, respectively (Table 1). The hatch of second generation egg masses occurred at 1,994, 1,543, and 1,157 GDD for bases 7.2, 10.0, and 12.8°C, respectively.

Results from measuring larval lengths revealed two generations occurring in both growing seasons (Fig. 4). Larvae increased in length upon hatching in May and reached a peak near 17 June (713 GDD, base 12.8) in 2005 and near 6 July (830 GDD, base 12.8) in 2006. The second generation of larvae increased in length until peaking near 22 August (2046 GDD, base 12.8) in 2005 and near 6 September (1946 GDD, base 12.8) in 2006.

The evidence for two generations of *O. leucostigma* is further supported by the abundance of larvae peaking on 17 June (713 GDD, base 12.8) and 12 August (1873 GDD, base 12.8) in 2005 and on 21 June (630 GDD, base 12.8) and 23 August (1750 GDD, base 12.8) in 2006 (Fig. 5). Additionally, we observed two peaks in egg masses and adults in both years, and two peaks in pupae in 2005

Table 1. Mean ± SE growing degree day accumulation (bases 7.2, 10, and 12.8 from 1 March) at egg hatch of first and second generation tussock moth in 2005, 2006, and 2007

Generation	Base temp. (°C)	Yearly mean GDD			Overall mean GDD
		2005[a]	2006	2007	
1	7.2	447 ± 0	496 ± 6.5	438 ± 2.6	460.3 ± 18.0
	10.0	304 ± 0	331 ± 5.0	305 ± 2.7	313.3 ± 8.8
	12.8	209 ± 0	208 ± 3.8	200 ± 2.6	205.7 ± 2.8
2	7.2	1,870 ± 19.5	1,945 ± 23.0	2,167 ± 6.8	1,994.0 ± 89.2
	10.0	1,463 ± 19.1	1,482 ± 21.3	1,683 ± 11.9	1,542.7 ± 70.4
	12.8	1,126 ± 18.4	1,086 ± 19.4	1,259 ± 11.4	1,157.0 ± 52.3

[a] Values with SE value of zero reflect egg hatch occurring on the same day from egg masses of the initial collection.
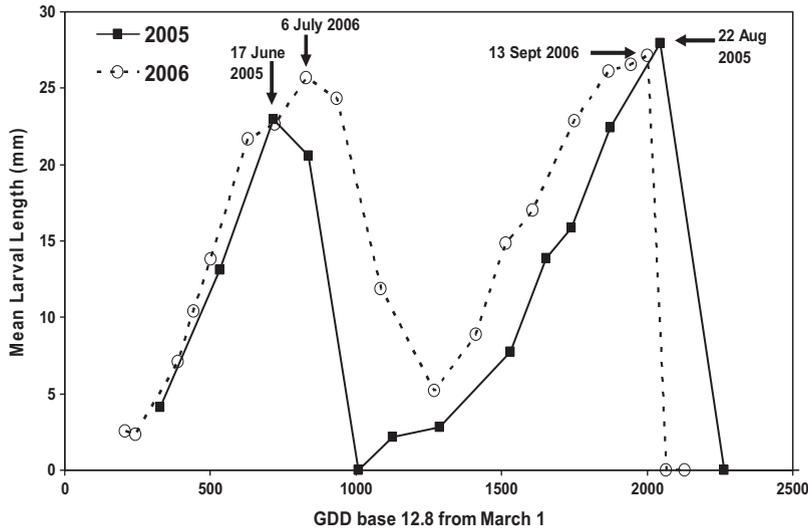
Fig. 4. Length of *O. leucostigma* larvae (mean ± SE) on caged blueberry bushes at the Trevor Nichols Research Complex in Fennville, MI, in 2005 and 2006, as a function of GDD accumulation. Arrows show the dates of peak larval size.

(Fig. 5). In 2006, many pupae from the first generation did not hatch as adults, resulting in difficulty separating dead first generation pupal cases from alive second generation pupae. As a result of this, we do not report the second generation pupae in Fig. 5.

Discussion

The results from this study provide insight into the biology of *O. leucostigma* in the Great Lakes region and can guide the implementation of integrated pest management (IPM) programs to minimize the economic influence of this insect in blueberry production. Our trap comparison indicated that large plastic delta traps are the most effective at trapping adult male moths through the season and that they should be placed at the perimeter of blueberry fields adjacent to woodland. Pheromone lures remaining in traps all season maintained similar effectiveness to those changed regularly, suggesting no need to replace lures.

The practical and economic feasibility of each trap design was considered in addition to how many moths were caught. Of the four trap designs tested, the large plastic delta trap was best able to survive field conditions. The others were damaged more extensively by machine harvesters, rain, and overhead irrigation than the large plastic delta traps. The diamond traps were made of cardboard and they lasted for only a month before needing replacement. Additionally, the large plastic delta and wing traps could be easily stored and reused for more than one season, thus reducing their long-term cost. Despite the large plastic delta traps being more expensive ($7.50, Great Lakes IPM 2008 catalog) than the small diamond ($4.20), large diamond ($5.26), and wing trap ($5.30), they were the most cost-effective traps for the reasons given above.

Over three growing seasons, *O. leucostigma* exhibited two distinct generations on blueberry in southwest Michigan. The phenology of egg hatching by this species was best predicted (i.e., with the least variation among the three years) using a base threshold temperature of 12.8°C. Verification of this lower development threshold came from the laboratory study at varying temperatures in which the lower threshold was found to be 12.3°C. This was in close agreement with the lowest variability among years found in the timing of egg hatch by *O. leucostigma* when degree-days were calculated at a base temperature of 12.8°C.

The timing of larval activity of the first generation found in this study reveals that *O. leucostigma* larvae are present on bushes from late May until early July (415–885 $GDD_{12.8C}$) (Fig. 5), with a peak in the size of the larvae at ≈770 $GDD_{12.8C}$. This timing coincides with the period of larval activity of another primary lepidopteran pest of blueberries in this region, the cranberry fruitworm, *Acrobasis vaccinii* Riley (Pyralidae) (Mallampalli and Isaacs 2002). Insecticides are typically applied to control this univoltine insect in early June, making it likely that this provides control of *O. leucostigma* if they are present at the same time and the application achieves good coverage of the foliage. Fields infested with *O. leucostigma* but not *A. vaccinii* might therefore be the most at risk from infestation by the former species during the period before harvest because the first generation will be able to survive and reproduce, leading to a second generation with larvae active in July and August.

Although the GDD accumulations from 1 March for eclosion of the second generation eggs can provide general target values for this event, it is likely that accuracy of chemical control timing will be increased from knowing the accumulation of GDD from first moth captures (biofix) to egg hatch. This approach has
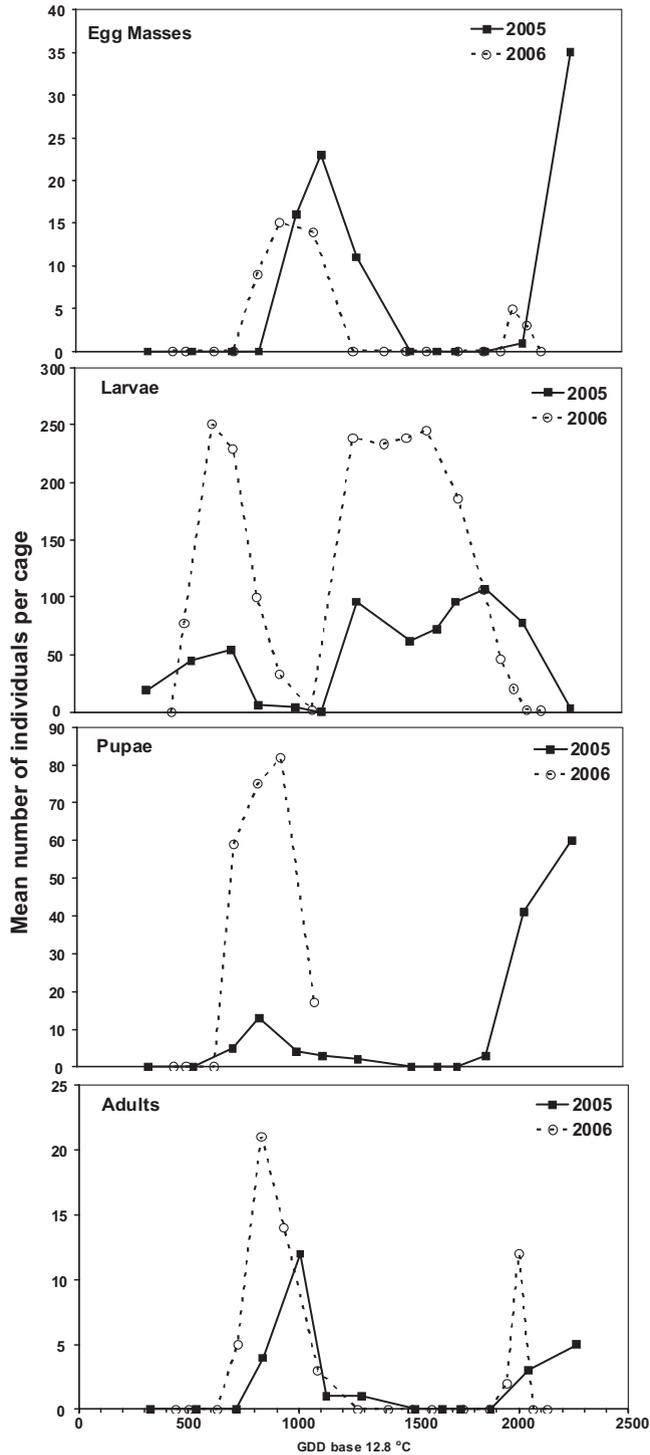
Fig. 5. Mean abundance of *O. leucostigma* egg masses, larvae, pupae, and male moths in four cages over blueberry bushes, at the Trevor Nichols Research Complex in Fennville, MI, during the summer 2005 and 2006. Pupae in 2006 could not be accurately counted due to contamination by those from the first generation.

been used effectively to improve control of codling moth (Riedl and Croft 1974, Riedl et al. 1976) and other insect pests in apple because it provides more accurate identification of egg hatch timing than counting heat accumulated since early spring. In the current study, second generation egg hatch occurred at

318.4 ± 32.8 GDD$_{12.8C}$ after first sustained capture of male moths in cages, and so an insecticide application at 400 GDD$_{12.8C}$ after biofix would be expected to provide control of the young larvae of the second generation before they are large enough to contaminate fruit and irritate harvesters. Such information also can be integrated into online weather systems, such as www.enviroweather.msu.edu, to predict when second generation egg-hatch will occur based on expected weather conditions.

Our detection of two distinct generations of *O. leucostigma* in this study contradicts the previous report of a single generation by Wilson (1991) in southwestern Michigan. The voltinism of this species may vary within a small geographic area due to the variation in GDD accumulation with proximity to Lake Michigan. From the data presented here, ≈ 2000 growing degree-days are needed for two generations of larvae, but this insect overwinters as egg masses and so there needs to be sufficient heat accumulation for emergence, mating, and oviposition of the second cohort of *O. leucostigma* moths, which occurred around 22 August in 2005 and 13 September in 2006 after accumulation of 1971 ± 25 GDD. There can be minimal heat accumulation above the 12.8°C threshold later in the growing season, so *O. leucostigma* may be at its limit for bivoltinism in this region where cooler seasons may limit development to a single generation.

These studies provide results to enable implementation of a monitoring program to minimize infestation of blueberry by *O. leucostigma*. The phenology studies indicate that application of insecticide at ≈ 300 GDD base 12.8°C will target egg hatch and young larvae of the first generation. This timing is likely to coincide with application of insecticides for control of fruitworm pests during bloom, which also will be active on *O. leucostigma* larvae. Targeting the first generation of *O. leucostigma* for chemical control has an additional benefit in that the lower amount of blueberry and weed foliage enables improved penetration of pesticides into the crop canopy compared with July when the second generation is active (Hanson et al. 2000). Growers concerned about this pest's risk of contaminating their harvest and who do not treat the first generation should deploy large plastic delta traps baited with sex pheromone and placed at the perimeter of wooded field borders to monitor the level and timing of second generation *O. leucostigma*. This can also be used to determine the level of success achieved by first generation control actions and to decide whether chemical applications are needed against the second generation. The second opportunity to prevent larval contamination of blueberry harvest is to apply an appropriate insecticide 350–450 GDD base 12.8°C after the first consistent catch of male moths that emerge in late June and early July.

Combining the monitoring system and phenology model is expected to minimize the likelihood of blueberry contamination and injury by *O. leucostigma*. In combination with regular crop scouting programs and use of selective insecticides that allow survival of the natural enemies of *O. leucostigma*, the monitoring protocol and phenology model described in this study are expected to prevent defoliation of bushes by larvae of this species and enable harvest of blueberries free of this potential insect contaminant.

Acknowledgments

References Cited

Baskerville, G. L., and P. Emin. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50: 515–517.

Binns, M. R., and J. P. Nyrop. 1992. Sampling insect populations for the purpose of IPM decision making. Annu. Rev. Entomol. 37: 427–453.

Cunningham, J. C., and W. J. Kaupp. 1995. Insect viruses, pp. 327–340. *In* J. A. Armstrong and W.G.H. Ives [eds.], Forest insect pests in Canada. Natural Resources Canada, Science and Sustainable Development Directorate, Ottawa, Canada.

Dustan, A. G. 1923. The natural control of the white-marked tussock moth under city and forest conditions. Proc. Acadian Entomol. Soc. 8: 109–126.

Embree, D. G., D. E. Elgee, and G. F. Estabrooks. 1984. *Orgyia leucostigma* (J. E. Smith), whitemarked tussock moth (Lepidoptera: Lymantriidae), pp. 359–361. *In* J. S. Keller and M. A. Hulme [eds.], Biological control programme against insects and weeds in Canada 1969–1980. Commonwealth Agricultural Bureaux, Slough, England.

Fettig, C. J., J. G. Fidgen, and S. M. Salom. 2005. A review of sampling procedures available for IPM decision-making of forest and shade tree insects in North America. J. Arboricult. 31: 38–47.

Gilmer, P. M. 1923. The poison and poison apparatus of the white-marked tussock moth, *Hemerocampa leucostigma* Smith and Abbot. J. Parasitol. 10: 80–86.

Grant, G. G. 1977. Interspecific pheromone responses of tussock moths and some isolating mechanisms of eastern species. Environ. Entomol. 6: 739–742.

Grant, G. G., K. N. Slessor, W. M. Liu, and M. Abou-Zaid. 2003. (Z,Z)-6,9-heneicosadien-11-one, labile sex pheromone of the whitemarked tussock moth, *Orgyia leucostigma*. J. Chem. Ecol. 29: 589–601.

Hanson, E., J. Hancock, D. C. Ramsdell, A. Schilder, G. VanEe, and R. Ledebuhr. 2000. Sprayer type and pruning affect the incidence of blueberry fruit rots. HortScience 35: 235–238.

Harrison, S. 1997. Persistent, localized outbreaks in the western tussock moth *Orgyia vestula*: the roles of resource quality, predation and poor dispersal. Ecol. Entomol. 22: 158–166.

Howard, L. O. 1896. The shade-tree insect problem in the eastern United States, pp. 361–384. Yearbook of the

United States Department of Agriculture. Government Printing Office, Washington, DC.

Howard, L. O. 1897. A study in insect parasitism: a consideration of the parasites of the white-marked tussock moth, with an account of their habits and interrelations, and with descriptions of new species. U. S. Dep. Agric. Tech. Bull. 5: 1–57.

Johnson, W. T., and H. H. Lyon. 1991. Insects that feed on trees and shrubs, 2nd ed. Cornell University Press, Ithaca, NY.

Jones, V. P., M. D. Doerr, J. F. Brunner, C. C. Baker, T. D. Wilburn, and N. G. Wiman. 2005. A synthesis of the temperature dependent development rate for the obliquebanded leafroller, *Choristoneura rosaceana*. J. Insect Sci. 5: 24. (insectscience.org/5.24).

Mallampalli, N., and R. Isaacs. 2002. Distribution of egg and larval populations of cranberry fruitworm (Lepidoptera: Pyralidae) and cherry fruitworm (Lepidoptera: Tortricidae) in highbush blueberries. Environ. Entomol. 31: 852–858.

Maron, J. L., S. Harrison, and M. Greaves. 2001. Origin of an insect outbreak: escape in space or time from natural enemies? Oecologia (Berl.) 126: 595–602.

Martineau, R. 1984. Insects harmful to trees. Multiscience Publications Ltd., Montreal, QC, Canada.

Ooi, P. L., K. T. Goh, H. S. Lee, and C. L. Goh. 1991. Tussockosis: an outbreak of dermatitis caused by tussock moths in Singapore. Contact Derm. 24: 197–200.

Perlman, F., E. Press, J. A. Googins, A. Malley, and H. Poarea. 1976. Tussockosis: reactions to Douglas fir tussock moth. Ann. Allergy 36: 302–307.

Riedl, H., and B. A. Croft. 1974. A study of pheromone trap catches in relation to codling moth (Lepidoptera: Olethreutidae) damage. Can. Entomol. 106: 525–537.

Riedl, H., B. A. Croft, and A. J. Howitt. 1976. Forecasting codling moth phenology based on pheromone trap catches and physiological-time models. Can. Entomol. 108: 449–460.

Rose, A., and O. H. Lindquist. 1994. Insects of Eastern spruces, fir, and hemlock. Natural Resources Canada, Canadian Forestry, Ottawa, ON, Canada.

Rose, A. H., and O. H. Lindquist. 1982. Insects of eastern hardwood trees. Canadian Forestry service, Forestry Tech Rep 29. Government of Canada, Ottawa, ON, Canada.

van Frankenhuyzen, K., P. Ebling, G. Thurston, C. Lucarotti, T. Royama, R. Goscott, E. Georgeson, and J. Silver. 2002. Incidence and impact of *Entomophaga aulicae* (Zygomycetes: Entomophthorales) and a nucleopolyhedrovirus in an outbreak of the whitemarked tussock moth (Lepidoptera: Lymantriidae). Can. Entomol. 134: 825–845.

Wagner, D. M. 2005. Caterpillars of eastern North America. Princeton University Press. Princeton, NJ.

Wilson, L. F. 1991. Location and condition of whitemarked tussock moth (Lepidoptera: Lymantriidae) cocoons in a Michigan black walnut plantation. Great Lakes Entomol. 24: 153–157.

Yoo, H.J.S. 2006. Local population size in a flightless insect: importance of patch structure-dependent mortality. Ecology 87: 634–647.