

Egg hatch of forest tent caterpillar (Lepidoptera: Lasiocampidae) on two preferred host species

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Abstract—Synchrony between herbivore and host phenology can be an important factor in herbivore fitness. The survival of first-instar forest tent caterpillar (FTC) (*Malacosoma disstria* Hübner; Lepidoptera: Lasiocampidae) larvae and performance of surviving larvae are reduced when egg hatch and host budbreak are asynchronous. Budbreak in trembling aspen (*Populus tremuloides* Michaux; Salicaceae) and largetooth aspen (*Populus grandidentata* Michaux; Salicaceae), two preferred hosts of FTC, differ by ~14 days. We examined the phenological requirements of FTC egg hatch to see if an inherent difference exists between FTC egg masses on the two hosts, and if the difference would promote synchrony with each host. Egg masses from a haphazard selection of clones of each host were collected in a mixed stand of trembling and largetooth aspen in New Brunswick, Canada. Egg masses were subjected to controlled temperature regimes in the laboratory, and hatch was monitored daily. Despite the differences in host phenologies and the obvious benefits of being synchronised with host phenology, egg masses collected from trembling aspen began hatching only 3 days earlier, and completed hatching only 2 days earlier, than egg masses collected from largetooth aspen. Bet hedging is discussed as a possible strategy to explain the absence of host-specific synchrony between egg hatch of FTC and the hosts it selects for oviposition.

Résumé—Des masses d'œufs de livrée des forêts (*Malacosoma disstria* Hübner; Lepidoptera: Lasiocampidae) ont été recueillies sur des peupliers faux-trembles et des peupliers à grandes dents dans un peuplement mélangé de l'ouest du Nouveau-Brunswick, au Canada. Ces masses d'œufs ont été soumises à des régimes de température contrôlée en laboratoire, et une surveillance a été exercée quotidiennement afin d'établir le moment de l'éclosion. La phénologie du débourrement des deux hôtes diffère d'environ 14 jours, et des effets négatifs ont été observés chez les chenilles obligées de se nourrir de feuillage plus âgé. Toutefois, en dépit des différences liées à la phénologie des hôtes et des avantages évidents découlant de la synchronisation de l'éclosion avec la phénologie des hôtes, les masses d'œufs recueillies sur le peuplier faux-tremble (*Populus tremuloides* Michaux; Salicaceae) ont commencé à éclore trois jours avant, et avaient toutes éclos seulement deux jours avant celles récoltées sur le peuplier à grandes dents (*Populus grandidentata* Michaux; Salicaceae). La stratégie de minimisation des risques (bet hedging) apparaît comme une explication possible à l'absence de synchronisation spécifique à l'hôte entre l'éclosion des œufs de la livrée et la phénologie du débourrement de l'hôte sur laquelle les femelles déposent leurs œufs.

Introduction

Seasonality is the predictable “occurrence of [a life-stage event] within a definite limited period or periods of the astronomic (solar), calendar year” (Lieth 1974); seasonal development is a requisite for the persistence (long-term survival) of every insect population (Gray 2012). For temperate insects, this implies that winter is

passed in a cold-hardy stage, that emergence of a feeding stage is coincident with presence of suitable host material, and that these events will coincide sufficiently each year for the continued survival of the population (Gray 2010). Beyond mere survival of the population, synchrony between herbivore and host phenology has significant consequences for herbivore fitness (van Asch and Visser 2007). Early spring-feeding

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Lepidoptera such as the forest tent caterpillar (FTC), *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), can experience reduced survival and performance if their spring hatch is not coincident with the emergence of new foliage (budbreak) (Scriber and Slansky 1981; Hunter 1990; Quiring 1992; Ostaff and Quiring 2000). Larvae that emerge before budbreak are without food, and those that emerge after budbreak must feed on older foliage that has begun a progressive reduction in nitrogen and water content and an increase in leaf toughness (Mattson and Scriber 1987; Hunter and Lechowicz 1992).

The FTC is a widely distributed pest in North America and feeds on a wide variety of hardwoods (Baker 1972): trembling aspen (*Populus tremuloides* Michaux; Salicaceae), largetooth aspen (*Populus grandidentata* Michaux; Salicaceae), and sugar maple (*Acer saccharum* (Marshall); Sapindaceae) are the most common hosts in eastern Canada. In mid to late July, a female FTC lays a single cylindrical band of eggs containing about 150–350 eggs (Baker 1972) around a small twig at the tip of a host branch, fully formed pharate first-instar larvae appear after 3 weeks (Witter 1979). Winter is spent as a larva within the egg, with hatch occurring in the following spring. Populations erupt periodically every 10–16 years (Mattson and Erickson 1978), with local-scale infestations lasting 2–3 years but occasionally longer than 4 years, depending on forest fragmentation (Roland 1993). Asynchrony between budbreak and larval emergence has been reported for FTC attacking trembling aspen (Parry and Goyer 2004) and sugar maple under certain temperature conditions (Fitzgerald and Costa 1986). Late-emerging larvae feeding on older foliage experienced reduced survival (Parry *et al.* 1998), a prolonged larval period from slower growth rates and extra instars, and lower pupal mass (Jones and Despland 2006).

Raske (1974) reported that within-population FTC egg hatch is relatively synchronous: >90% of total hatch was completed within 4 days of the first hatch. However, Lorimer (1979) found lower within-population synchrony of hatch: only 60% of total hatch was completed within 4 days of first hatch, and 90% was not complete for 8 days, suggesting an adaptive response to budbreak variability in the host. Studies report a range of degree days (231–450) before the onset

of egg hatch (Hodson and Weinman 1945; Ives 1973; Mattson and Erickson 1978).

Parry *et al.* (1998) suggest that FTC and other early emerging aspen folivores have evolved a life-history strategy that risks the consequences of occasional poor springs to exploit the narrow phenological window when host-plant quality is optimal (*i.e.*, young) and pressure from natural enemies is low. This strategy would suggest that the temperature–time requirements for FTC egg hatch on early flushing host species should differ from those on late-flushing host species. Many aspen stands contain a mixture of trembling aspen and largetooth aspen, and Barnes (1969) found that trembling aspen clones generally flushed 2 weeks earlier than largetooth aspen clones in the same site. Trembling aspen flowers, foliates, and disperses seeds about 1–3 weeks earlier than largetooth aspen in the same location (Laidly 1990).

We collected egg masses from two hosts (trembling aspen and largetooth aspen) in a mixed stand. In a laboratory experiment, we subjected the egg masses to controlled temperatures and monitored egg hatch to test the hypothesis that inherent differences exist in the phenological requirements between eggs oviposited on the two host species, and that any such difference could promote synchrony between egg hatch and budbreak of the two hosts that differ in budbreak phenology.

Materials and methods

FTC egg masses were collected during the fall from 45 trembling aspen and 15 largetooth aspen from an approximately three-quarter ha plot near Woodstock, New Brunswick, Canada (Table 1). Our objective was to compare the phenological requirements of FTC populations on the two hosts, not among clones within the hosts. Therefore, it was only necessary that our sampling included multiple clones from each host in order to avoid any bias arising from potential differences in FTC requirements among host clones. Trembling aspen and largetooth aspen clone sizes each vary between 0.02 and 0.03 ha (Barnes 1969), so it is most likely that our samples came from several clones, although we did not confirm the actual number with genetic tests. Five branches from each of the upper, mid, and lower crown were haphazardly selected, and

Table 1. Mean (\pm SE) and range for mensurational characteristics of trembling aspen ($n = 45$) and largetooth aspen ($n = 15$) trees sampled for forest tent caterpillar egg masses.

Characteristic	Trembling aspen	Largetooth aspen
Tree height (m)	10.3 \pm 0.5 (4.6–15.8)	10.2 \pm 0.9 (5.8–17.1)
DBH (cm)	11.8 \pm 0.8 (4.8–24.6)	10.8 \pm 1.2 (4.3–19.8)
Crown length (m)	7.2 \pm 0.4 (3.7–19.1)	7.6 \pm 0.7 (4.2–12.5)

DBH, diameter at breast height.

all current-year branch tips with egg masses were clipped, bagged, labelled, returned to the laboratory, and stored in a refrigerator at 5°C.

Four hundred and eighty-six egg masses from trembling aspen and 162 from largetooth aspen were haphazardly selected; each egg mass was placed in a glass vial, and vials were arranged on an aluminium plate in which a temperature gradient (5.8–24.1°C) was maintained by the internal circulation of cold and warm water in opposite ends. Mercury switches controlled water flow and temperatures ($\pm 0.2^\circ\text{C}$). Eighteen egg masses from trembling aspen and six egg masses from largetooth aspen were subjected to each of 27 temperatures on the gradient. Observations from the lowest temperature (5.8°C) were eliminated because of poor egg hatch (see below). Within each of the remaining 52 temperature–host combinations, egg hatch was recorded each day, and cumulative percentage hatch was calculated from each day’s observation when hatch was completed. Median developmental time (d) was estimated for each of the combinations by interpolation between the two observations that bracketed 50% cumulative hatch. Median developmental rates (d^{-1}) were compared between the larval populations from each host by the nonparametric sign test of Fisher (Hollander and Wolfe 1973).

Based on the results of the Fisher test (see the “Results” section), the relationship between temperature and developmental rate was described individually for the larval population from each host. Equation [10] of Logan *et al.* (1976)

$$R = \alpha \left\{ [1 + ke^{-\rho T}]^{-1} - e^{-\tau} \right\} \quad (1)$$

was fit to the estimated median developmental rates from the larvae of each host. In equation [1], R is the developmental rate (d^{-1}); T is degrees (C) above the lowest experimental temperature (6.8°C); ρ is the rate increase to the optimum

temperature; α and k are empirical parameters; and τ is a scaling variable

$$\tau = \frac{T_M - T}{\Delta T}, \quad (2)$$

where T_M is the maximum lethal temperature, and ΔT is the width of the “boundary layer” (*i.e.*, the temperature span over which the developmental rate function changes its behaviour from a positive to a negative first derivative). Parameter values for equation [1] were selected for the 26 median developmental rates of the larvae of each host on the basis of maximum likelihood by giving a weight of R^{-1} to each iteration within PROC NLIN of SAS (SAS Institute 1999). Jennrich and Moore (1975) showed that maximum likelihood estimates are obtained by a least squares criterion when squared differences have been so weighted.

Temperature-independent estimates of developmental times (= normalised times) were calculated by dividing each observed developmental time by the median developmental time of the temperature–host combination. The number of observations was not uniform among all temperature–host combinations, so the number of observations in each combination was standardised to give them equal weight before comparing developmental times: *i.e.*, the number of observations in each combination (n) was multiplied by \bar{n}/n , where \bar{n} is the mean number of observations across all combinations. Differences between the populations in their variability in temperature-independent developmental times were then analysed by applying the nonparametric rank test of Ansari–Bradley (Hollander and Wolfe 1973) to the 3900 normalised and standardised developmental times (two populations \times 26 temperatures \times 75 [standardised] hatches per temperature).

Based on the results of the Ansari–Bradley test (see the “Results” section), a temperature-independent description of population variability

in developmental times was made for the larvae of each host (Wagner *et al.* 1984). The normalised and standardised developmental times were grouped into classes of width 0.05, and a cumulative Weibull function (Law and Kelton 1982)

$$F(x) = 1 - \exp \left[- \left(\frac{x - \gamma}{\beta} \right)^\alpha \right],$$

where $F(x)$ is the cumulative probability of hatch at normalised time x , and β , ϕ , and λ are parameters to be estimated, was fit to the cumulative probabilities of each class. Parameter estimation was done by maximum likelihood as described above.

The cumulative probability of hatch within t days ($F(t)$) is then estimated as

$$F(t) = 1 - \exp \left[- \left(\frac{\sum_0^t R - \gamma}{\beta} \right)^\alpha \right], \quad (4)$$

where $\sum_0^t R$ is the cumulative development at time t (*i.e.*, the cumulative developmental rates from equation [1]).

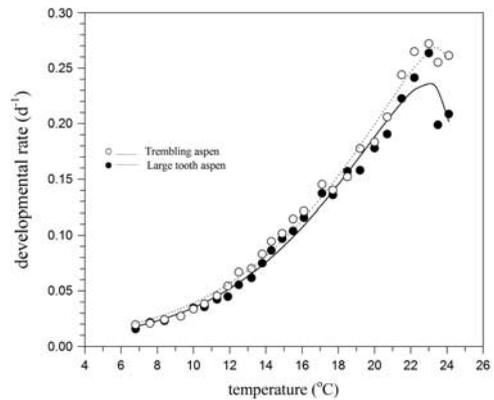
The hatch pattern for each population was simulated using the relationships described above (equations [3] and [4]) and the daily minimum and maximum temperatures from Woodstock, New Brunswick (site of the egg mass collection) from 1971 to 2000 (Earth Info 2010). Hourly temperatures were estimated from the daily minima and maxima by the sine wave function of Allen (1976), and the simulated daily emergence was recorded.

Results

The mean number of eggs per mass per temperature was 130 ± 3 (range 79–162). Within the egg masses, $14.7\% \pm 1.9\%$ (range 0%–40.6%) of the eggs did not contain an overwintering (pharate) larvae. For eggs that did contain pharate larvae, emergence was $74.7\% \pm 4\%$ (range 15.9%–93.1%). At the lowest temperature (5.8°C), only three larvae emerged (all from one egg mass from largetooth aspen), and this temperature treatment was eliminated from the analysis.

Median developmental times were significantly shorter in eggs from trembling aspen than those from largetooth aspen ($B = 22$; $P(> B) < 0.0001$). Therefore, the relationship between temperature and developmental rate was described for larvae of each host separately. The temperature–developmental rate relationships were described very well by

Fig. 1. Estimated developmental rates for forest tent caterpillar eggs in egg masses collected from trembling aspen and largetooth aspen.



equation [1] ($R^2 = 0.991$ and $R^2 = 0.981$ for the populations from largetooth aspen and trembling aspen, respectively). A maximum developmental rate of $\sim 0.24 \text{ d}^{-1}$ at 23°C, and 0.27 d^{-1} at 23.5°C, for eggs from largetooth aspen and trembling aspen, respectively, was estimated from equation [1] (Fig. 1). Parameter values are given for both populations in Table 2.

Population variability in temperature-independent developmental times was significantly less in the population of eggs from largetooth aspen than from the population from trembling aspen (Fig. 2) ($W = 2.56$; $P(> W) < 0.005$). Therefore, population variability in developmental times was described separately for each population. Equation [3] described >0.99 of the variability in developmental times within each population (Fig. 2).

Simulated egg hatch under the 1971–2000 temperature conditions of the collection site began (cumulative hatch $\geq 5\%$) as early as 30 March, and ended (cumulative hatch $>95\%$) as late as 17 May for egg masses on trembling aspen. Simulated egg hatch for eggs on largetooth aspen began as early as 31 March and ended as late as 18 May. The average hatch duration was 17.5 days ($s_{\bar{x}} = 1.1 \text{ d}$) on trembling aspen and 16.7 days ($s_{\bar{x}} = 1.0 \text{ d}$) on largetooth aspen.

Discussion

The FTC is fairly described as a generalist when one considers the variety of genera on which it feeds throughout its range (*Populus* Linnaeus

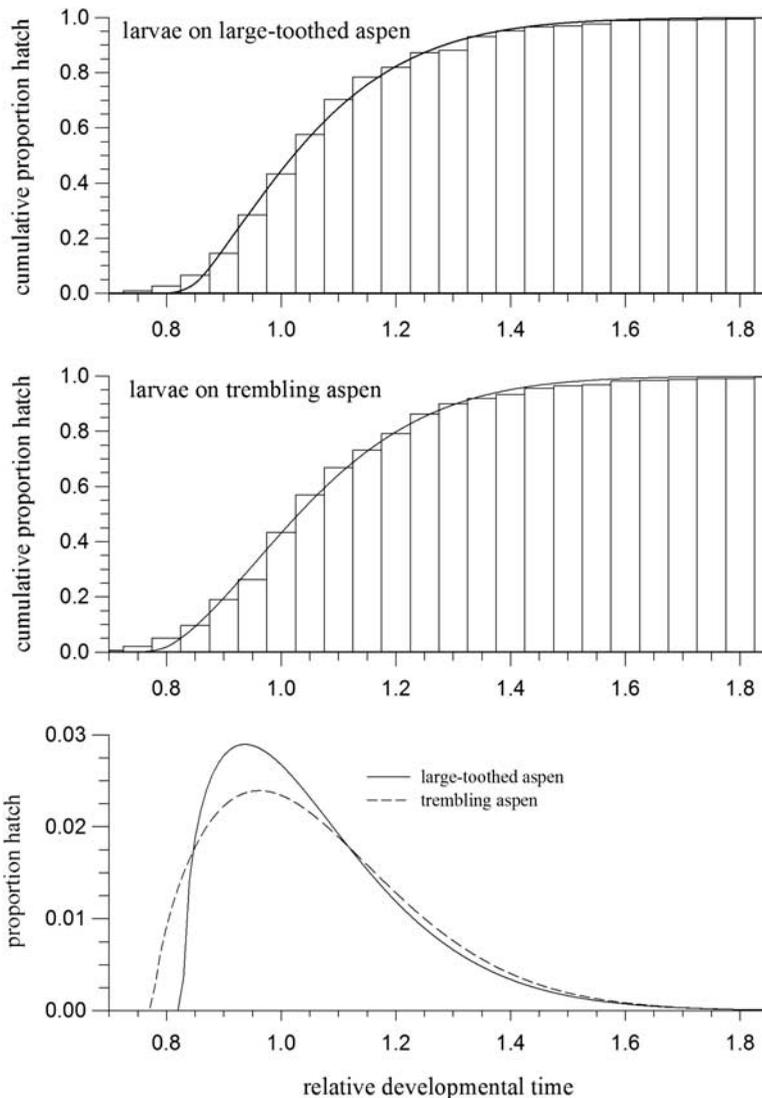
Table 2. Estimated parameter values for median developmental rates and temperature-independent variability in developmental times for populations of forest tent caterpillar taken from two host species.

Host	Median developmental rate*					Temperature-independent variability†		
	α	k	ρ	ΔT	T_M	λ	β	ϕ
Largetooth aspen	0.3954	21.1900	0.2242	0.7670	18.5955	1.4126	0.2541	0.8253
Trembling aspen	0.4671	21.5071	0.2100	0.6601	18.9312	1.6611	0.3232	0.7709

* $R = \alpha \left\{ [1 + ke^{-\rho T}]^{-1} - e^{-\tau} \right\}$, where $\tau = \frac{T_M - T}{\Delta T}$

† $F(x) = 1 - \exp \left[- \left(\frac{x - \lambda}{\beta} \right)^\alpha \right]$.

Fig. 2. Estimated population variability in developmental rates for forest tent caterpillar eggs in egg masses collected from trembling aspen and largetooth aspen.

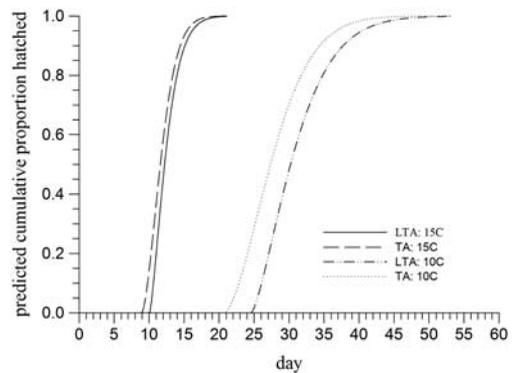


(Salicaceae), *Salix* Linnaeus (Salicaceae), *Alnus* Miller (Betulaceae), *Betula* Linnaeus (Betulaceae), and *Prunus* Linnaeus (Rosaceae)). However, at smaller scales, even broad generalists exhibit higher degrees of specialisation (*i.e.*, local specialisation, *sensu* Fox and Morrow (1981)) as the local population adapts to the temporally and spatially restricted availability of suitable hosts. The deleterious effects that newly emerged larvae experience when forced to feed on older foliage is one factor that would promote synchrony between FTC egg hatch and budbreak of the hosts available at the local level (Parry *et al.* 1998; Jones and Despland 2006; van Asch and Visser 2007).

Differences between the two larval populations (laid on early flushing trembling aspen and laid on later flushing largetooth aspen) in median developmental rates and in variability in developmental times were both statistically significant. However, these differences produce only very small differences in expected hatch patterns between the populations. For example, at constant 15°C, eggs on trembling aspen hatch <1 day (0.73 days) sooner than eggs on largetooth aspen (averaged from observations of 5%, 50%, and 95% cumulative hatch). At constant 10°C, the eggs from trembling aspen hatch an average of 3.3 days earlier than the eggs on largetooth aspen (Fig. 3). Under the 1971–2000 temperature conditions of the collection site, the simulated egg hatch on trembling aspen begins an average of 3.1 days sooner ($s_{\bar{x}} = 0.6$ d) than on largetooth aspen, and hatch is completed on trembling aspen an average of 2.3 days sooner ($s_{\bar{x}} = 0.3$ d). The duration of the hatching period on the two hosts is <1 day different. These differences are substantially less than the 14 days that the budbreak of trembling aspen precedes that of largetooth aspen. We did not test for differences in FTC phenological requirements among host clones. However, differences in budbreak among clones does not eliminate the host differences: budbreak of trembling aspen still precedes that of largetooth aspen by ~14 days. Therefore, it does not appear that FTC egg hatch is independently synchronised with the budbreak of the two hosts on which eggs were oviposited.

We can only speculate as to why FTC lays eggs on two hosts that have a 14-day difference in budbreak phenologies when its phenological pattern of egg hatch is almost identical on the two hosts. Some authors have suggested a general

Fig. 3. Differences in egg hatch patterns of egg masses collected from trembling aspen and largetooth aspen, simulated for constant 10°C and 15°C.



principle (Hopkin’s Host Selection Principle) in which adults have an oviposition preference for the host species on which they matured (reviewed in Barron 2001). But such an inter-generational preference should eventually lead to phenotypes that are specialised *vis-à-vis* the phenology of budbreak on their respective preferred hosts. In our observations of FTC hatch, we see no marked specialisation.

On the other hand, we may have observed an example of bet hedging (or risk-spreading) in host selection for oviposition where a “don’t put all your eggs in one basket” strategy (Seger and Brockman 1987), or “diversified risk-spreading” (Hopper 1999) is prevalent. A significant body of literature has accumulated regarding the theory of bet hedging (Hopper 1999), classifications of bet hedging, and its potential to explain some life-history characteristics of insects. Briefly, bet hedging is a strategy, especially beneficial in temporally variable environments, whereby a lower mean arithmetic fitness is preferred because it confers a lower variance in fitness. The type of bet hedging we are suggesting here is classified by Seger and Brockman (1987) as the “probabilistic diversification of the phenotypes expressed by a single genotype”, and by Hopper (1999) as “diversified risk-spreading”. The currency of fitness is the gene frequency that results over multiple generations. The resulting gene frequency (over time) is multiplicative, and so long-term fitness is measured by the geometric mean, not the arithmetic mean, over the multiple generations. As a trivial example, consider two genotypes: *A* has little

phenotypic variation for a given trait (e.g., host selection) and *B* has large phenotypic variation for the trait. In a temporally variable environment, the generational survival of genotype *A* (averaged over its all very similar phenotypes) is 0.8, 0.8, 0.1, and 0.8; generational survival of genotype *B* (averaged over its many and varied phenotypes) is 0.6, 0.6, 0.4, and 0.6. Genotype *A* has a higher mean arithmetic fitness ($\bar{x} = 0.62$) than genotype *B* ($\bar{x} = 0.55$), but the lower fitness variance of *B* ($s_{\bar{x}} = 0.10$ versus $s_{\bar{x}} = 0.35$) gives *B* a higher mean geometric fitness than *A* ($\left(\prod_{i=1}^4 x_i\right)^{1/4} = 0.54$ versus 0.48) and confers better long-term survival on genotype *B* in the temporally variable environment.

Parry *et al.* (1998) speculated that a narrow phenological window wherein host quality decreases rapidly after budbreak and increased invertebrate predation in later hatching cohorts have exerted a strong selective pressure on larvae to emerge from eggs as early as possible in the spring. In the event that egg hatch precedes budbreak, larvae are able to survive without food for a number of days. Hanec (1966) reported 30%, 79%, and 80% survival at 21°C, 16°C, and 10°C, respectively, after 10 days without food. But when egg hatch follows budbreak of trembling aspen, larvae from eggs oviposited on that host species will suffer from the poorer foliage quality. In a phenotypically diverse genotype, individuals will have laid eggs in the “other basket”: egg masses on largetooth aspen are likely to hatch in time for larvae to feed on the youngest and most nutritious foliage. In most years, the selection of trembling aspen has a better outcome for the FTC population, but the selection of largetooth aspen by a portion of the population spreads the risk.

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References

Allen, J.C. 1976. A modified sine wave method for calculating degree days. *Environmental Entomology*, **5**: 388–396.

- Baker, W.L. 1972. Eastern forest insects. United States Department of Agriculture, Forest Service, Washington, DC, United States of America.
- Barnes, B.V. 1969. Natural variation and delineation of clones of *Populus tremuloides* and *P. grandidentata* in northern Lower Michigan. *Silvae Genetica*, **18**: 130–142.
- Barron, A.B. 2001. The life and death of Hopkins' host-selection principle. *Journal of Insect Behavior*, **14**: 725–737.
- Earth Info. 2010. Global daily [compact disc]. EarthInfo, Inc., Boulder, Colorado, United States of America. Available from www.earthinfo.com.
- Fitzgerald, T.D. and Costa, J.T. 1986. Trail based communication and foraging behavior of young colonies of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *Annals of the Entomological Society of America*, **79**: 999–1007.
- Fox, L.R. and Morrow, P.A. 1981. Specialization: species property or local phenomenon. *Science*, **211**: 887–893.
- Gray, D.R. 2010. Hitchhikers on trade routes: a phenology model estimates the probabilities of gypsy moth introduction and establishment. *Ecological Applications*, **20**: 2300–2309. doi:10.1890/09-1540.
- Gray, D.R. 2012. Using geographically robust models of insect phenology in forestry. *In Phenology. Edited by X. Zhang*. In Tech Publishing, Rijeka, Croatia. pp. 3–20.
- Hanec, W. 1966. Cold-hardiness in the forest tent caterpillar, *Malacosoma disstria* Hubner (Lasiocampidae, Lepidoptera). *Journal of Insect Physiology*, **12**: 1443–1449.
- Hodson, A.C. and Weinman, C.J. 1945. Factors affecting recovery from diapause and hatching of eggs of the forest tent caterpillar, *Malacosoma disstria* Hbn. University of Minnesota Agricultural Experiment Station Technical Bulletin, **170**: 1–31.
- Hollander, M. and Wolfe, D.A. 1973. Nonparametric statistical methods. John Wiley and Sons, New York, United States of America.
- Hopper, K.R. 1999. Risk-spreading and bet-hedging in insect population biology. *Annual Review of Entomology*, **44**: 535–560.
- Hunter, A.F. and Lechowicz, M.J. 1992. Foliage quality changes during canopy development of some northern hardwood trees. *Oecologia*, **89**: 316–323.
- Hunter, M.D. 1990. Differential susceptibility to variable plant phenology and its role in competition between two insect herbivores on oak. *Ecological Entomology*, **15**: 401–408.
- Ives, W.G.H. 1973. Heat units and outbreaks of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *The Canadian Entomologist*, **105**: 529–543.
- Jennrich, R.I. and Moore, R.H. 1975. Maximum likelihood estimation by means of nonlinear least squares. *American Statistical Association Proceedings of the Statistical Computing Section*, 57–62.

- Jones, B.C. and Despland, E. 2006. Effects of synchronization with host plant phenology occur early in the larval development of a spring folivore. *Canadian Journal of Zoology*, **84**: 628–633.
- Laidly, P.R. 1990. *Populus gradidentata* Michx. Bigtooth aspen. In *Silvics of North America*, vol. 2: Hardwoods. Edited by R.M. Burns and B.H. Honkala. United States Department of Agriculture, Forest Service, Washington, DC, United States of America. pp. 544–550.
- Law, M.A. and Kelton, W.D. 1982. Simulation modeling and analysis. McGraw-Hill, New York, United States of America.
- Lieth, H. 1974. Phenology and seasonality modeling. Springer-Verlag, New York, United States of America.
- Logan, J.A., Wollkind, D.J., Hoyt, S.C., and Tanigoshi, L.K. 1976. An analytic model for description of temperature dependent rate phenomena in arthropods. *Environmental Entomology*, **5**: 1133–1140.
- Lorimer, N. 1979. Differential hatching times in the forest tent caterpillar (Lepidoptera: Lasiocampidae). *Great Lakes Entomologist*, **12**: 199–201.
- Mattson, W.J. and Erickson, G. 1978. Degree-day simulation and hatching of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *Great Lakes Entomologist*, **11**: 59–61.
- Mattson, W.J. and Scriber, J.M. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, fiber and mineral considerations. In *Nutritional ecology of insects, mites, spiders and related invertebrates*. Edited by F. Slansky and J.G. Rodriguez. John Wiley, New York, United States of America. pp. 105–146.
- Ostaff, D.P. and Quiring, D.T. 2000. Role of the host plant in the decline of populations of a specific herbivore, the spruce budmoth. *Journal of Animal Ecology*, **69**: 263–273.
- Parry, D. and Goyer, R.A. 2004. Variation in the susceptibility of host tree species for geographically discrete populations of forest tent caterpillar. *Environmental Entomology*, **33**: 1477–1487.
- Parry, D., Spence, J.R., and Volney, W.J.A. 1998. Budbreak phenology and natural enemies mediate survival of first instar forest tent caterpillar (Lepidoptera: Lasiocampidae). *Environmental Entomology*, **27**: 1368–1374.
- Quiring, D.T. 1992. Rapid change in suitability of white spruce for a specialist herbivore, *Zeiraphera canadensis*. *Canadian Journal of Zoology*, **70**: 2132–2138.
- Raske, A.G. 1974. Hatching rates for forest tent caterpillar in the laboratory. Natural Resources Canada, Canadian Forest Service – Atlantic Forestry Centre, St. John's, Newfoundland, Canada. pp. 24–25.
- Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia*, **93**: 25–30.
- SAS Institute. 1999. SAS/STAT[®] user's guide, version 8. SAS Institute, Inc., Cary, North Carolina, United States of America.
- Scriber, J.M. and Slansky, F. 1981. The nutritional ecology of immature insects. *Annual Review of Entomology*, **26**: 183–211.
- Seger, J. and Brockman, H.J. 1987. What is bet-hedging? *Oxford Surveys in Evolutionary Biology*, **4**: 182–211.
- van Asch, M. and Visser, M.E. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology*, **52**: 37–55.
- Wagner, T.L., Wu, H.-I., Sharpe, P.J.H., and Coulson, R.N. 1984. Modeling distributions of insect development time: a literature review and application of the Weibull function. *Annals of the Entomological Society of America*, **77**: 475–487.
- Witter, J.A. 1979. The forest tent caterpillar (Lepidoptera: Lasiocampidae) in Minnesota: a case history review. *Great Lakes Entomologist*, **12**: 191–196.