

## Effects of synchronization with host plant phenology occur early in the larval development of a spring folivore

B.C. Jones and E. Despland

**Abstract:** Early spring feeding Lepidoptera depend on synchronization of larval emergence with host plant phenology for optimal growth and development. Physical and chemical characteristics of foliage change over the course of the growing season, and a delay in larval emergence therefore results in larvae foraging on lower quality food. We examine the effect of synchronization of larval emergence with leaf phenology on the entire larval stage of the forest tent caterpillar, *Malacosoma disstria* Hübner, 1820 (Lepidoptera: Lasiocampidae). Caterpillars were reared from egg hatch to pupation on trembling aspen, *Populus tremuloides* Michx; 10 days separated egg hatch in the early and late treatments. Late-hatching caterpillars experienced reduced growth in the early instars, but growth in the later instars did not differ between treatments. Reduced growth early in development resulted in both prolongation of the larval stage through the occurrence of additional instars, and lower pupal mass. Aspen foliage quality changes rapidly during leaf expansion, and the late-hatching caterpillars likely missed the narrow window of opportunity for young larvae to feed on high-quality developing foliage. This study demonstrates the importance of early-instar ecology in Lepidoptera.

**Résumé :** Pour atteindre une croissance et un développement optimaux, les lépidoptères qui se nourrissent au printemps dépendent d'une synchronisation de leur émergence larvaire avec la phénologie de la plante-hôte. Les caractéristiques physiques et chimiques du feuillage changent au cours de la saison de croissance et un délai dans la synchronisation a donc comme conséquence que les larves s'alimentent d'une nourriture de moindre qualité. Nous examinons l'effet de la synchronisation avec la phénologie des feuilles sur l'ensemble de la période larvaire de la livrée des forêts, *Malacosoma disstria* Hübner, 1820 (Lepidoptera: Lasiocampidae). Nous avons élevé les chenilles depuis l'éclosion des oeufs jusqu'à la nymphose sur le peuplier faux-tremble, *Populus tremuloides* Michx; dix jours séparent l'éclosion des groupes hâtif et tardif. Les chenilles à éclosion tardive ont une croissance réduite durant les premiers stades, mais la croissance des stades plus avancés ne diffère pas selon les groupes. La croissance réduite au début du développement a pour conséquence un prolongement de la vie larvaire et même l'addition de stades supplémentaires, ainsi qu'une masse nymphale plus petite. La qualité du feuillage du peuplier diminue rapidement durant l'expansion des feuilles et les chenilles à éclosion tardive manquent vraisemblablement la fenêtre d'opportunité étroite représentée par le feuillage en expansion. Notre étude souligne l'importance de l'écologie des premiers stades larvaires chez les lépidoptères.

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### Introduction

Early spring feeding Lepidoptera demonstrate synchronization of larval emergence with host leaf flush. There is much evidence that synchronization of emergence with a phenological window of opportunity is important for larval development (Feeny 1970; Ayres and MacLean 1987; Raupp et al. 1988; Stoyenoff et al. 1994; Martel and Kause 2002). Foliage quality tends to deteriorate as the growing season progresses; in particular, nitrogen and water content de-

crease and leaf toughness increases (Mattson and Scriber 1987). Early spring feeding Lepidoptera can experience reduced survival and performance if they miss the phenological window of young foliage (Scriber and Slansky 1981). Reduction in performance can manifest itself through both reduced growth and extended duration of the larval phase. Both of these factors have direct implications for fitness. Reduction in mass of females leads to lower potential fecundity, and an extended larval phase results in longer exposure to natural enemies (Parry et al. 1998).

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For instance, the gypsy moth, *Lymantria dispar* (L., 1958), showed reduced growth in the early larval stages when feeding on older foliage (Hunter and Lechowicz 1992). Schroeder (1986) demonstrated that late-instar eastern tent caterpillar (*Malacosoma americanum* (Fabr., 1793)) larvae experienced reduced growth when reared on mature as opposed to immature foliage from black cherry, *Prunus serotina* Ehrh. Other early spring feeding caterpillar species showed similar dependence on immature foliage for maximal growth rates: the hemlock looper, *Lambdina fiscellaria fiscellaria* (Guenée, 1857) (Carroll 1999); the autumnal moth, *Epirrita autumnata* (Borkhausen, 1794) (Kause et al. 1999); the buckmoth caterpillar, *Hemileuca lucina* H. Edwards, 1887 (Stamp and Bowers 1990); and the winter moth, *Operophtera brumata* (L., 1758) (Tikkanen and Julkunen-Tiitto 2003). Many early spring feeders are outbreaking species, and the narrow window of opportunity for optimal growth may play a role in generating outbreak dynamics (Hunter 1991).

The forest tent caterpillar, *Malacosoma disstria* Hübner, 1820, is an early spring feeder and an important defoliator throughout much of North America. Populations reach epidemic levels cyclically, but the factors causing the initiation of outbreaks are poorly understood (Cooke and Roland 2003). However, it is hypothesized that phenological synchronization of forest tent caterpillars with their host plant may be a mechanism (Parry et al. 1998). The primary host of the forest tent caterpillar in the northern part of its range is trembling aspen, *Populus tremuloides* Michx. Forest tent caterpillar larval development generally lasts about 5 to 7 weeks (Ives and Wong 1988). During this time, trembling aspen foliage undergoes a reduction in foliar nitrogen and water concentration, an increase in leaf toughness (Ricklefs and Matthew 1982; Hunter and Lechowicz 1992), and a substantial change in secondary metabolites (Lindroth et al. 1987; Osier et al. 2000; Barbehenn et al. 2003). Therefore, early- and late-instar larvae forage upon foods of different chemical and physical composition, and caterpillars that hatch late experience reduced food quality compared with insects hatching in time with budbreak.

Parry et al. (1998) compared forest tent caterpillars reared on freshly flushed aspen foliage with those that hatched 6 days after budbreak over the first larval instar. No differences in mortality were observed in the absence of predation, but late-hatching caterpillars moulted to the second instar significantly later. However, it is not clear whether this delay early in development affects overall larval performance. It is also not known how foliage age affects caterpillars in later instars. This experiment quantifies the effects of delayed larval emergence throughout forest tent caterpillar larval development. We hypothesized that caterpillars hatching late relative to leaf flush would be affected more heavily early in development than in later larval instars. To test the hypothesis, growth and development time were compared between caterpillar sib-groups removed from dormancy 10 days apart and reared on aspen foliage. Measurements were taken at each larval instar to determine when effects of host phenology occurred.

## Materials and methods

Egg bands were supplied by the Canadian Forest Service

Great Lakes Forestry Centre in Sault Ste. Marie, Ontario, Canada. Ten egg bands were removed from dormancy on 13 May 2003 to synchronize with local bud flush in the Montréal region (Quebec, Canada). Eggs hatched within 4 days; larvae emerging from these eggs constituted the early hatching treatment. To reduce the probability of infection with pathogens, the bands were sterilized by soaking in 5% sodium hypochlorite for 2 min, washed with running tap water for 5 min, and rinsed with 0.05% sodium hypochlorite (Grisdale 1985). Each egg band was placed upon an aspen leaf in a separate 10 cm × 20 cm plastic container with a mesh lid. The bottom of each container was lined with a layer of damp paper towel covered with a layer of wax paper. The petiole of each leaf was inserted into a plastic florist's tube filled with water. Foliage was collected from three different aspen stands in Mount Royal Park (Parc du Mont-Royal) in Montréal. Stands were exposed to the west and were mixed with other deciduous species. Stands were visited in regular rotation and the same three or four trees of similar size (<4 m) were used. Terminal twigs were removed from the lower and middle portions of the crown. Leaves were sterilized by rinsing with 1% hypochlorite solution and washed with tap water, against the possible presence of pathogens. Foliage was replaced in containers ad libitum when a leaf became desiccated or was wholly consumed. The containers were placed in an incubator at 22 °C with a photoperiod of 16 h light : 8 h dark. On 23 May 2003, 6 more egg bands were set using the same protocol to establish a late hatching treatment. Eggs hatched within 4 days. Therefore, there was a 10-day difference in egg hatch between the early and late treatments. Upon moulting to the second instar, each sib-group was reduced to a maximum of 20 individuals. Only 3 of the 10 egg bands in the early hatching treatment produced sufficient numbers of larvae. Hence, there were 3 sib-groups that hatched early, and 6 that hatched later. The forest tent caterpillar is gregarious; therefore, larvae were kept in sib-groups for the duration of the experiment. The experiment continued until all larvae had pupated.

Containers were examined twice per day for newly moulted larvae and to replace foliage. Data collection began at the third instar owing to the fragility and very low mass of first- and second-instar caterpillars. First-instar larvae from the early hatching treatment and first- and second-instar larvae from the late treatment weighed less than 1 mg. This made handling difficult and the probability of fatally damaging larvae particularly high. To measure larval performance, moulting date and mass were recorded at each moult for each larva in all sib-groups. Larvae were weighed at the beginning of an instar, within 12 h of moulting. After pupation, mass and sex were recorded for each individual.

To analyze overall performance of larvae, a two-way factorial analysis of variance was used to test the effects of foliage treatment and sex on pupal mass and time to pupation. Sib-groups were nested in the treatment groups to test for variability between sib-groups.

For the analysis of patterns of development, it was not possible to follow individual trajectories from one instar to the next because caterpillars were reared in groups. Instead, the average time from hatch to each instar and the average mass at each instar were compared between treatments. Lin-

ear regression was used to determine whether the growth trajectories of larvae from the two treatments were the same. Mass and total time to reach each instar were plotted against the instar number: the slopes and y-intercepts of these regression lines were compared between the two treatments using analysis of covariance (ANCOVA) (Sokal and Rohlf 1995). The slope represents the rate of growth (for the mass regression) or development (for the time regression) between the third and final instars; the y-intercept represents the growth or development rate up to the third instar.

## Results

### Overall performance

Table 1 shows differences in mortality rate and the total number of larval instars both between treatments and between sib-groups. Larvae from the early hatching treatment underwent 5 to 7 instars, with the majority completing 6 instars before pupation. All individuals in the late hatching treatment underwent at least 7 instars before pupating. The number of larval instars differed significantly between treatments ( $\chi^2_{[3]} = 895$ ,  $P < 0.001$ ). There was no difference in mortality rate between the two treatments, but mortality varied widely between sib-groups, ranging from 0% to over 50%.

The difference in the number of instars completed before pupation led to a 20% difference in development time between treatments, with larvae from the late hatching treatment taking more time to pupate ( $F_{[1,7]} = 14.417$ ,  $P = 0.006$ ; see Fig. 1). Within each treatment there was also significant variation between sib-groups in time to pupation ( $F_{[7,93]} = 9.940$ ,  $P < 0.001$ ). However, the time to pupation did not differ significantly between the sexes ( $F_{[1,93]} = 2.821$ ,  $P = 0.096$ ), nor was there a significant interaction between treatment and sex ( $F_{[1,93]} = 0.006$ ,  $P = 0.940$ ).

Pupae from the early hatching treatment were more than 20% heavier than pupae from the late treatment ( $F_{[1,7]} = 21.956$ ,  $P = 0.002$ ; see Fig. 1). Significant differences were also detected between sib-groups within each treatment ( $F_{[7,91]} = 4.086$ ,  $P = 0.001$ ). Female pupae were significantly heavier than male pupae ( $F_{[1,91]} = 138.412$ ,  $P < 0.001$ ). There was no significant interaction between sex and treatment on pupal mass ( $F_{[1,91]} = 3.536$ ,  $P = 0.063$ ).

### Pattern of development

Larval mass and cumulative development time were regressed against instar for comparison between the two treatments. For each treatment, only larvae that underwent the same number of instars (6 for the early hatching treatment and 7 for the late treatment) were used, to avoid confounding effects associated with metamorphosis in the ultimate instar. Larval mass was log-transformed to normalize the distribution of data before analysis. Larvae from the late hatching treatment lagged behind their early hatching counterparts in both mass and development rate from the third instar onward (see Fig. 2). The additional seventh instar in the late hatching treatment reduced the difference in mass, at the expense of further prolonging development (see Fig. 2).

Testing for homogeneity of slopes revealed no significant difference between treatments in the relationship between cumulative development time and instar ( $F_{[1,6]} = 0.23$ ,  $P > 0.25$ ) or in the relationship between mass and instar ( $F_{[1,6]} =$

2.90,  $0.10 < P < 0.25$ ). This indicates that between instar 3 and instar 6, neither growth rate nor development rate differed between the two treatments. The ANCOVA revealed a significant difference in y-intercepts between treatments, for both mass ( $F_{[1,389]} = 544.701$ ,  $P < 0.001$ ) and cumulative development time ( $F_{[1,390]} = 42.987$ ,  $P < 0.001$ ). This indicates differences between treatments in growth and development rates before the third instar.

## Discussion

Late-hatching forest tent caterpillars grew and developed more slowly in the first two larval instars than did caterpillars hatching in time with aspen budbreak. Although growth and development rates from the third instar onward did not differ between treatments, this delay early in development led to a prolongation of the larval stage via the addition of larval instars, and to lower pupal mass.

In our experiment, delayed growth and development in the first few larval instars led to supernumerary larval instars. Additional instars indicate that there may be a mass threshold for pupation; if the threshold is not reached, then the larva will continue the moulting cycle until a critical mass is attained (Nijhout 1994). Late-hatching forest tent caterpillar larvae experienced reduced growth in earlier instars and were therefore less heavy at each instar than larvae from the early hatching treatment. Thus, additional instars were necessary to attain the threshold size for pupation (Fig. 2). Additional instars can occur when an insect is subjected to environmental stress (Sehnal 1985; Danks 1987). For example, insect larvae reared on suboptimal food can be induced to undergo additional instars (Beck 1950; Wigglesworth 1972; Nijhout 1994; Kidd and Orr 2001; Verdine and Sanna-Passino 2003). In the forest tent caterpillar, the number of larval instars is plastic (Muggli and Miller 1980; Smith et al. 1986): we show that it can depend on growth rate early in development.

Late-hatching caterpillars in our experiment fed readily on the leaves provided to them but grew less and developed more slowly, presumably because of lower foliar nutritional quality. Indeed, aspen foliage changes during the course of the growing season through reduced nitrogen and water content, increased phenolic glycosides and condensed tannins, and increased leaf toughness (Hunter and Lechowicz 1992; Osier et al. 2000). All of these factors are suggested to have adverse effects on the development of forest tent caterpillar larvae (Hemming and Lindroth 1999; Kopper and Lindroth 2003).

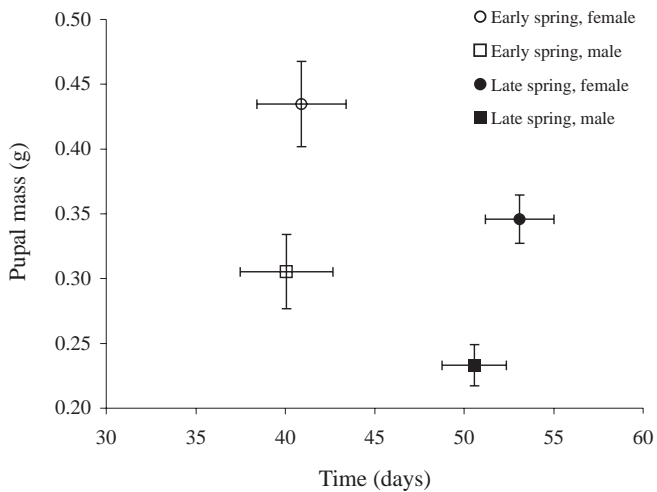
A difference in growth and development rates between treatments in the early larval instars but not in the later stadia could be due to two different mechanisms: either the caterpillars are more sensitive to variations in leaf quality when they are younger than when they are older, or foliage quality changes rapidly early in the season and then stabilizes later on. The present experiment does not allow us to distinguish between these hypotheses, and the literature provides support for both. Indeed, young larvae are generally more sensitive to food quality, including nitrogen content and secondary chemistry, and older caterpillars are able to feed on a wider range of hosts (Lindroth and Bloomer 1991; Waldbauer and Friedman 1991). Younger caterpillars are

**Table 1.** Number of larval instars completed before pupation by early- and late-hatching forest tent caterpillars (*Malacosoma disstria*).

Treatment	Sib-group	Larval mortality (%)	Total no. of pupae	No. of larvae pupating at instar			
				5	6	7	8
Early hatching	1	4.8	20	9	11		
	4	61.5	5		5		
	10	0	6		3	3	
Late hatching	101	7.7	12			12	
	102	52.4	10			4	6
	103	0	15			15	
	104	14.3	12			3	9
	105	6.7	14			14	
	106	21.4	11			6	5

**Note:** For each sib-group, the table shows mortality between the third instar and pupation, the total number of caterpillars that pupated successfully, and the number of caterpillars requiring 5, 6, 7, or 8 instars before pupation.

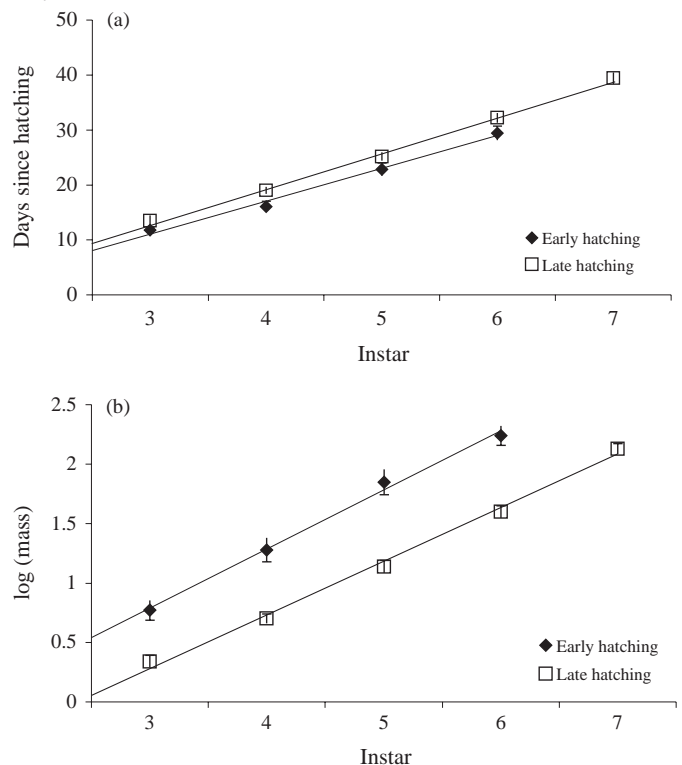
**Fig. 1.** Effect of early and late hatching treatments (mean  $\pm$  95% confidence interval) on pupal mass and time to pupation for both male and female forest tent caterpillars (*Malacosoma disstria*).



also more sensitive to mechanical leaf traits (e.g., toughness) owing to their smaller mouthparts and less developed musculature (Hochuli 2001).

Moreover, water and nitrogen content decreases rapidly during aspen leaf expansion and then stabilizes for the rest of the growing season (Ricklefs and Matthew 1982; Hunter and Lechowicz 1992). Osier et al. (2000) showed that in the first 2 weeks following leaf-out, aspen leaf nitrogen decreased from around 4.5% of foliar dry mass to about 3% and leaf water content fell from approximately 72% to approximately 68%. Water content continued to drop over the next month, reaching approximately 60%, whereas nitrogen content showed only a slight further decrease to 2.5%. Condensed tannins increased significantly in the first 2 weeks following budbreak and then stabilized, whereas phenolic glycosides showed no clear pattern. Changes in leaf water and nitrogen content were very consistent among all the clones studied, whereas secondary metabolites varied considerably between clones (Osier et al. 2000). Similar findings have been obtained in other studies (Ricklefs and Matthew 1982; Barbehenn et al. 2003; Kopper and Lindroth 2003), including one conducted very near to our sampling

**Fig. 2.** Mean values ( $\pm$ 95% confidence interval) for performance at each instar for both early and late hatching forest tent caterpillars: (a) total number of days since hatching and (b) log of the mass (in grams). Only individuals that underwent 6 or 7 instars before pupation are included. Lines represent best-fitting linear regressions. Regression equations are as follows: (a) duration: early hatching,  $y = 5.94x - 6.70$ ,  $R^2 = 0.87$ ; late hatching,  $y = 6.32x - 6.02$ ,  $R^2 = 0.78$ ; (b)  $\log(\text{mass})$ : early hatching,  $y = 0.50x - 0.72$ ,  $R^2 = 0.83$ ; late hatching,  $y = 0.43x - 0.98$ ,  $R^2 = 0.82$ . Invisible interval bars imply very narrow confidence intervals.



site (Hunter and Lechowicz 1992). Thus, in our experiment, early-hatching caterpillars would have had access to foliage with high water and high nitrogen concentrations for the first few days of their development, whereas those hatching 10 days later would have missed this narrow window of opportunity and would have been exposed to lower concentrations of water and nitrogen throughout their larval stage.

The consequences associated with delayed hatching differ between species, particularly between evergreen and deciduous feeders. In some evergreen-feeding species, young larvae are unable to feed on tough, mature foliage from previous years, and larvae that hatch too soon are at risk of starvation (Cockfield and Mahr 1993). In another evergreen feeder, the spruce budworm (*Choristoneura fumiferana* (Clemens, 1865)), the opposite is observed: the best performance is observed among caterpillars that emerge before budbreak and feed on the previous years' foliage before switching to the high-quality new growth. Caterpillars thus require access to high-quality foliage late in development to complete larval development before the end of shoot growth and the associated decline in food quality (Lawrence et al. 1997; Carroll 1999). Contrary to what we have shown for the forest tent caterpillar, reduced performance of late-hatching budworms is thus due to poor growth in the final larval instar.

In several temperate-zone, early-spring deciduous feeders, late-hatching caterpillars are able to feed on the older foliage available to them but exhibit decreased growth owing to lower food quality (Ayres and MacLean 1987; Hunter and Lechowicz 1992; Parry et al. 1998). In these species, mortality in the field can be higher among late-hatching larvae owing to phenological differences in predation (Parry et al. 1998) or to increased dispersal away from the less palatable older foliage (Hunter and Lechowicz 1992). Our study shows that in a species where first-instar larvae are able to feed on older foliage without an increase in mortality (Parry et al. 1998), there is nonetheless a nutritional cost to consuming older foliage early in development.

It has been pointed out that not enough attention is given to the ecology of early instars when discussing lepidopteran host use: most studies are conducted on late or final-instar larvae, yet most mortality occurs during the early stadia (Hochuli 2001; Zalucki et al. 2002). Young larvae face different challenges than older larvae when feeding. They have greater sensitivity to secondary plant compounds (Lindroth and Bloomer 1991) and exhibit smaller mandibles that are morphologically different from those of older larvae (Hochuli 2001). Indeed, caterpillars exhibit instar-specific adaptations linked to the changing selection pressures they face during development (Hochuli 2001; Despland and Hamzeh 2004). Mortality is often high and extremely variable in the early larval stadia (Zalucki et al. 2002) and, as we have shown here, differences in growth and development rate in the first two instars can significantly influence performance measures at pupation. Given that both plant chemistry and insect requirements change during the course of larval development, plant-insect interactions and the interplay between plant and insect phenology need to be studied directly in young larvae, since effects early in larval ontogeny cannot necessarily be inferred from work on older developmental stadia.

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