

# Macrogeographic clines in fecundity, reproductive allocation, and offspring size of the forest tent caterpillar *Malacosoma disstria*

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**Abstract.** 1. The fecundity of the forest tent caterpillar varies considerably across its geographic range. Field data indicate that populations in the southern United States (Gulf States) produce nearly twice as many eggs as females from Canada or the Lake States, with little or no difference in the size of adult females.

2. In controlled rearing experiments, female forest tent caterpillar from the southern United States (Louisiana) had much larger clutch sizes than same sized females from northern populations in Michigan or Manitoba, Canada. Increased fecundity in Louisiana females was achieved through a significant reduction in egg size and a concomitant increase in the allocation of resources to egg production.

3. Comparison of 10 forest tent caterpillar populations spanning a 27° latitudinal gradient, validated the results of detailed comparisons among the three populations above by confirming the strong negative correlation between latitude and clutch size.

4. Neonate forest tent caterpillars from Manitoba were significantly larger than larvae from either Michigan or Louisiana. Michigan larvae were intermediate in size. It is postulated that large neonates are advantageous in thermally limiting environments. More than three times as many degree-days are available to Louisiana neonates during the first 2 weeks after hatching. A consistently favourable climate during the vulnerable post-hatching period may have allowed the evolution of larger clutches at the expense of neonate size in southern populations.

**Key words.** Clutch size, latitudinal gradient, life-history strategy, offspring size, reproductive trade-offs.

## Introduction

A fundamental tenet of evolutionary theory is that life-history strategies that maximise reproductive success in a particular environment will be favoured by natural selection (Lack, 1954; Stearns, 1992). In many organisms, egg size is correlated with the fitness of offspring (e.g. Lloyd, 1987; Sinervo & McEdward, 1988; Roff, 1992; Stearns, 1992; Sinervo, 1993). Thus, selection should act to maximise egg size. Because maternal investment in reproductive propagules is high and in many cases fixed, however, as energy expended on individual offspring increases, the number of offspring must decrease.

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Smith and Fretwell (1974) postulated that changes in egg size among populations represent variation in optimal egg size driven by different selective regimes. Furthermore, in species subjected to variable environmental conditions, minimum viable offspring size will be smaller in *good* habitats than in *poor* habitats because an offspring should require fewer resources to become established under favourable conditions (Lloyd, 1987; McGinley *et al.*, 1987).

A useful approach to addressing questions about the contribution of environment to reproductive trade-offs is to examine the relationship between fecundity and propagule size along a latitudinal gradient. Parker and Begon (1986) hypothesised that in seasonal environments, production of fewer but larger eggs should be favoured where the growing season is short. This hypothesis appears to be supported among insects where, within a species, egg size tends to increase in

populations from higher latitudes or cooler regions. For example, in *Drosophila*, egg size was larger at high latitudes on two continents (Azevedo *et al.*, 1996). Latitudinal clines in egg size have also been identified in a leaf feeding beetle (Ando, 1983) and a gerrid, *Aquarius remigis* (Blanckenhorn & Fairbairn, 1995).

Few studies have focused on geographic variation in egg size and fecundity in the Lepidoptera. The spruce budworm *Choristoneura fumiferana* Clemens (Tortricidae) exhibited a strong latitudinal cline in the proportional allocation of resources to individual eggs (Harvey, 1983). Females from northern latitudes produced fewer but significantly larger eggs for any given body mass. Harvey (1983) attributed this difference to greater yolk provisioning of northern eggs, presumably as an adaptation to aid survival of young larvae over the longer, colder winters. Similarly, Ayres and Scriber (1994) found that Canadian tiger swallowtail butterflies *Papilio canadensis* R & J (Papilionidae) from Alaska produced larger eggs than those from Michigan. They suggested that the larger eggs and concomitantly faster growth rates of the larger neonates compressed development time in a thermally limited environment.

Substantial geographic variation in life-history traits might be expected in species such as the forest tent caterpillar *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). It is found from northern Canada to the Gulf of Mexico and from the Atlantic to the Pacific, a range spanning some 30° of latitude (Prentice, 1963; Stehr & Cook, 1968). This insect utilises a taxonomically diverse array of deciduous trees in climatic environments ranging from boreal to sub-tropical. The forest tent caterpillar has maintained an early spring feeding habit and a univoltine life cycle throughout its distribution. Comparisons among regional populations with respect to either ecological or evolutionary parameters have been surprisingly few, despite this caterpillar's status as a major forest pest. One study has shown that there are substantive genetic differences in some enzymes between populations from the southern and northern United States (Lorimer, 1979a,b). It is unknown whether such differences affect aspects of life history or population dynamics for this species.

One component of the biology of the forest tent caterpillar that clearly differs among regional populations is fecundity. Females deposit all their eggs in a single clutch, laid in a band encircling the distal end of live twigs on selected host plants. This egg-laying habit allows accurate estimation of fecundity in the field because each mass is the full egg complement of an individual female. Comparison of fecundity data suggests that clutch size is much lower in populations in Canada and the northern United States than in Louisiana. For example, Ives (1971) found that forest tent caterpillar populations from Alberta (latitude 53–56°N) averaged 94–248 eggs per mass. Similarly, surveys conducted in northern Minnesota (latitude 48°N) found that egg masses ranged from 120 to 240 eggs (Witter *et al.*, 1975). In marked contrast, egg masses from populations in Louisiana (latitude 30°N) averaged 307–397 eggs (Smith & Goyer, 1986; Goyer *et al.*, 1987). In the only comparative study among populations, Lorimer (1979c) showed that females from northern Michigan (latitude 47°N)

produced fewer eggs for a given pupal mass than did females from southern Indiana (latitude 39°N). Such data must be interpreted cautiously, however, because the number of eggs produced by forest tent caterpillar varies considerably with population density and successive years of outbreak (see Ives, 1971; Witter *et al.*, 1975; Smith & Goyer, 1986). Thus, comparisons of data among northern and southern populations may be confounded because densities are not standardised. Furthermore, number of eggs in this species is highly correlated with pupal and adult mass, so it is possible that females in southern populations attain larger sizes than northern females and that their differences in fecundity simply reflect this relationship.

To address questions about geographic variation in fecundity, the first issue was whether female mass could account for variation in fecundity between southern and northern populations. Laboratory rearing experiments were conducted to assess fecundity, total allocation of resources to reproduction, and mass of individual eggs for three populations of forest tent caterpillar, spanning the latitudinal range of the species. Using data sets from similarly conducted experiments to supplement data collected for this paper, the allocation of female resources to eggs was compared for populations along a 27° latitudinal gradient. Also described is how egg size and number relate to the mass of neonates. The selective mechanisms that may drive changes in optimal neonate size among regional populations are discussed.

## Materials and methods

### *Adult size in field populations*

To determine whether females in southern populations were sufficiently large to account for their much greater fecundity, estimates of mean pupal masses reported from field populations in the literature and from unpublished data sets were compared. Given the caveats about density and fecundity discussed, this approach although coarse was still sufficient to indicate any pupal mass variation among populations large enough to account for the reported fecundity differences of 100–200 eggs per female.

### *Egg collections for laboratory rearing*

Eggs for experimental work in 1998 and 1999 were collected in late autumn and early winter 1997 and 1998 respectively, from three forest tent caterpillar populations. Northern populations were represented by egg bands collected from trembling aspen *Populus tremuloides* Michaux near Flin Flon, Manitoba (latitude 54°N). Mid-latitude eggs were collected from northern red oak *Quercus rubra* L., sugar maple *Acer sacharrum* Marshall, and crab-apple *Malus* sp. in East Lansing, Michigan (latitude 42°N). Southern egg bands were collected from water tupelo *Nyssa aquatica* L. near Sorrento, Louisiana (latitude 30°N). To minimise possible maternal effects, collections were made from low- to

moderate-density populations that were unlikely to have been stressed by starvation or high disease levels. Survey data from the Canadian Forest Service (J. Brandt and J. Weber, unpublished) indicated that the Manitoba populations were part of a new, expanding outbreak, characterised by large egg bands (moderate defoliation, mean=175 eggs per band,  $n=54$ ). Collections by the authors (D. Parry, Michigan, light defoliation, mean=240 eggs per band,  $n=25$ ; R. Goyer, Louisiana, no visible defoliation, mean=390 eggs per band) established the density and population characteristics for Michigan and Louisiana populations respectively. Once collected, eggs were returned to the laboratory and held in a refrigerator at  $\approx 3^\circ\text{C}$  and 70% RH until used in experiments.

Egg bands from different populations had experienced varying amounts of cold prior to collection. In order to synchronise hatch and adjust all populations to the phenology of bud break in Michigan, subsets of the collected egg bands were used to determine the number of days required for hatch to commence in each population. Once thermal requirements for hatch had been established, egg bands were removed from cold storage at the appropriate time prior to initiation of the experiment to ensure synchronous emergence among populations. After removal from cold storage, the frothy spumaline covering on each egg band was removed carefully using a razor blade. The eggs were then placed in a bleach solution (5% sodium hypochlorite) for 2 min to remove any pathogens (particularly nuclear polyhedrosis virus) from the egg surface (modified from Williams *et al.*, 1996).

### Rearing

Larvae representing a minimum of 12 families (maximum of 30) from each of the three populations were then reared outdoors in screened cages held under a 30% shade frame on the Michigan State University campus. During rearing, leaf turgor was maintained by inserting the clipped ends of branches into a water-filled, 500-ml Erlenmeyer flask in each cage. A mesh covering prevented larvae from falling into the flasks. The hatch and rearing of larvae from all three populations were timed to correspond with the phenology of local forest tent caterpillars (East Lansing, Michigan, mean hatch date 2 April 1998 for six egg bands in natural habitats, 9 April 1999 for 13 egg bands). Manitoba and Michigan larvae were reared on either northern red oak or trembling aspen. Although caterpillars grew larger when reared on aspen than on oak, there was no difference between the slope or intercept of regressions of fecundity on pupal mass for these two hosts, so all data were pooled (Manitoba, slope:  $F_{1,89}=0.48$ ,  $P=\text{NS}$ ; intercept:  $F_{1,90}=2.48$ ,  $P=\text{NS}$ ; Michigan, slope:  $F_{1,81}=2.21$ ,  $P=\text{NS}$ ; intercept:  $F_{1,82}=1.55$ ,  $P=\text{NS}$ ). Louisiana caterpillars perform less well on aspen due to rapid phenological maturing of the foliage and were therefore provided with sweet gum *Liquidambar styracifolia* L. or northern red oak. Analysis of the regression parameters showed that, as with caterpillars from Michigan and Manitoba, host plants had no effect on the pupal mass–fecundity relationship (Louisiana: slope,  $F_{1,87}=1.29$ ,  $P=\text{NS}$ ; intercept,  $F_{1,88}=0.53$ ,  $P=\text{NS}$ ), so data

from red oak and sweet gum were pooled. Previous studies on Canadian populations also showed that although pupal mass, fecundity, and development time were affected by rearing on five different host plants, the relationship between female mass and the number of eggs produced was not changed significantly (Parry *et al.*, 1992; D. Parry and J. R. Spence, unpublished).

### Fecundity, reproductive allocation, and egg size

Within 24–36 h of pupation, pupae were removed from the cages, weighed on an electronic balance, and placed individually in 1-oz diet cups until adult emergence. On emergence, females were immediately frozen and stored at  $-15^\circ\text{C}$  for later dissection. Eggs were teased from female abdominal tissue and counted under water using a table-mounted magnifying lens. To ensure accuracy, a different observer repeated egg counts. If the counts did not match, the eggs were recounted.

To determine whether the regression slopes for Manitoba, Michigan, and Louisiana populations were homogeneous, a statistical model with latitude as a covariate, fecundity as the dependent variable, pupal mass as the independent variable, and the interaction term population  $\times$  mass was run (PROC GLM in SAS; SAS Institute, 1996). In this model, only the  $F$ -test for the interaction term is of interest; if it is not significant, slopes are homogeneous (Sokal & Rohlf, 1981). To test for homogeneity of intercepts, the model was run again with the interaction term removed. If there were overall differences between slopes and intercepts, pairwise comparisons were performed using the same model. The sequential Bonferroni correction (Rice, 1989) was applied to  $P$ -values from the pairwise comparisons to avoid inflating the group-wide type I error rate.

In 1999, a minimum of 25 newly emerged females was selected from Louisiana, Michigan, and Manitoba, representing a range of pupal masses common to all three populations (0.300–0.700 g). As above, females were dissected and eggs counted. Eggs were rinsed carefully with distilled water to remove extraneous tissue then placed in a drying oven at  $35^\circ\text{C}$  for 72 h. Once dry, the entire egg complement of each female was weighed on an electronic balance, accurate to 0.01 mg. The statistical model above was used to determine homogeneity of slopes and intercepts for the pupal mass–fecundity and pupal mass–allocation relationships. The reproductive allocation (mass of each female's full egg complement) was divided by the number of eggs to obtain the average weight of each egg. The mass of individual eggs among populations was compared using a one-way ANOVA.

To determine the relative contributions of changing egg size and increasing reproductive allocation to fecundity differences among populations, the following equation was derived:

$$\Delta a/w_2 - [(a_1 \times \Delta w)/(w_1 \times w_2)] = \Delta F \quad (1)$$

where:  $\Delta F$  = fecundity difference between populations,  $\Delta a$  = change in mass allocated to egg complement between

populations,  $\Delta w$  = change in egg weight between populations,  $w_1$  = egg weight population 1,  $w_2$  = egg weight population 2,  $a_1$  = mass allocated to egg complement in population 1, assuming the following equality  $F = a/w$ , where  $F$  = fecundity,  $a$  = mass of egg complement, and  $w$  = weight of individual eggs. From this equation, the relative contribution of egg size and allocation to changes in fecundity for pairwise comparisons between Louisiana and Michigan, Louisiana and Manitoba, and Michigan and Manitoba was determined.

Additional data on the relationship between allocation to eggs, accessory glands, and adult female mass for 10–15 individuals were collected from each population. Prior to dissection, newly emerged adult females were placed in a drying oven for 3 days then weighed. Females were dissected as above and the accessory glands and entire egg complement were returned to the drying oven prior to weighing. Females were selected from each population over an approximately equal size range. Proportions were arcsin-square root transformed prior to analysis to improve normality. A one-way ANOVA with female mass as the independent variable was used to test for differences among populations in the proportion that egg complement and accessory glands contributed to adult female weight.

#### *Regional population comparisons*

Published and unpublished data sets for 10 populations of forest tent caterpillar where female pupal mass and fecundity were recorded were used to calculate the least-square regression equation for the relationship between fecundity and pupal mass. This regression equation was used to estimate the fecundity for a 500-mg female (the mean weight of females from all sampled populations), and this value was regressed on the latitude from which each population was sampled. Because the regression equations for each of these populations do not intersect at biologically relevant values (above 150 mg for females), the nature of the relationship between fecundity and latitude is similar for any given pupal mass.

#### *Neonate size*

To determine neonate size, individual egg bands from each of the three populations ( $n=51$ ,  $n=22$ ,  $n=8$  for Manitoba, Michigan, Louisiana respectively) were placed in plastic diet cups lined with moistened filter paper and allowed to hatch at room temperature. After the majority of the eggs had hatched ( $\approx 24$ – $36$  h), 10 neonates were selected randomly by dipping a moistened fine-tip paintbrush into the mass of caterpillars clustered on each egg band. Because the sample larvae were required for subsequent experiments, the live (wet) mass of 10 larvae from each egg band was recorded using an electronic balance (accurate to 0.1 mg). Mean neonate mass from each egg band was used as the dependent variable in a one-way ANOVA to determine whether there were differences among populations.

#### *Degree-days available for post-hatch larval growth*

Both published and unpublished data on the phenology of egg hatch in northern populations (Michigan and Alberta, Canada) and a southern population (Louisiana) were used to estimate the number of degree-days available for larval growth following hatch. Alberta hatch records are for populations at the same latitude as the Manitoba population used for other experiments in this study ( $\approx 54^\circ\text{N}$ ). Hatch data used in these analyses were as follows: Alberta 1961–65 (Ives, 1973) and 1990 (D. Parry, unpublished); Michigan 1997–98 (D. Parry, unpublished); and Louisiana 1981–83 (Smith, 1983) and 1998–99 (D. Parry, unpublished).

Daily maximum and minimum temperatures were obtained from Environment Canada (for Grande Prairie, Alberta), Michigan State University (for East Lansing, Michigan), and the National Climate Data Center (for Baton Rouge, Louisiana). These data were used to calculate the number of degree-days available for larval growth in the first 14 days post hatching. To determine the base threshold for larval growth, neonates from Manitoba and Louisiana were reared at  $2^\circ\text{C}$  intervals ranging from 8 to  $16^\circ\text{C}$ . Larvae were unable to complete the first instar when reared at temperatures  $\leq 10^\circ\text{C}$ . Thus, a  $10^\circ\text{C}$  threshold was used for larval growth, the same value as Hodson (1941) determined for Minnesota populations of forest tent caterpillar. Accumulated degree-days were estimated by subtracting the threshold temperature from average daily temperature (mid-point of daily maxima and minima) and summing over a 14-day post-hatch period. It is recognised that this technique underestimates degree-day accumulation when temperatures are close to the threshold, but is sufficient to detect broad patterns among regions.

## **Results**

#### *Mass of adult females in field populations*

The mean pupal mass of field-collected females was similar in northern and southern populations ( $F_{1,12}=0.55$ ,  $P=\text{NS}$ ; Table 1), indicating that differences among regional populations are insufficient to account for fecundity differences of 100–200 eggs reported in the literature. In laboratory rearing, spanning a decade and representing many thousands of individuals from at least 10 different populations from Alberta, Saskatchewan, Manitoba, and British Columbia, the largest individual pupal masses recorded for northern females were 800 mg (D. Parry, unpublished). In laboratory-reared forest tent caterpillars ( $n>300$ ) from two populations in Louisiana, maximum individual pupal mass values of 840 mg were recorded, similar to that of northern populations.

#### *Fecundity, reproductive allocation, and egg size*

The interaction term mass  $\times$  population in the test for homogeneity of slopes was significant ( $F_{2,175}=5.61$ ,  $P<0.01$ ), indicating that there were overall differences between the

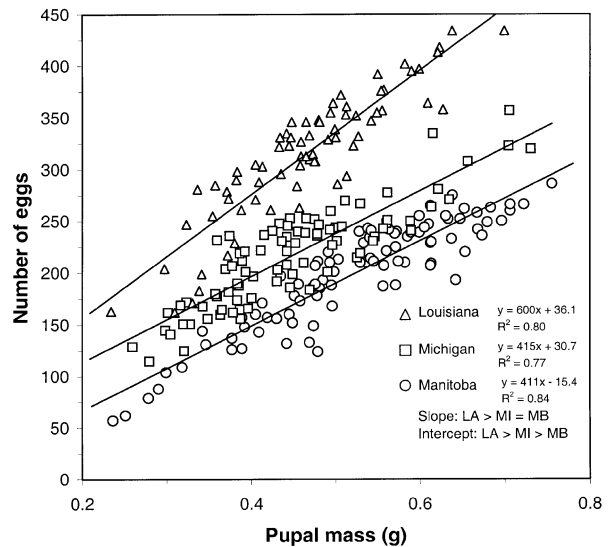
**Table 1.** Pupal mass of female forest tent caterpillars collected from field populations in the southern United States (Alabama and Louisiana) and Canada (Alberta and British Columbia). Louisiana data from Smith (1983), Alabama data from Stark and Harper (1982), Canadian data from D. Parry and J. R. Spence (unpublished). Defoliation level is given for each collection site because this variable often indicates significant food stress and a concomitant reduction in pupal mass.

Population	Site	Year	Latitude (°N)	Pupal mass (g ± SE)	<i>n</i>	Defoliation level
Louisiana	Sorrento	1981	30.2	0.505 ± 0.02	66	Severe
	Sorrento	1982	30.2	0.579 ± 0.06	38	Moderate
	Verrett	1982	30.0	0.464 ± 0.02	57	Moderate
	Alligator	1982	29.5	0.615 ± 0.02	111	Moderate
Alabama	Live Oak	1979	30.5	0.530 ± 0.09	25	Moderate
	Alligator Lake	1979	31.0	0.240 ± 0.06	25	Severe
	Bayou Zeast	1979	30.5	0.500 ± 0.08	25	Severe
	Hubbard Landing	1979	31.1	0.540 ± 0.10	25	Moderate
	Mean			0.497 ± 0.048		
Alberta	George Lake	1989	53.6	0.528 ± 0.01	61	Moderate
	Calling Lake	1989	55.1	0.421 ± 0.01	50	Severe
	Alder Flats	1989	52.6	0.438 ± 0.02	50	Severe
	Elk Island	1991	53.4	0.582 ± 0.02	100	Moderate
British Columbia	Wasa Lake	1989	49.5	0.334 ± 0.01	50	Severe
	Mean			0.461 ± 0.038		

slopes for the three populations reared in 1998 (Fig. 1). Intercepts for each population were also significantly different ( $F_{2,177} = 467.6$ ,  $P < 0.001$ ). Pairwise comparisons with sequential Bonferroni correction (actual  $P$ -values presented here) indicated that both the slope and the intercept differed between Louisiana and Michigan females (slope:  $F_{1,167} = 20.9$ ,  $P < 0.001$ ; intercept:  $F_{1,168} = 509.3$ ,  $P < 0.001$ ) and Louisiana and Manitoba females (slope:  $F_{1,172} = 26.5$ ,  $P < 0.001$ ; intercept:  $F_{1,173} = 1291.3$ ,  $P < 0.001$ ). The slope did not differ between Michigan and Manitoba females although intercepts were significantly different (slope:  $F_{1,171} = 0.02$ ,  $P = \text{NS}$ ; intercept:  $F_{1,172} = 188.1$ ,  $P < 0.001$ ).

In 1999, the relationship between pupal mass and fecundity was similar to that in 1998 (Fig. 2a). Overall, there were significant differences between the slopes and intercepts for the three populations (slope:  $F_{2,77} = 21.3$ ,  $P < 0.001$ ; intercept:  $F_{2,79} = 349.8$ ,  $P < 0.001$ ). Pairwise comparisons indicated that the relationship between fecundity and pupal mass differed significantly between Louisiana and Manitoba (slope:  $F_{1,49} = 34.8$ ,  $P < 0.001$ ; intercept:  $F_{1,50} = 597.2$ ,  $P < 0.001$ ) and between Louisiana and Michigan (slope:  $F_{1,55} = 26.7$ ,  $P < 0.001$ ; intercept:  $F_{1,56} = 255.6$ ,  $P < 0.001$ ). There was no difference between the slopes of Manitoba and Michigan ( $F_{1,50} = 0.14$ ,  $P = \text{NS}$ ) although the intercepts were significantly different ( $F_{1,51} = 175.4$ ,  $P < 0.001$ ).

The overall relationship between pupal mass and reproductive allocation also differed significantly (slope:  $F_{2,77} = 3.1$ ,  $P < 0.05$ ; intercept:  $F_{2,79} = 150.1$ ,  $P < 0.001$ ) for the three populations (Fig. 2b). Pairwise comparisons indicated that Louisiana and Manitoba populations were significantly different (slope:  $F_{1,49} = 26.7$ ,  $P < 0.05$ ; intercept:  $F_{1,50} = 292.4$ ,  $P < 0.001$ ). There was no difference between the slopes of Louisiana and Michigan ( $F_{1,55} = 3.5$ ,  $P = \text{NS}$ ) or Manitoba and Michigan ( $F_{1,50} = 0.7$ ,  $P = \text{NS}$ ). The intercepts

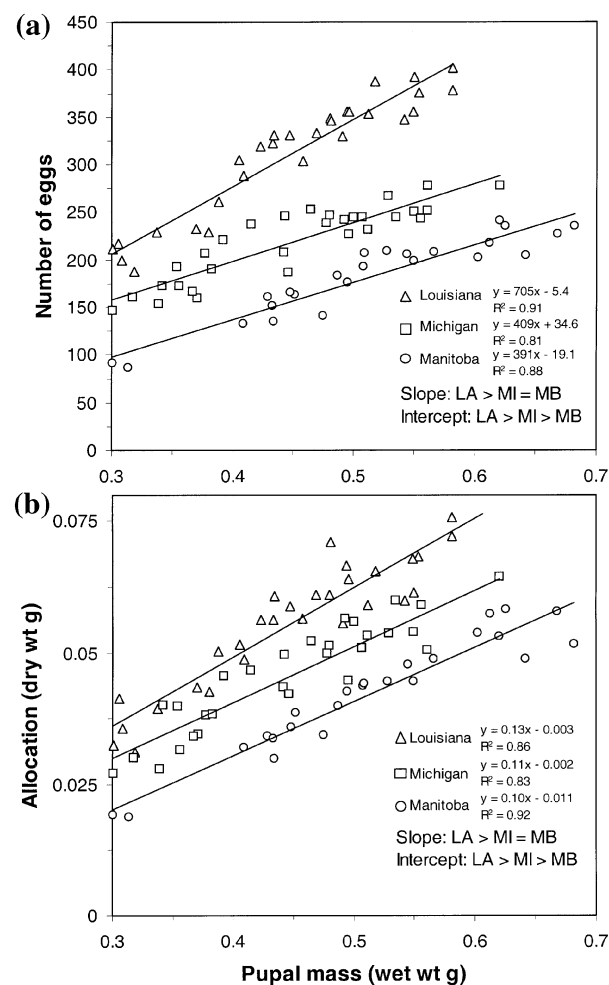


**Fig. 1.** Least-square regressions of the number of eggs (fecundity) on female pupal mass for forest tent caterpillar populations from Manitoba (MB), Michigan (MI), and Louisiana (LA). Data from caterpillars reared under standardised conditions in 1998.

were significantly different ( $F_{1,56} = 72.1$ ,  $P < 0.001$  and  $F_{1,51} = 90.7$ ,  $P < 0.001$  for comparisons of Louisiana and Michigan, and Michigan and Manitoba respectively).

Multiple comparisons (Tukey–Kramer HSD,  $P < 0.05$ ) following ANOVA showed that the dry mass of individual eggs varied significantly among the populations (Table 2). Eggs from Manitoba were 10% heavier than eggs from Michigan and 23% heavier than eggs from Louisiana. Eggs from

Michigan were 14% heavier than eggs from Louisiana. Individual egg weight was correlated positively with pupal mass in the Manitoba population ( $y = 0.07854x + 0.1907$ ,  $P < 0.01$ ,  $r^2 = 0.24$ ) and the Michigan population



**Fig. 2.** Least-square regressions of (a) the number of eggs (fecundity) on female pupal mass and (b) allocation of resources to eggs for forest tent caterpillar populations from Manitoba (MB), Michigan (MI), and Louisiana (LA). Data from caterpillars reared under standardised conditions in 1999.

**Table 2.** Comparison of individual egg weight (dry) in three populations of forest tent caterpillar. Eggs were from the same females used in Fig. 2.

Egg weight			ANOVA				
Population	<i>n</i>	Mean (mg) $\pm$ SE $^\dagger$	Source	d.f.	MS	<i>F</i>	<i>P</i>
Manitoba	24	0.231 $\pm$ 0.0032 <sup>a</sup>	Population	2	0.01842	74.04	<0.001
Michigan	30	0.209 $\pm$ 0.0028 <sup>b</sup>	Error	80	0.00025		
Louisiana	29	0.179 $\pm$ 0.0029 <sup>c</sup>	Total	82			

$^\dagger$ Means followed by different letters are significantly different at  $P < 0.05$  (Tukey–Cramer HSD).

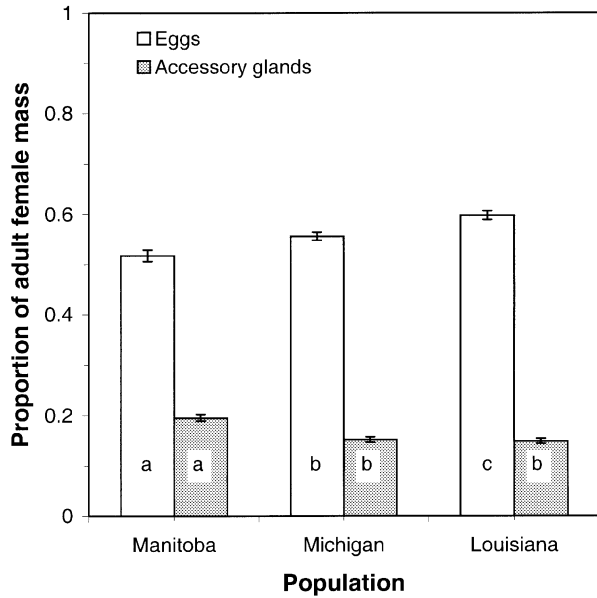
( $y = 0.02217x + 0.1688$ ,  $P < 0.009$ ,  $r^2 = 0.22$ ) but not the Louisiana population ( $y = 0.0222x + 0.1688$ ,  $P < 0.40$ ,  $r^2 = 0.02$ ).

Estimates of fecundity and allocation for a 485-mg female (overall mean for the 13 populations in Table 1) were generated using regression equations from Fig. 2a (fecundity: Louisiana  $y = 705.25x - 5.379$ , Michigan  $y = 409.32x + 34.578$ , Manitoba,  $y = 390.85x - 19.112$ ) and Fig. 2b (allocation: Louisiana  $y = 0.1314x - 0.0033$ , Michigan  $y = 0.106x - 0.0018$ , Manitoba  $y = 0.103x - 0.0107$ ). From values obtained using the regression equations, individual egg weight (egg weight = allocation/fecundity) was derived for each population. A 485-mg female from Louisiana produced 104 more eggs than a same-sized female from Michigan and 166 more eggs than the equivalent Manitoba female. Using eqn 1, the increased fecundity in Louisiana over Michigan females was 42% due to the reduction in egg size and 58% due to the increase in allocation. The difference between the number of eggs in Louisiana and Manitoba females was 29% due to changes in egg size and 71% due to changes in allocation. The difference between Michigan females and Manitoba females was 22% attributable to changes in egg size and 78% due to changes in allocation.

The proportion of adult female mass attributable to eggs differed significantly among populations (ANOVA:  $F_{2,34} = 17.0$ ,  $P < 0.001$ ). Eggs composed a smaller proportion of adult mass in Manitoba, an intermediate level in Michigan, and the largest proportion in Louisiana (Tukey–Cramer HSD,  $P < 0.05$ ; Fig. 3). The contribution of accessory glands to adult female weight also varied among populations (ANOVA:  $F_{2,34} = 16.3$ ,  $P < 0.001$ ). Multiple comparisons indicated that accessory glands made up a larger proportion of mass in females from Manitoba than in either Michigan or Louisiana females (Fig. 3).

#### Comparison of regional populations

There was a highly significant, negative correlation between fecundity and latitude for 10 populations of forest tent caterpillar (Fig. 4), suggesting that differences in egg size, allocation, and fecundity in the three population comparisons (Manitoba, Michigan, Louisiana) are robust and may be general for *M. disstria* throughout North America.



**Fig. 3.** Proportion of adult female mass attributable to eggs and to accessory glands. Means followed by different letters are significantly different at  $P < 0.05$  (Tukey–Cramer HSD). Analysis was performed on arcsin-square root transformed proportions. Actual proportions are shown.

#### Neonate mass

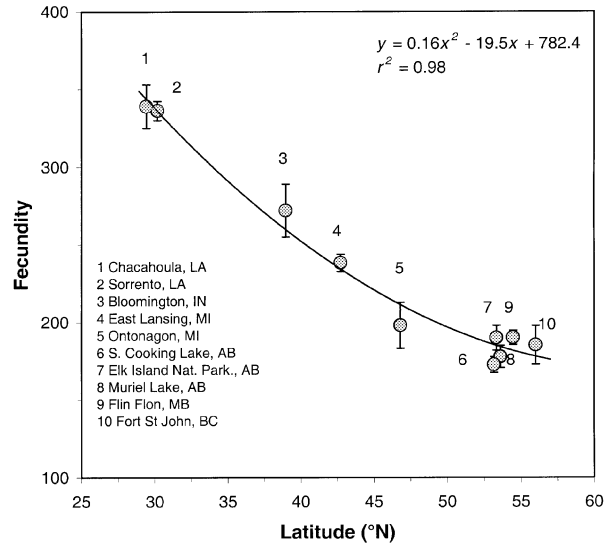
The mass of neonates at emergence differed significantly among the three populations ( $F_{2,78} = 39.75$ ,  $P < 0.001$ ; Table 3). Neonates from Manitoba were 26.3% heavier than caterpillars from Louisiana and 6% heavier than those from Michigan. Michigan neonates were 21.7% heavier than newly hatched larvae from Louisiana. These results are similar to that shown above for the mass of individual eggs, indicating that populations characterised by large eggs produce large neonates.

#### Degree-days available for post-hatch larval growth

As expected, the number of degree-days available during the first 2 weeks after hatch varied significantly among populations (Table 4). On average, Louisiana caterpillars had more than three times as many degree-days available for growth following hatch than did populations in Alberta or Michigan. There was no significant difference between the number of degree-days available to larvae in Alberta and Michigan populations.

#### Discussion

The study found a strong latitudinal cline in the mass of eggs, the allocation of resources to eggs, and in the mass of neonate forest tent caterpillar at emergence. Northern populations



**Fig. 4.** Regression of fecundity for 500-mg females from 10 different forest tent caterpillar populations on the latitude where they were collected. Fecundity was estimated from the following linear regression equations derived for each population. 1. Chacahoula, Louisiana ( $y = 564.9x + 56.4$ ,  $r^2 = 0.85$ ,  $n = 15$ ). 2. Sorrento, Louisiana ( $600.0x + 36.1$ ,  $r^2 = 0.80$ ,  $n = 86$ ). 3. Bloomington, Indiana ( $y = 578.5 - 16.1$ ,  $r^2 = 0.78$ ,  $n = 53$ ). 4. East Lansing, Michigan ( $414.9x + 30.7$ ,  $r^2 = 0.77$ ,  $n = 85$ ). 5. Ontonagon, Michigan ( $y = 448.4 - 20.2$ ,  $r^2 = 0.73$ ,  $n = 53$ ). 6. South Cooking Lake, Alberta ( $y = 380.4x - 17.8$ ,  $r^2 = 0.76$ ,  $n = 61$ ). 7. Elk Island National Park, Alberta ( $424.1x - 22.1$ ,  $r^2 = 0.72$ ,  $n = 35$ ). 8. Muriel Lake, Alberta ( $y = 359.0x - 1.6$ ,  $r^2 = 0.84$ ,  $n = 21$ ). 9. Flin Flon, Manitoba ( $411.01x - 15.4$ ,  $r^2 = 0.84$ ,  $n = 90$ ). 10. Fort St John, British Columbia ( $y = 302.6x + 34.0$ ,  $r^2 = 0.68$ ,  $n = 17$ ). Data for forest tent caterpillar populations 1, 6, 7, 8, 10, D. Parry, unpublished; 2, 4, 9, this study; populations 3 and 5, Lorimer, 1979c.

(Manitoba and Michigan) of forest tent caterpillar had larger eggs and neonates, but females from these populations produced significantly fewer eggs for any given pupal mass than did their southern (Louisiana) counterparts. In addition, southern females allocated more total resources to egg production than other populations. These data show that there are significant trade-offs in egg production and that selective forces operating on reproductive parameters probably differ across the latitudinal range of the species.

Such geographic clines in egg numbers and egg size have been identified in a few other widely distributed North American forest Lepidoptera. A strong latitudinal gradient in spruce budworm egg size and number has been shown (Harvey, 1983). Northern females produced fewer but significantly larger eggs than conspecifics from lower latitudes. Harvey (1983) proposed that larger egg size in the spruce budworm was adaptive at northern latitudes because they contained more yolk, enabling survival through the longer winters, however the weight of larvae either prior to or following diapause termination was not recorded so it is unknown whether *C. fumiferana* also shows a latitudinal gradient in neonate size. In the swallowtail butterfly

**Table 3.** Comparison of individual neonate weight (wet) in three populations of forest tent caterpillar. Individual neonate weights were estimated from 10 neonates per egg band.

Neonate weight			ANOVA				
Population	<i>n</i> egg bands	Mean (mg) ± SE†	Source	d.f.	MS	<i>F</i>	<i>P</i>
Manitoba	51	0.255 ± 0.0028 <sup>a</sup>	Population	2	0.0159	39.75	<0.001
Michigan	22	0.239 ± 0.0043 <sup>b</sup>	Error	78	0.0004		
Louisiana	8	0.188 ± 0.0051 <sup>c</sup>	Total	80			

†Means followed by different letters are significantly different at  $P < 0.05$  (Tukey–Cramer HSD).

**Table 4.** Degree-days available for forest tent caterpillar larval growth in three populations during the first 14 days after hatch. A 10 °C base, established experimentally for all three populations, was used for calculating degree-days (see text).

Available degree-days			ANOVA				
Population	Years	Mean ± SE†	Source	d.f.	MS	<i>F</i>	<i>P</i>
Alberta	6	62.5 ± 15.7 <sup>a</sup>	Population	2	33250.9	22.6	<0.001
Michigan	2	78.2 ± 27.1 <sup>a</sup>	Error	10	6769.5		
Louisiana	5	213.1 ± 17.2 <sup>b</sup>	Total	12			

†Means followed by different letters are significantly different at  $P < 0.05$  (Tukey–Cramer HSD).

*P. canadensis*, Ayres and Scriber (1994) found that Alaskan females produced larger eggs, larger neonates, but smaller adults than a population in Michigan. For *P. canadensis*, which overwinter as pupae, larger eggs and neonates are clearly not an adaptation for winter survival. Using a model, Ayres and Scriber (1994) demonstrated that the increased size of Alaskan eggs and neonates is advantageous where growing seasons are limited because it allows completion of development under the abbreviated time period available for larval growth. In the model, Michigan swallowtail larvae were unable to complete development under an Alaskan climate scenario.

More than 9 months of the year are spent by forest tent caterpillars in the egg stage. There is little or no difference in the length of time spent as an egg in northern and southern populations, however the climate in the southern United States may be more energetically demanding on diapause and post-diapause eggs as it is not uncommon to have temperatures in the 25–30 °C range in January and February in Louisiana. Ives (1973) showed that, for northern populations at least, warm temperatures during overwintering could cause premature exhaustion of energy reserves, leading to death. This suggests that provisioning of eggs is unlikely to be the reason for their greater size in northern populations.

During periods of cool weather, trees may grow faster relative to caterpillars, creating a phenological asynchrony that reduces their performance and ultimately survival (Blais *et al.*, 1955; Fitzgerald & Costa, 1986; Ayres, 1993). Delays in development driven by capricious climate and ephemeral host plant quality may enhance the success of a suite of effective

natural enemies (see Parry *et al.*, 1997, 1998). Because caterpillar growth is nearly an exponential function of size (e.g. Reavy, 1993; Ayres & Scriber, 1994), at hatch, larger neonates may be better able to exploit the phenological window available to them because development time to pupation is shorter. Under the much warmer conditions in the southern United States, phenological asynchrony may be less important. Caterpillars from Louisiana took significantly longer to complete larval development on six different host tree species and under both a cool northern temperature and warm southern temperature regime (D. Parry and R. A. Goyer, unpublished). It is hypothesised here that in thermally limited northern environments, completion of larval development within the phenological window bounded by declining host quality and natural enemies is only possible if development time is shortened by starting at a larger size.

Nonetheless, there are many factors other than developmental rate that may favour the selection for larger neonates (Reavy, 1993, and references therein). At northern latitudes, spring-feeding caterpillars must often function at temperatures that hover around or are below their developmental threshold. The threshold for the growth of first-instar forest tent caterpillars from all populations examined is 10 °C (Hodson, 1941; this paper), however for the 6 years in which data could be obtained, average daily temperature for the first 2 weeks following hatch was 7.3 °C in Alberta. Compensatory thermoregulatory behaviours such as aggregation and basking are used by tent caterpillars to elevate their basal temperature significantly above ambient. Through basking and aggregation,

temperatures in excess of 24 °C above ambient are achieved by eastern tent caterpillars (Joos *et al.*, 1988; Fitzgerald, 1995). Because the forest tent caterpillar exhibits many of the same thermoregulatory behaviours, similar elevations in basal temperature are likely. Neonate forest tent caterpillars may also confer some thermodynamic advantage by having a larger body in cooler climates although this needs to be tested.

In northern populations, post-hatch larvae may be exposed to inclement weather that can include snow and below freezing temperatures (Blais *et al.*, 1955; Witter, 1979). It is possible that under such extreme climatic conditions, larger initial sizes may confer considerable advantages to neonates. Cool spring weather may delay bud break, and forest tent caterpillars from Canadian populations are very resistant to starvation (Smith & Raske, 1968). Forest tent caterpillars have not been tested for resistance to starvation in southern populations; this would be an interesting comparison. These hypotheses are not mutually exclusive and it is quite conceivable that several factors operating simultaneously drive selection for larger neonates.

The interplay between environment and neonates is probably more critical at the northern limit of forest tent caterpillar distribution. The absolute northern limit of forest tent caterpillar range is unknown, however outbreaks do not occur north of 62° latitude despite the presence of large areas of suitable host (trembling aspen) in parts of Canada's Mackenzie River basin and in interior Alaska. It has long been held that the northern limit of forest tent caterpillar is determined by the maximum supercooling point of its freeze-intolerant eggs (Hanec, 1966). While low overwintering temperatures may determine the absolute northern limit of this species, recent work (Currie & Volney, 1995; Roland *et al.*, 1998) has suggested that the frequency of cold temperatures following hatch is a better predictor of the northern limit for outbreaks. This suggests that environmental conditions following hatch probably exert strong selection on neonates.

It is important to consider constraints on selection for larger neonates. These may simply be physiological restrictions on maximum egg size or they may be due to competing selective pressures. Because forest tent caterpillars are gregarious, there may be strong selection for large group sizes that may counterbalance selection for large neonates. Survival has been shown to increase with group size in some species of tent caterpillar (Shiga, 1976). Furthermore, forest tent caterpillar is distributed continuously throughout North America so gene flow between southern and northern populations may be high (see Costa & Ross, 1994), counteracting selection for extremes in egg size or fecundity although this paper shows that some isolating barriers must be present.

In comparisons of different regional forest tent caterpillar populations, the largest contribution to higher fecundity resulted from increased allocation of resources to reproduction. The physiological mechanism underlying the increase in allocation is unclear. Several morphological characteristics such as wing and body length did not vary significantly between populations. Some of the increase in allocation appears to be at the expense of the large paired accessory glands responsible for secreting the spumaline covering of egg

masses. Data (Fig. 4) suggest that although the proportion of adult mass attributable to eggs increases from north to south, the mass of accessory glands shows the opposite trend. The function of spumaline is unknown although it has been speculated that it may insulate the eggs, protect them from parasitoids, or have hygroscopic properties (Stehr & Cook, 1968; Darling & Johnston, 1982). After reproductive tissue, the next largest component of adult female mass is flight muscle. It is unknown whether either flight muscle or energy allocation to flight varies among populations although this may be a fruitful area of future research. Large differences in flight energetics are probable given the substantive regional changes in nocturnal temperatures when females are flying.

Reproductive strategies in the Lepidoptera range from *income* breeding, where all resources for reproduction are accumulated by the larva – hence the adults are drawing from stored resources only, to *capital* breeding, where feeding by adults contributes significantly to egg production (Tammara & Haukioja, 1996). Of the three studied lepidopterans exhibiting latitudinal clines in egg size, the forest tent caterpillar is a strict *income* breeder, spruce budworm has weak adult feeding (Miller, 1996), and feeding by swallowtail adults contributes to reproductive success (Wheeler, 1996). In addition, other aspects of life history vary considerably among these species. Spruce budworm are spring feeders that overwinter as larvae, *P. canadensis* is a summer feeder, overwintering as pupae, and forest tent caterpillars are spring feeders, spending the winter as eggs. Furthermore, both the forest tent caterpillar and spruce budworm are characterised by outbreak population dynamics whereas *P. canadensis* populations are relatively stable. Similar geographic clines in three unrelated groups with highly disparate life-history strategies suggest that trade-offs between egg production and size along latitudinal gradients might be indicative of a more general pattern. Although neither spruce budworm nor tent caterpillars are limited by the end of the growing season as swallowtails are, both these spring-feeding species are affected strongly by phenologically driven declines in foliage quality, which effectively constrain the functional length of the larval period. Thus, limitation on the length of phenological windows available for larval development could be the common denominator driving selection for large offspring among a diverse group of lepidopterans.

Fecundity is a fundamental component of population growth. Very high fecundity may be partially responsible for the unusual population dynamics exhibited by forest tent caterpillar in the Gulf States. Across Canada and the northern Lake States (Minnesota, Wisconsin, Michigan), the periodicity between large-scale, regional outbreaks averages 10 years (e.g. Hodson, 1941; Hildahl & Reeks, 1960) whereas in Louisiana and Alabama, outbreaks occur on average every 5 years (Harper & Hyland, 1981; Rejmanek *et al.*, 1987). It is postulated that the high reproductive rate of southern females coupled with low mortality from natural enemies produces fast-cycling, starvation-driven population dynamics. In Canada, where fecundity is half that in the Gulf States, population growth rates are also dampened by an effective suite of predators and parasitoids operating across a range of densities (Witter & Kulman, 1979; Parry, 1995; Parry *et al.*,

1997). Southern swamp populations lack efficient guilds of larval parasitoids and pupal parasitism is reduced considerably relative to northern populations (Stark & Harper, 1982; Smith & Goyer, 1986). At this level, evolutionary trade-offs in life history interact with the ecology of natural enemies to produce population dynamic phenomena not seen elsewhere in the forest tent caterpillar's range. This suggests that simplistic, single-cause generalisations about the population dynamics of forest tent caterpillar need to be tempered with the knowledge that variation in basic life-history processes is significant and those processes underlying outbreaks may vary from region to region. Latitudinal changes in basic life-history strategies highlight the need to integrate evolutionary components into understanding the ecology of this insect.

Most discussion of trade-offs between clutch and propagule size assumes that the allocation to resources remains constant. In the forest tent caterpillar, decreases in offspring size and increases in allocation to reproduction occur concurrently. This reproductive strategy has not been discussed previously, at least with respect to insects. This study showed that populations of forest tent caterpillar either produce large eggs with concomitantly low fecundity at northern latitudes or have high fecundity but smaller eggs in southern populations. Because caterpillars from the different populations were reared under standardised conditions, it is clear that the relationship between fecundity, allocation, and offspring size is genetically based. Congruent with predictions that offspring size should increase in environments where developmental rates are lower (Kolding & Fenchel, 1981; Parker & Begon, 1986; Perrin, 1988), forest tent caterpillar populations from northern regions (Manitoba and Michigan) with cool climates (and thus slower development) are characterised by larger eggs and neonates. Slowed growth in tent caterpillars, at least in the early stages, is associated with higher mortality (Parry *et al.*, 1998), suggesting that natural selection should act to compress development time under these conditions.

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