Life History and Age-Specific Mortality of Eastern Tent Caterpillar (Lepidoptera: Lasiocampidae)

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ABSTRACT   *Malacosoma americanum* (F.) (Lepidoptera: Lasiocampidae) was recently implicated in early fetal losses and late-term abortions of pregnant mares in the thoroughbred and saddlebred industry centered in central Kentucky. The direct role of the caterpillars in these losses prompted the need for a more thorough understanding of life history and age-specific biology, to develop more precise management strategies and reduce future losses. During 2003 and 2004, egg masses and tents were destructively and sequentially sampled, respectively, to observe development and mortality agents. Eggs were significantly impacted by parasitization. Larval development was linear, yet asynchronous, with individual tents containing up to four instars simultaneously. Predators were the major mortality factor impacting the first three instars; parasitoids and pathogens had the greatest impact on fourth, fifth, and sixth instars. These data demonstrate that the eastern tent caterpillar is impacted by a variety of biotic mortality agents throughout the Bluegrass region of Kentucky, and the potential impacts on natural enemies must be considered when designing any direct suppression strategies targeting populations.

KEY WORDS   eastern tent caterpillar, life history, mortality, mare reproductive loss syndrome

DURING SPRING 2001, mare reproductive loss syndrome struck the equine industry throughout the thoroughbred-producing region of central Kentucky, causing early fetal losses and late-term abortions in >3,000 mares (Webb et al. 2004). Foal loss has been correlated with exposure of pregnant mares to the larval cuticle of eastern tent caterpillars, *Malacosoma americanum* (F.) (Lepidoptera: Lasiocampidae), by ingestion (Webb et al. 2004). Consequently, minimizing pregnant mare contact with eastern tent caterpillars is a critical component of management strategies to reduce foal losses due to mare reproductive loss syndrome. A greater understanding of caterpillar behavioral ecology and naturally occurring mortality agents will enhance our abilities to effectively manage caterpillar populations.

The eastern tent caterpillar is a common, native tree-feeding lepidopteran that can cause localized defoliation of its rosaceous hosts. In early summer, females deposit their egg masses in bands covered with protective spumaline around small-diameter twigs of black cherry, *Prunus serotina* Ehrhart (Rosales: Rosaceae) (Stacey et al. 1975). Egg masses overwinter, hatching concurrently with bud break in early spring (Fitzgerald and Willer 1983). Caterpillars feed gregariously and communally construct silken tents that expand as they develop, and often coalesce with nearby tents (Fitzgerald and Willer 1983). Foraging occurs three times daily in early instars but is less

synchronous as caterpillars age (Fitzgerald 1980). When not foraging, caterpillars remain within the tent.

Although detailed life table studies addressing age-specific mortality rates of eastern tent caterpillars are lacking (Fitzgerald 1995), biotic mortality factors lead to local population fluctuations, with peaks occurring at 9–12-yr intervals (Stacey et al. 1975). Parasitization affects *M. americanum* egg, larval, and pupal survival (Kulman 1965, Stacey et al. 1975, Darling and Johnson 1982), and predation impacts larval populations (Fitzgerald 1995, Ayre and Hitchon 1968, Evans 1983). Despite providing protection from predators, Stehr and Cook (1968) suggest that overcrowding in tents also may enhance the spread of parasitic and pathogenic agents that commonly infect tent caterpillars. Disease agents such as viruses (Steairs 1972) and microsporidia (Nordin 1976) can cause mortality. Extensive studies of the closely related forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), indicate that both biotic and abiotic factors regulate populations (Witter et al. 1972, 1975, Witter and Kulman 1979). High temperatures impede successful egg development (Hodson 1941), and less commonly, low temperatures cause mortality of pharate larvae (Smith and Goyer 1986).

Management of eastern tent caterpillars to reduce the incidence of mare reproductive loss syndrome is complex. Dispersal abilities of both adults (Fitzgerald

1995) and larvae (Rieske 2002, Rieske and Townsend 2005), application restrictions associated with grazing horses, and environmental concerns, all make widespread insecticide applications impractical or ineffective (Townsend 2002a, b). Our objectives were to describe the life history and age-specific mortality factors of eastern tent caterpillars developing in central Kentucky, thereby enhancing our ability to predict population behavior and develop more precise management strategies.

Materials and Methods

In March 2003, three sites were established (Woodford County, Kentucky) consisting of black cherry-dominated fencerows with east-west orientation. Each wooded fencerow was ≈15 m in depth and 220 m in length. To ensure an adequate number of caterpillars for our study, egg masses were collected in February and March from infestations outside of the study area. Twenty black cherry trees with branches accessible from both sides of the fence were selected. Twenty surface-sterilized egg masses (0.1% sodium hypochlorite for ≈5 min) were wired to branches at 1.2–3.2 m on the north side of each selected tree, and 20 on the south. Egg masses, egg hatch, caterpillar feeding behavior, and relative tent size were monitored at 24-h intervals.

Site Characterization. Sites were characterized by selecting three trees, to which egg masses were previously wired, one at the midpoint and one at each end, and measuring tree height, height to branching point, and height of herbaceous cover on the north and south sides of the fencerows for each tree. The distance from the ground cover to the branching point was calculated to describe the vertical complexity of the site. Species identification and relative abundance of all trees >0.08 m in diameter at 1.3 m was assessed.

Eastern Tent Caterpillar Development. Caterpillar age structure and parasitism rates were determined by destructive sampling beginning 9 d posthatch and repeated at 3–5-d intervals. One or two tents were chosen randomly from the north and south sides of the fencerow plot. Collections were made before midday foraging bouts (1500 hours EST) (Fitzgerald et al. 1988) to ensure that the majority of caterpillars were within the tent. The egg mass, tent, and associated caterpillars were placed in plastic bags on ice, returned to the laboratory, and stored at 0°C for later processing.

We collected all remaining tents 43–50 d posthatch (4 May) and placed each in a 51 by 26-cm aquarium, covered with fine mesh screening to prevent the loss of wandering larvae. The aquaria were set on end in a shaded outdoor area to allow for airflow and to prevent accumulation of rainwater. Fresh black cherry foliage from the study site was provided daily. Tents were collected from the aquaria at 3-d intervals and stored at 0°C as described above. Cocoons that formed within the aquaria were collected daily and placed in individual plastic containers (29.6 ml) to monitor parasitoid and moth emergence. Five tents

remained at each site and were monitored daily for an additional 7 d, after which all ETC had abandoned the tent. The time from initial egg hatch to our final tent observation was 62 d.

In the laboratory, the contents of each collected egg mass were exposed by removing the spumaline with a razor blade (Witter et al. 1972). The total number of eggs per egg mass, and the percentage of hatched, parasitized, and nonviable were assessed. Caterpillars, predators, parasites, and inquilines were removed from collected tents, counted, and stored at 0°C. The head capsules of all caterpillars ($n = 6260$) were measured to determine instar (Fitzgerald 1995).

Eastern Tent Caterpillar Associates. Two fencerow sites were specified for sequential sampling in 2004 to characterize caterpillar associates and to assess parasitoid impact. Beginning 13 d posthatch (7 April) six naturally occurring tents were collected at 3–5-d intervals from the lower (1.9–4.5 m) and upper (4.75–12.5 m) tree canopy. At site I, two tents were randomly collected, one from the upper canopy and one from the lower canopy. Because endemic populations were higher at site II, four tents were randomly collected at each interval; two from the north side of the fencerow, one from the upper canopy and one from the lower canopy. Similarly, two tents were also collected from the south side. Ten collections were completed over a period of 37 d, yielding a total of 56 tents.

Tents, caterpillars, and associated branches of foliage were immediately transferred to the greenhouse (23°C, photoperiod of 12:12 [L:D]), where the cut branch ends were placed in ≈1-liter containers of water within round, dark mesh cages (30.5 × 61 cm). A transparent, inverted cone fitted with an 8-ml collection vial served as the top of the cage. Larvae were provided fresh black cherry foliage, collected from original sites, as needed and reared to pupation, after which the cocoons were placed in plastic collection boxes (29.6 ml) until adult emergence. Tent caterpillar associates (predators, parasites, and inquilines) were collected from the collection vials at 24-h intervals, and stored in 70% ethanol before identification. Steve Krauth (University of Wisconsin) identified all collected associates, and voucher specimens were deposited in the University of Wisconsin Insect Research Collection. The incidence of parasitization (percentage), and parasitoid and predator species composition were assessed and all tent associates noted.

Statistical Analysis. Analysis of variance (ANOVA) was used to assess site differences, including canopy height, height of understory herbaceous growth, and the distance from herbaceous growth to the lowest branching point. Data analyzing time from hatch to initial tent formation were not normally distributed; therefore, analysis was completed using the nonparametric Kruskal–Wallis method (Kruskal and Wallis 1952). Interaction and main effects were tested using linear contrasts on the rank means. Larval survivorship (percentage) was analyzed using PROC GLM (SAS Institute 1997) with site, cardinal exposure, collection interval, and number of predators and parasitoids as main effects. The number of predators, parasitized

Table 1. Characterization of sites used to assess *M. americanum* development in central Kentucky, 2003 and 2004

Site	Cherry composition (%)	Mean ht (m)		Gap (m)[a]
		Canopy	Herbaceous	
I	54	12.5 (1.3)b	2.84 (0.4)a	1.42 (0.5)a
II	40	11.52 (0.3)b	1.98 (0.5)a	3.09 (1.1)a
III	32	16.55 (0.2)a	0.29 (0.1)b	3.64 (0.3)a

[a] Gap is distance from herbaceous cover to branching point.

caterpillars, and associates was assessed for fit to the Poisson model; however, due to overdispersion scaled deviance was used to estimate the variance. Data were analyzed using PROC GENMOD (SAS Institute 1997) with site, cardinal exposure, collection interval, and level within canopy as main effects. Least squared means were compared by a chi-square analysis to determine the relationship between site and the freqency of parasitized larvae. An ANOVA was conducted to determine significant differences in the number of pupae collected per tent at each site, cardinal exposure, and canopy level. Differences of least squared means were conducted to determine significant differences in the numbers of adult males, adult females, and pupae that failed to emerge. The dependent variable was number of pupae and independent variables were status (male, female, and failed to emerge), site, cardinal exposure, and canopy level. ANOVA also was conducted to determine whether the number of pupae, male and female moths varied with collection date, and whether the length of developmental time for male and female adults varied. The dependent variables were pupal collection date, moth collection date, and time from pupal collection date to emergence of moths. Independent variables were status (male, female, or failed to emerge), site, cardinal exposure, and canopy levels.

Results

Site Characterization. Sites I and II were similar with respect to tree height ($P = 0.41$) and height of herbaceous ground cover ($P = 0.14$) (Table 1). Site III contained the lowest proportion of black cherry, the tallest trees, and the lowest herbaceous ground cover. The gap between ground cover and tree branching was greatest at site III and least at site I, but this difference was not statistically significant ($P = 0.56$).

Egg Development. Egg hatch began 15 March, coinciding with 89 degree-days (DD) [$DD_{(Base\ 3)}$] (UK Ag Weather Data), and continued through 1 April [248 $DD_{(Base\ 3)}$]. Egg masses contained 130–457 eggs (mean ± SE, 275 ± 5.4). Within collected egg masses, 81.0 ± 1.2% of eggs hatched, 14.1 ± 1.0% were parasitized, and 4.9 ± 0.6% failed to hatch for unknown reasons.

Larval Development. The time from hatch to initial tent formation was 5.9 ± 0.3 d. The rate at which site III caterpillars formed tents was significantly faster than tent formation at sites I and II ($F = 25.74$; df = 1, 111; $P < 0.0001$). There was also an overall exposure
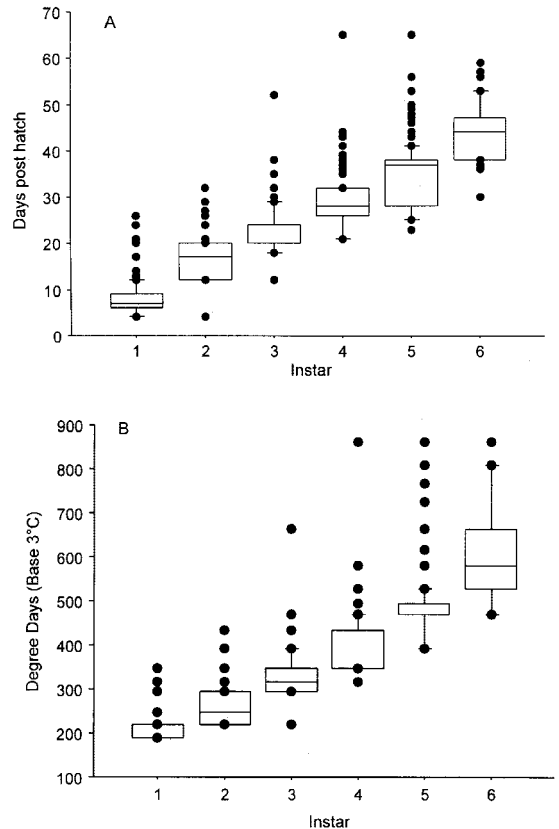

Fig. 1. Developmental rate and stadium length of *M. americanum* in central Kentucky based on the number of days posthatch (A) and degree-day (base 3°C) accumulations (B). (A, developmental time (days posthatch) = 6.91 * (instar) + 1.26; $R^2 = 0.86$, $P = <0.0001$) (B, developmental time $DD_{(Base\ 3)} = -72.09 + 566.29 * (instar) - 414.43 * (instar)^2 + 150.63 * (instar)^3 - 24.73 * (instar)^4 + 1.51 * (instar)^5$; $R^2 = 0.83$, $P < 0.0001$). Graph demonstrates the 10th, 25th, 50th, 75th, and 90th percentiles for each variable. Plotted points represent values above the 90th percentile and below the 10th percentile.

effect ($F = 11.05$; df = 1, 111; $P = 0.0012$) with caterpillars on the south sides of the fencerow forming tents more rapidly than those with northern exposure.

Eastern tent caterpillar development is highly predictable and is linearly related to time elapsed (Fig. 1A) and with a fifth order relationship to degree-day accumulations (Fig. 1B). However, development is asynchronous, with considerable variability within each instar (Fig. 1; Table 2). Second instars were within tents 4 d after initial egg hatch and well before the majority of caterpillars had hatched. Sixth instars were first found 31 d posthatch, when the majority of eastern tent caterpillars were fourth and fifth instars (Fig. 1A and B). This asynchrony is further illustrated by the variation in tent composition (Table 2). During most of our collection intervals, developing tents contained three or four developmental stages. Overall, development of each instar progresses linearly with collection date. However, tents collected on 7 May

Table 2.　Instar distribution (%) of *M. americanum* in destructively sampled tents in central Kentucky, 2003

Date	n^a	Σ of larvae	Instar						Unable to age	Cumulative $DD_{(Base\ 3)}$
			1	2	3	4	5	6		
24 Mar.	4	534	94.3	0.0	0.0	0.0	0.0	0.0	5.6	188
27 Mar.	4	668	56.0	38.1	0.12	0.0	0.0	0.0	5.8	219
1 April	3	302	17.2	79.5	0.0	0.0	0.0	0.0	3.2	248
4 April	3	620	0.9	39.0	57.5	0.0	0.0	0.0	2.6	294
8 April	3	274	1.0	10.2	83.9	0.3	0.0	0.0	4.7	317
13 April	5	499	10.0	19.1	29.6	36.7	0.0	0.0	0.5	348
16 April	4	421	0.0	25.9	24.4	29.7	18.9	0.0	1.1	393
19 April	3	450	0.0	0.0	6.2	73.4	18.9	0.0	0.5	433
22 April	7	901	0.0	0.0	4.2	28.7	55.6	11.2	0.3	468
25 April	6	454	0.0	0.0	0.0	5.6	86.8	7.5	0.0	494
28 April	6	276	0.0	0.0	0.0	1.4	29.4	69.2	0.0	528
1 May	5	147	0.0	0.0	0.0	0.3	43.3	43.9	12.5	581
4 May	7	169	0.0	0.0	0.0	0.0	4.1	95.9	0.0	616
7 May	7	90	0.0	0.0	25.0	0.0	1.7	73.3	0.0	665
10 May	6	62	0.0	0.0	0.0	0.0	15.8	84.2	0.0	725
13 May	6	35	0.0	0.0	0.0	0.0	33.3	66.7	0.0	766
16 May	6	106	0.0	0.0	0.0	0.0	0.7	95.9	3.4	809
19 May	5	10	0.0	0.0	0.0	25.0	16.7	50.0	8.3	862
22 May	3	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	902

^{a} n is number of tents collected.

and 19 May were atypical in that they contained larvae younger than the predicted developmental stage.

　　Larval survivorship (Fig. 2) decreased significantly with time ($F = 124.92$; df = 1, 88; $P = <0.0001$) and at a constant rate, suggesting that mortality rates do not vary with instar. Survival was not affected by site ($F = 0.07$; df = 2, 88; $P = 0.93$) or exposure ($F = 1.26$; df = 1, 88; $P = 0.26$).

　　Larval Mortality. We witnessed a number of predation events involving early instar eastern tent caterpillars. Jumping spiders (Araneae: Salticidae) were observed preying on first instars on 18 March, and on second instar caterpillars 3 April. One episode of ant (Hymenoptera: Formicidae) predation on a second instar caterpillar occurred on 30 March. A spined soldier bug, most likely *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), was observed preying on

Fig. 2. Survivorship (percentage) of *M. americanum* from egg through sixth instar [survivorship = −11.73 * (stage at collection) + 81.82; $R^2 = 0$ 0.76, $P < 0.0001$].

a single fourth instar on 12 April and another on 16 April.

　　Fifteen percent of all collected tents contained predators. Spiders (Salticidae and Anyphaenidae) comprised 63%; the ants, *Camponotus* spp. and *Crematogaster ashmeadi* (Emery) (Hymenoptera: Formicidae), comprised 33%; and a single beetle (Coleoptera: Carabidae) comprised the remaining 4%. The number of predators within collected tents varied slightly by site ($F = 2.69$; df = 2, 91; $P = 0.07$) with site II tents containing the greatest number of predators ($n = 16$) and site I containing the least ($n = 5$). Cardinal exposure significantly impacted predator numbers within collected tents ($F = 8.75$; df = 1, 91; $P = 0.004$); 75% were collected from tents with northern exposure. The number of predators collected did not change over time ($F = 0.25$, df = 1, 90, $P = 0.62$). However, a single anomalous tent collected 22 May was excluded from the analysis because it contained nine ants, or 30% of all collected predators. In spite of their prevalence, when numbers of predators on and within tents were compared with percentage of larval survival, the presence of predators did not significantly impact overall caterpillar survival ($F = 0.12$; df = 1, 9; $P = 0.74$) during any point in development.

　　Parasitization was influenced by site ($F = 8.43$; df = 2, 91; $P = 0.0004$) but not by cardinal exposure ($F = 0.62$; df = 1, 91; $P = 0.43$). Tents collected from site III contained greater numbers of parasitized caterpillars than sites I ($\chi^2 = 11.81$, $P = 0.0006$) and II ($\chi^2 = 7.25$, $P = 0.007$). Sites I and II ($\chi^2 = 0.79$, $P = 0.37$) were not different. Parasitization rates increased over time ($F = 51.85$; df = 1, 91; $P < 0.0001$).

　　Eastern Tent Caterpillar Associates. The total number of parasitoids emerging from all life stages in sequentially collected tents (Table 3) did not differ among sites ($F = 1.18$; df = 1, 73; $P = 0.28$) or by direction ($F = 0.20$; df = 1, 73; $P = 0.65$). Parasitoid numbers were marginally higher in tents collected
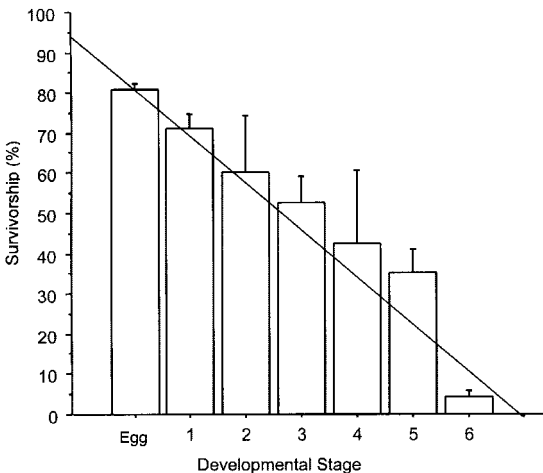
Table 3. Parasites and associates reared from sequentially sampled *M. americanum* tents in central Kentucky, spring 2004

Stage at emergence	Order	Family	Species	Host association	Prevalence	n^a	%
Egg	Hymenoptera	Scelionidae	*Telenomus* sp.	Parasitoid	Common	10	10.6
		Eulophidae	*Tetrastichus* sp.	Parasitoid	Common	5	5.3
Larva	Hymenoptera	Braconidae	*Apanteles* sp.	Parasitoid	Common	1	1.1
			Meteorus hyphantriae Riley	Parasitoid	Common	3	3.2
		Ichneumonidae	*Hyposoter fugitivus* (Say)	Parasitoid	Abundant	49	52.1
		Elasmidae	*Elasmus atratus* Howard	Hyperparasitoid	Common	1	1.1
		Pteromalidae		Hyperparasitoid or Parasitoid	Common	1	1.1
	Diptera	Ephydridae	*Scatella obsolete* Loew	Associate	Common	12	12.8
		Muscidae	*Mydaea* sp.	Associate	Common	1	1.1
		Sciaridae		Associate	Common	1	1.1
Pupa	Hymenoptera	Eulophidae	*Sympiesis fragariae* Miller	Parasitoid	Rare	2	2.1
		Ichneumonidae	*Agrypon anale* Say	Parasitoid	Common	8	8.5

[a] n is total number collected.

from the lower canopy than in tents collected from the upper canopy ($F = 3.69$; df $= 1$, 73; $P = 0.059$).

Sixty-five percent of collected parasitoids emerged from larval eastern tent caterpillar, 59% of these were *Hyposoter fugitivus* (Say) (Hymenoptera: Ichneumonidae), which preferentially parasitized caterpillars in the lower canopy ($F = 8.49$; df $= 1$, 73; $P = 0.005$). Site ($F = 0.02$; df $= 1$, 73; $P = 0.89$) and exposure ($F = 0.45$; df $= 1$, 73; $P = 0.51$) had no impact on larval parasitization, but larvae in tents in the lower canopy were more heavily parasitized than were larvae in tents collected from the upper canopy ($F = 7.25$; df $= 1$, 73; $P = 0.009$).

Pupal Development and Mortality. Site ($F = 0.57$; df $= 1$, 92; $P = 0.45$), direction ($F = 2.22$; df $= 1$, 92; $P = 0.14$), and canopy level ($F = 0.16$; df $= 1$, 92; $P = 0.69$) did not significantly impact the number of pupae that developed within sequentially collected tents. Of the pupae that emerged as adults, 44% were females and 56% were males; the difference was not statistically significant ($t = 1.86$; df $= 1$, 92; $P = 0.67$). Males formed pupae ≈0.83 d earlier than females ($t = 2.32$; df $= 1$, 704; $P = 0.021$) and emerged 2.4 d earlier ($t = 2.37$; df $= 1$, 704; $P = 0.018$). However, the length of the pupal stage did not differ significantly ($t = 1.57$; df $= 1$, 704; $P = 0.118$), suggesting that either female larval development is slower or that females remain within their pupal case as pharate adults for longer. Whereas 53% of collected pupae failed to emerge, parasitoids were collected for <1%, making it evident that undetected factors were impacting populations. No literature previously reported *Sympiesis fragariae* Miller (Hymenoptera: Eulophidae), a pupal parasitoid, from eastern tent caterpillar or within Kentucky (Choate and Rieske 2005).

Discussion

We assessed eastern tent caterpillar development and mortality factors in the thoroughbred-producing Bluegrass region of Kentucky in the context of the caterpillar's role in reproductive failure of pregnant mares. Accidental ingestion of caterpillars by pregnant grazing mares leads to early fetal losses and late term abortions.

All eastern tent caterpillar life stages were impacted by biotic mortality agents. We observed egg parasitization rates approaching 15%, which is considerably higher than studies of more northern eastern tent caterpillar populations (Witter and Kulman 1979). *Tetrastichus malacosomae* Girault (Hymenoptera: Eulophidae) and *Telenomus clisiocampidae* Riley (Hymenoptera: Scelionidae) parasitize eastern tent caterpillar eggs at very low rates (Williams 1916, Stacey et al. 1975, Darling and Johnson 1982). However, we observed egg parasitization by these two species at much higher levels than previously reported (Stacey et al. 1975), suggesting that these parasitoids may be more prevalent or more effective in this region or that additional mortality factors are at play. Although these were the only two egg parasitoids collected in our study (Table 2), two other egg parasitoids have been recorded impacting eastern tent caterpillar populations (Stacey et al. 1975, Darling and Johnson 1982).

Larval developmental rate (Fig. 1A) was greatest in tents with southern exposure and most rapid at site III, perhaps because sparser herbaceous growth and mature vegetation allowed greater sunlight penetration (Table 1). In the closely related western tent caterpillar, *Malacosoma californicum pluviale* Dyar (Lepidoptera: Lasiocampidae), egg masses and tents are more abundant on branches with southern exposure (Moore et al. 1988). *M. americanum* within tents exposed to direct sunlight grow more rapidly than those in the shade (Casey et al. 1988).

Caterpillar development within tents was surprisingly asynchronous. This may be due to the asynchrony of egg hatch, with some egg masses taking as many as 3 d to hatch entirely, or to the coalescing of individual tents as they enlarged. The lack of intraspecific competition may provide early hatching larvae with optimal conditions for more rapid development.

Early instars were more heavily impacted by predators. We witnessed several predation events during early caterpillar development involving three different groups (ants, spiders, and stink bugs). The fact that these events were witnessed during such brief bouts of observation suggests that these predators have a substantial impact on caterpillar populations.

Several species of ants have been recorded feeding on colonies of first and second instars in northern regions (Green and Sullivan 1950, Ayre and Hitchon 1968). Salticidae have not been reported impacting eastern tent caterpillar populations; however, they are opportunistic predators and were observed feeding on a first and a second instar. Four species of *Podisus* (Hemiptera) have been identified as natural enemies of eastern tent caterpillars in the northeastern United States (Evans 1983), but their role in regulating populations may be insignificant if early spring temperatures are cool enough to slow feeding activity (Evans 1982).

Similar to other *Malacosoma* studies (Witter et al. 1972, Smith and Goyer 1986), we did not observe parasitoid emergence from the first three instars. However, parasitization was the major mortality factor for late instars and pupae. Eight parasitoid species were collected, but the ichneumonid *H. fugitivus* accounted for >50% of the parasitoids collected. Rates of parasitization varied with collection date, and parasitoid emergence was greatest (22%) on 11 May 2004. Parasitization was greatest at site III, perhaps due to greater parasitoid activity or greater parasitoid efficiency, because the sparse herbaceous growth and the large gap between the herbaceous cover and tree branching may have simplified foraging. With the exception of the pupal parasitoid *S. fragariae,* which had not been previously reported from this host (Choate and Rieske 2005), all collected parasitoids had been previously documented on *M. americanum* (Krombein et al. 1979).

A number of tent caterpillar associates collected were algal and fungal feeders (Table 3) and were associated with decaying plant and animal tissue, as well as excrement within collected tents (Blair and Foote 1984, Skidmore 1985, Lindquist 1996).

During daily observations and tent collections, pathogens were observed causing mortality of fifth and sixth instars. Nordin (1976) reported *Nosema* sp. infections impacting 3.7% of larvae and pupae. However, 92% of emerging adults harbored the infection, suggesting that *Nosema* may impact adult fecundity and possibly other developmental factors (Nordin 1974). When combined, pathogens such as *Nosema* sp., nuclear polyhedrosis virus, bacteria, fungi, and nematodes may result in the loss of >58% of larvae (Nordin 1974).

More than one-half of the pupae we collected failed to emerge as adults. Daily monitoring of parasitoid emergence and dissection of pupae that failed to emerge showed that <1% were detectably parasitized, suggesting that some other mortality agent is at play. Nordin (1974) observed 36% mortality of late instar eastern tent caterpillar and pupae in Fayette Co. due to infection by nuclear polyhedrosis viruses and the microsporidian *Nosema* sp. In addition to direct mortality, *Nosema* sp. is transovarially transmitted, impacting adult fecundity and developing progeny (Nordin 1974). The prevalence of various pathogens within central Kentucky *M. americanum* populations suggests that they may play a significant role in pupal mortality.

A variety of biotic and abiotic factors impact *M. americanum* development and all interact to decrease populations linearly over time. No single mortality factor is responsible for significant decreases in population numbers during nonoutbreak years. However, the interactions of predators, parasitoids, pathogens, and to a lesser extent abiotic factors, lead to population fluctuations every 9–12 yr (Stacey et al. 1975). Years of peak populations are of greatest concern to the equine industry, due to the increased risk of caterpillar contact by pregnant, grazing mares.

Knowledge of eastern tent caterpillar development and mortality factors is key to gaining a full understanding of tent caterpillar population dynamics. This understanding is critical for the development of effective management strategies to reduce the incidence of mare reproductive loss syndrome. Our data suggests that manipulating herbaceous ground cover may enhance the incidence of parasitization, thereby reducing tent caterpillar populations. Our work provides a knowledge base from which tools can be developed to assist farm managers and horse owners in managing tent caterpillar populations in a manner consistent with concerns of the equine industry.

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