

**APPLE OR CHERRY? HOST SELECTION QUANDARY
FOR THE EASTERN TENT CATERPILLAR**S. E. BLATT¹, D. A. KNOX and R. HARMSSEN

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Abstract*Proc. ent. Soc. Ont.* 131: 123-131

Egg parasitism of eastern tent caterpillar, *Malacosoma americanum* (Fab.) (Lepidoptera: Lasiocampidae), was investigated in 1991, 1993 and 2000. Comparison of egg parasitism was made on two different rosaceous hosts: apple, *Malus pumila* Mill., and choke cherry, *Prunus virginiana* L. Three species of Hymenopteran egg parasitoids were recovered from the egg masses and identified as *Tetrastichus malacosomae* Girault (Eulophidae), *Telenomus clisiocampae* Riley (Scelionidae) and *Ooencyrtus clisiocampae* (Ashmead) (Encyrtidae). Egg parasitism was higher on cherry than on apple. Egg masses collected from cherry and apple trees in 1991 experienced 7.5% and 4.8% parasitism, respectively, and 4.6% and 3.5% parasitism, on cherry and apple, respectively, in 2000. *Tetrastichus malacosomae* parasitized 5.1% and 2.5% of the eggs on cherry and apple, respectively, in 1991, and parasitized 1.8% and 0.3% of the eggs on cherry and apple, respectively, in 2000. Mortality of first instar caterpillars was investigated in 1993 and again in 2000. Caterpillars on cherry were more likely to survive to second instar than were caterpillars on apple, regardless if the egg mass originated on the host or was transplanted.

Introduction

Predator avoidance is but one means of primary defense among insects (Evans and Schmidt 1990). For many Lepidoptera, these defenses include allopatry, eucrypsis, mimesis and elimination of evidence, eg. frass, that can act as location cues (Lederhouse 1990). To avoid parasitoids, particularly those closely associated with the resource (Vinson 1976; Van Alphen and Vet 1986; Casas 1989; Denno et al. 1990; Voelkl 1994), Lepidoptera can seek out enemy-free space by switching host plants (Lawton 1986; Gold et al. 1989; Gross 1993). This tactic has been observed in *Malacosoma disstria* (Hübner), the forest tent caterpillar (Roland 1997). We wondered if this tactic would be effective for other species in *Malacosoma* and if the benefit of host switching would persist throughout the early life stages.

The eastern tent caterpillar, *Malacosoma americanum* (Fab.), is an oligophagous defoliator of members of the Rosaceae (Stehr and Cook 1968), and subject to egg parasitism that may reduce realized fecundity by as much as 15% (Darling and Johnson 1982). Published studies on egg parasitism have paid little attention to the relative rates of parasitism on different host trees. The preferred host plants of *M. americanum* are two native cherries, black cherry, *Prunus serotina* Ehrh., and choke cherry, *P. virginiana* L. Relative to other potential host species, these impart higher levels of larval survival and greater adult fitness (Segarra-Carmona and Barbosa 1983;

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Peterson et al. 1987). However, *M. americanum* can also be found on other hosts such as wild crabapple (*Malus coronaria* Mill.), hawthorn (*Crataegus* spp.), plum (*Prunus* spp.) and the introduced apple, *Malus pumila* Mill. Records of fitness and survival on these hosts are less well documented (Porter 1958; Stehr and Cook 1968; Segarra-Carmona and Barbosa 1983).

In our study, we examined the egg parasitoids of *M. americanum* on two of its hosts, choke cherry and the introduced apple. If host switching is an effective means to achieve enemy-free space, it must reduce the impact of parasitism relative to that incurred by remaining on the original, or preferred, host species. Further, the newly emerged caterpillars must be able to survive on the alternative host. Our objectives were to determine: 1. if choosing *M. pumila* is an effective means to achieve enemy-free space, and 2. if this choice is negated by an increased caterpillar mortality on the new host.

Materials and Methods

Avoiding egg parasitism by achieving enemy-free space

In 1991, four sites were selected in eastern Ontario approximately 10–20 kilometers north of Kingston. Site selection was based on the availability of enough apple and cherry trees occurring in roughly equal proportions, and there being a large enough area in which to sample. Two of the sites were at the Little Cataraqui Conservation Area (LC and LC2) off Perth Road just north of Kingston. Two other sites were located on farms north of Unity Road in Glenburnie (H and MR), approximately six kilometers northeast of LC and LC2.

Shortly following eclosion of *M. americanum* eggs in early May 1991, equal numbers of cherry and apple trees harboring caterpillar tents were searched until an egg mass was found. The egg mass was then removed by cutting off the section of the branch that harbored the egg mass, with a pair of pruning secateurs. Within three of the four sites, 20 trees of each species were found and sampled. As there were many cherry and apple trees at the MR site, 23 trees of each species were sampled. In total, 166 egg masses were collected from 83 cherry and 83 apple trees. Upon inspection in the lab, two egg masses from cherry and three from apple were excluded from the data set and subsequent analyses. Three of these, one from apple and two from cherry, were egg masses from *M. disstria*. The remaining two were collected from a species of hawthorn (*Crataegus* spp.), which had been misidentified as apple during collection.

Egg masses were transferred to clean 125 ml milk bottles and maintained at 21°C with a photophase:scotophase light regime of 12:12 L:D. As parasitoids emerged, they were recovered and placed into vials of 70% ethanol for preservation, one vial for each egg mass. Parasitoids were identified in the lab.

In 1993, egg masses from the caterpillar mortality study near the Queen's University Biological Station were brought into the lab and the parasitoids reared out, and identified following the protocol from 1991.

In April of 2000, this experiment was repeated at the H site. Egg masses on 33 apple and 29 cherry were located and flagged. After the caterpillars had left the egg masses, egg masses were collected by clipping the branch with pruning secateurs. Egg masses were then placed in culture tubes, labeled and sealed with cotton. In total, 133 egg masses were found. Egg masses were brought into the lab and maintained at room temperature, 12D:12L light regime and a relative humidity of 40%. Parasitoids began emerging within two weeks and continued until 22 June. Upon emergence, parasitoids were cooled in the refrigerator, then transferred to 70% ethanol until identification. When emergence had ceased, each egg mass was dissected and the status of the non-emerged eggs was evaluated as either undeveloped, or parasitized. Several specimens of each type were sent to Dr. C. Darling at the Royal Ontario Museum for definitive identification. Voucher specimens of each species are currently housed at the museum.

Statistical analyses: In 1991, the data did not meet the requirements for normality, even with transformation, so Kruskal-Wallis (KW) tests were performed. The Statview statistical package on a Macintosh Plus computer was used to determine if the parasitoids preferred one site to another and if the number of non-viable eggs varied by site. Data were tested at two levels: total parasitoid counts and individual species counts. In all cases, $\alpha = 0.05$. As no site effects were found for parasitoid numbers ($Y = 4.664$, $P = 0.198$ for *Tetrastichus*, $Y = 5.513$, $P = 0.138$ for *Teleonomus* and $Y = 2.638$, $P = 0.451$ for *Ooencyrtus*) or non-viable eggs (H value = 0.094, $P = 0.9926$), data from all four sites were pooled.

In 1991, 1993 and 2000, percentage parasitism by parasitoid species and percentage emergence within each host was analyzed using one-tailed Mann-Whitney U tests (Zar 1984). In all cases, we hypothesize that percentage parasitism and emergence would be higher in cherry as compared with apple. As sample sizes in 1991 and 2000 were >20 , the normal approximation (z score) was utilized to determine significance.

Mean number of eggs per egg mass for all years was analyzed between host species using t-tests. In 1993 we were interested in caterpillar mortality more so than the specifics of the parasitoid species, hence no identification of the parasitoids occurred, and no analysis by species was possible.

Caterpillar mortality

Ten cherry trees and seven apple trees were selected from around the Queen's University Biology Station (Chaffey's Locks, Ontario) in 1993. Locating greater numbers of trees with egg masses proved difficult, suggesting that the tent caterpillar population had declined since 1991. Trees were tagged and the egg masses flagged to allow for easy relocation. Egg masses were checked daily until the first instar larvae emerged. Larvae were counted and the egg mass was removed to the laboratory for further study. Larvae were observed in the field until they returned to their 'tent' to molt to second instars, and were again counted. Percent parasitism of the eggs and mortality of first instar larvae were calculated.

In 2000, 29 cherry and 33 apple trees were selected and flagged at the H. site. As each tree harbored more than one egg mass, there were 133 egg masses located and used in this study. Twenty-one egg masses found on cherry were transplanted onto apple trees already harboring an egg mass. Twenty-one egg masses from apple were then transplanted onto cherry trees already harboring an egg mass. Egg masses were transplanted by clipping the branch harboring the egg mass and attaching it to the recipient tree using twist ties. Selecting trees already harboring an egg mass eliminates the possibility that the tree was not a suitable host for *M. americanum*. Trees selected for this transplanting study had to be large enough to safely harbor more than one caterpillar tent without the tents combining (Fitzgerald and Willer 1983). Egg masses were then checked until the first instar larvae emerged. These were counted in the field by taking a digital picture with a Kodak digital camera. Larvae were observed in the field until they returned to their 'tent' to molt into second instars, and were again counted. Final larval counts were obtained by removing the tent from the tree, separating the caterpillars from the silk in a white bucket and taking a digital picture. Each picture was then loaded into Microsoft PhotoSuite 5.0 and the caterpillars counted accurately. Percent parasitism of the eggs and mortality of first instar larvae were calculated.

Ideally, a control consisting of egg masses taken from cherry and transplanted onto other cherry trees and similarly for apple would have been included. We did not have enough egg masses to effectively facilitate this. We did, however, have three egg masses from cherry that we transplanted onto cherry. These showed similar egg counts, percentage emergence and percentage mortality to other egg masses collected from cherry or transplanted onto cherry. As the replicate number was only 3, we did not deem this sufficient enough to warrant inclusion in the analysis.

TABLE 1. Percent parasitism and percent larval mortality of *Malacosoma americanum* on two host-plant species located at four sites (pooled) near Kingston, Ontario in 1991, at Queen's University Biology Station in 1993, and at the H site in 2000.

Year		Host species		t-score, df, P value	Mann Whitney U-value, z score, P value
		Cherry	Apple		
1991	Total number of trees	81	80		
	Mean eggs/egg mass ± SE	264.31 ± 6.20	260.94 ± 5.63	0.40, 158, 0.68	
	% emergence ± SE	83.53 ± 2.43	86.31 ± 4.24		3151.5, 0.29, 0.38
	% parasitism ± SE (all parasitoids)	7.54 ± 1.67	4.80 ± 0.96		2371, 2.57, 0.005
	% parasitism ± SE by <i>T. malacosomae</i>	5.1 ± 2.09	2.5 ± 1.33		1897.5, 3.10, 0.001
1993	Total number of trees	10	7		
	Mean eggs/egg mass ± SE	219 ± 12.71	224 ± 41.47	-0.11, 7, 0.91	
	% emergence ± SE	78.33 ± 4.62	78.90 ± 8.94		30, n/a, > 0.10
	% parasitism ± SE (all parasitoids)	11.81 ± 3.04	6.54 ± 1.89		48, n/a, > 0.10
	% mortality ± SE	21.48 ± 3.51	40.02 ± 3.98		62, n/a, < 0.005
2000	Total number of trees	62	61		
	Mean eggs/egg mass ± SE	293.66 ± 10.45	291.03 ± 7.59	-0.20, 90, 0.42	
	% emergence ± SE	85.12 ± 1.63	87.04 ± 1.35		1803, 0.44, 0.329
	% parasitism ± SE (all parasitoids)	4.64 ± 0.76	3.51 ± 0.67		2183, 1.47, 0.07
	% parasitism ± SE by <i>T. malacosomae</i>	1.77 ± 0.32	0.31 ± 0.22		2775.5, 4.47, < 0.00001
	% mortality ± SE	57.27 ± 4.40	68.56 ± 3.75		1661, 2.02, 0.022

TABLE II. Percent parasitism of eggs within each host species by the three parasitoid species. Data from all four sites, pooled, in 1991 and from the H site in 2000.

Year	Parasitoid species	Host species		U, z, P value
		Cherry	Apple	
1991	<i>Tetrastichus malacosomae</i>	5.1	2.5	1897.5, 2.05, 0.002
	<i>Telenomus clisiocampae</i>	1.4	1.1	4185.5, 0.18, 0.573
	<i>Ooencyrtus clisiocampae</i>	1.0	1.1	5721.5, 1.66, 0.952
	All species	7.5	4.7	2371.0, 2.57, 0.005
2000	<i>Tetrastichus malacosomae</i>	1.8	0.3	2775.5, 4.47, <0.00001
	<i>Telenomus clisiocampae</i>	1.4	2.1	1872.0, 0.09, 0.463
	<i>Ooencyrtus clisiocampae</i>	1.4	0.9	1745.0, 0.74, 0.231
	All species	4.6	3.5	2183.0, 1.47, 0.070

Statistical analyses: Percentage parasitism and percentage mortality were compared between host species using one-tailed Mann-Whitney U tests $\alpha = 0.05$ (Zar 1984). Again, we hypothesized that percentage parasitism would be higher on cherry when compared with apple while percentage mortality would be higher on apple when compared with cherry.

Leaf development

Field observations of the stage of bud break were taken in 2000. Beginning in late April, trees were categorized by their buds on a weekly basis as either: gray, pink or green. 'Gray' buds were tightly closed with no crack in the outer casing being observed. 'Pink' buds had an obvious crack in the casing, a pink hue to the bud with the new leaves being visible upon close inspection. Trees designated 'green' had new leaves completely exposed; bud break was considered complete. A chi-square analysis was performed to determine if cherry trees were significantly developmentally advanced when compared with apple.

Results and Discussion

The number of eggs per egg mass and percent emergence of the caterpillars did not significantly differ between cherry and apple trees in any year (Table I). As all egg masses had similar numbers of eggs, and caterpillars on either host had similar success emerging, it is highly probable that the females were actively choosing apple, as well as cherry, for oviposition. Had the egg numbers and percent emergence been significantly lower, it might have suggested that the females were selecting apple as a 'best of a bad situation' strategy. Further, all sites had cherry and apple trees located <10 m apart, suggesting that the females had ample opportunity to evaluate both hosts prior to oviposition.

Three different species of egg parasitoid were reared and subsequently identified: *Tetrastichus malacosomae* Girault (Hymenoptera: Eulophidae), *Telenomus clisiocampae* Riley (Hymenoptera: Scelionidae) and *Ooencyrtus clisiocampae* (Ashmead) (Hymenoptera: Encyrtidae). With all parasitoid species together, overall percent parasitism in 1991 and 2000 was significantly higher on cherry than on apple, $\alpha = 0.05$ (1991) and $\alpha = 0.10$ (2000) (Table II). These results suggest that host switching provided a degree of escape from parasitism by a specialist parasitoid. In 1993, a slightly higher overall percent parasitism was encountered (Table I), but the difference was not significant, possibly because of inadequate sample size.

As the three species were not individually identified in 1993, it was not possible to compare the values for the three species separately. In both 1991 and 2000, all three species were found in apple and cherry egg masses (Table II). In 1991, *T. malacosomae* parasitized the most eggs (5.1% and 2.5% of eggs laid on cherry and apple, respectively), with *T. clisiocampae* parasitizing fewer (1.4% and 1.1%, on cherry and apple, respectively) and *O. clisiocampae* parasitizing the fewest (1.0% and 1.1%, on cherry and apple, respectively). In 2000, the situation was similar with *T. malacosomae* parasitizing the most eggs (1.8% and 0.3% on cherry and apple, respectively). *Telenomus clisiocampae* parasitized 1.4% and 2.1% of eggs, on cherry and apple, respectively with *O. clisiocampae* parasitizing 1.4% and 0.9% of eggs, on cherry and apple, respectively (Table II). Of all three species, the only one that differed significantly between the hosts was *T. malacosomae* that parasitized more eggs on cherry than on apple (Table II). This difference is probably the main contributor to any significance when all parasitoids are considered together. *Tetrastichus malacosomae* is a specialist parasitoid that has not been documented in egg masses of any other species (Knox 1992). *Malacosoma americanum* may have been selected to oviposit on apple as a result of the release from parasitism by *T. malacosomae* on this host plant.

Percentage mortality in 1993 was significantly higher for 1st instar larvae on apple than on cherry (Table I). This same analysis in 2000 was slightly more complex. Percentage mortality was analyzed between and within host species, and took into consideration those egg masses that had been transplanted. Egg masses transplanted from apple and cherry trees onto cherry and apple trees, respectively, were compared for caterpillar mortality and found to be not significantly different (tree of origin, apple: $n = 21$, mean = 72.86 ± 4.99 ; cherry: $n = 21$, mean = 62.96 ± 6.71 ; $U = 258.5$, $z = 0.94$, $P = 0.172$). Caterpillar mortality for egg masses from apple and transplanted onto cherry were compared with egg masses from apple that were not transplanted and found not to differ significantly (apple, not transplanted: $n = 33$, mean = 65.82 ± 5.26 ; apple, transplanted: $n = 21$, mean = 72.86 ± 4.99 ; $U = 323$, $z = 0.41$, $P = 0.34$). A similar result was obtained for cherry egg masses, comparing transplanted with non-transplanted egg masses (cherry, not transplanted: $n = 29$, mean = 53.16 ± 5.82 ; cherry, transplanted: $n = 21$, mean = 62.96 ± 6.71 ; $U = 238$, $z = 1.29$, $P = 0.09$). The only comparison that showed a significant difference was for egg masses that were not transplanted and compared between host species. In this case, caterpillars reared from egg masses on apple ($n = 33$, mean = 65.82 ± 5.26), experienced significantly higher mortality compared with caterpillars reared from egg masses on cherry ($n = 29$, mean = 53.16 ± 5.82 , $U = 602$, $z = 1.74$, $P = 0.041$). As there were no significant differences in percent mortality for egg masses that were transplanted compared with those that were not, either within host species or between host species, all egg masses were pooled by tree of origin. A Mann-Whitney U test was conducted to test the hypothesis that caterpillar mortality was higher for egg masses laid on apple as compared with cherry; this result was significant. Caterpillars reared from egg masses laid on apple ($n = 54$, mean = 68.56 ± 3.75) experienced higher mortality than their cherry counterparts ($n = 50$, mean = 57.27 ± 4.40 , $U = 1661$, $z = 1.74$, $P = 0.022$).

That caterpillar mortality is significantly higher on apple as compared with cherry may be a result of the phenology of the tree being asynchronous with larval development. On 28 April and 3 May 2000, there were significantly more cherry than apple trees in full leaf (green) (Table III). By 9 May, this difference had disappeared. However, given that the caterpillars had begun to emerge as early as 15 April, those on apple would have had to wait three weeks until green leaves were available, and only one week on cherry.

As *M. americanum* has most likely evolved on cherry (Hosie 1979), its development is timed to coincide with bud break of this host species. Apple, breaking bud later, does not provide adequate food resources for the developing larvae for the first few days following eclosion and consequently many larvae do not survive to the 2nd instar. Another factor resulting in reduced mortality on cherry may be the presence of hydrogen cyanide and benzaldehyde present in the

TABLE III. Field observations of bud break for 26 cherry and 25 apple trees at the H site in spring 2000.

Date	Stage of bud break	Number of trees		$\chi^2_{0.05,2}$ (P)
		Cherry	Apple	
April 28	Gray	2	17	25 (<0.00001)
	Pink	8	7	
	Green	16	1	
May 2	Gray	0	5	7.8 (0.019)
	Pink	10	11	
	Green	16	8	
May 9	Gray	0	0	Not calculable due to zeroes
	Pink	1	2	
	Green	25	24	

larval regurgitant (Peterson et al. 1987) which deters predators. These compounds originate within the cherry leaves prior to ingestion by the larvae, and are not present in apple leaves. Denno et al. (1990) found salicylate content of *Salix* spp. to influence host selection by willow beetles. Beetles on high salicylate *Salix* spp. were able to deter predators.

Irrespective of the possible co-evolution of cherry and eastern tent caterpillar, the benefit of selecting a new host as a means to reduce parasitism must still be evaluated in relative terms. If the number of caterpillars surviving to adulthood on the new host were greater than the number lost to parasitism on the old host, then switching would be the optimal strategy. This was not shown in our studies, as mortality on apple was much greater than that on cherry, even with reduced parasitism. Given this, the question of why a female would choose apple over cherry is still unclear. In contrast to our tent caterpillar situation, Roland (1986) found winter moth larvae to be equally parasitized by its parasitoid on both oak and apple, its alternative host. This occurred even though fewer parasitoid eggs were laid on apple. Unlike tent caterpillar egg masses that are parasitized directly, winter moth larvae must ingest parasitoid eggs to become parasitized. In this case, the differential foraging behavior of winter moth larvae on the two hosts influenced the rate of parasitism. Although the alternative host, apple, appears to be an enemy-free space due to reduced numbers of parasitoid eggs, larval behavior negates any benefit of selecting this host.

Despite our observations from three separate years spanning a period of nine years, we cannot effectively balance the positive and negative effects of eastern tent caterpillar utilizing apple as compared with cherry. However, when we measured larval mortality, the observed difference was greater than the benefit of avoiding egg parasitism. It is possible that this large difference in the early instars may be offset by fitness-affecting differences in survival and development for later larval stages between apple and cherry feeders. For instance, if we assume that later instars on both apple and cherry face the same probability of parasitism by larval parasitoids, an increased fitness may be achieved those caterpillars on an abundant food source. Given that apple trees are typically larger than choke cherry bushes, apple caterpillars may not need to disperse to locate a new food source incurring both the dangers of predation and starvation in the process. Unfortunately, making reliable observations of survival and growth on later larval instars may not be possible, since larvae on cherry disperse (Stehr and Cook 1968). We do not know whether larvae on apple also disperse.

As apple is a relatively recent newcomer to North America, we must assume that the currently observed ratio of oviposition on apple and cherry probably does not as yet reflect an equilibrium strategy. Whether natural selection based on escape from parasitism and possible starvation will eventually drive *M. americanum* towards extensive use of apple, or whether the effects of lack of synchrony and possible changes in parasitoid behavior will have the opposite effect, remains an unanswered question. A third possibility is that, with a fluctuating environment, changes in climate and land use, and variable levels of genetic adaptability in the interacting species concerned, a stable equilibrium may never evolve.

What this study has provided, is a good example of how the introduction of a new potential host plant can affect in a complex manner of opposing selective forces the life history strategies of a herbivore and its parasitoids.

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References

- Casas, J. 1989. Foraging behavior of a leafminer parasitoid in the field. *Ecological Entomology*, 14: 257-265.
- Darling, D.C. and N.F. Johnson. 1982. Egg mortality in the eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae): the role of accessory gland secretions and egg mass shape. *Proceedings of the Entomological Society of Washington*, 84: 448-460.
- Denno, R.F., S. Larsson and K.L. Olmstead. 1990. Role of enemy-free space and plant quality in host-plant selection by willow beetles. *Ecology*, 71: 124-137.
- Evans, D.L. and J.O. Schmidt. 1990. *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators*. Albany: University of New York Press. 482 pp.
- Fitzgerald, T.D. and D.E. Willer. 1983. Tent building behavior of the Eastern Tent Caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae). *Journal of Kansas Entomological Society*, 56: 20-31.
- Gold, C.S., M.A. Altieri and A.C. Bellotti. 1989. Relative oviposition rates of the cassava hornworm, *Eriomyia ello* (Lepidoptera: Sphingidae), and accompanying parasitism by *Telenomus sphingis* (Hymenoptera: Scelionidae), on upper and lower leaf surfaces of cassavas. *Entomophaga*, 34: 73-76.
- Gross, P. 1993. Insect behavioral and morphological defenses against parasitoids. *Annual Review of Entomology*, 38: 251-273.
- Hosie, R.C. 1979. *Native Trees of Canada*. Don Mills: Fitzhenry and Whiteside Ltd. 380 pp.
- Knox, D.A. 1992. Host plant variation in egg parasitism of the eastern tent caterpillar (*Malacosoma americanum*) in eastern Ontario. Master's Thesis. Ontario: Queen's University. 56 pp.
- Lawton, J.H. 1986. The effect of parasitoids on phytophagous insect communities. pp. 265-289 *In* J. Waage and D. Greathead (eds.) *Insect Parasitoids*. England: Academic Press, Inc. 389 pp.
- Lederhouse, R.C. 1990. Avoiding the hunt: primary defenses of lepidopteran caterpillars. pp. 175-190 *In* D.L. Evans and J.O. Schmidt (eds.) *Insect Defenses: Adaptive mechanisms and strategies of prey and predators*. Albany: State University of New York Press. 482 pp.
- Peterson, S.C., N.D. Johnson and J.L. LeGuyader. 1987. Defensive regurgitation of allelochemicals derived from host cyanogenesis by eastern tent caterpillars. *Ecology*, 68: 1268-1272.
- Porter, B.A. 1958. The Eastern Tent Caterpillar. U.S.D.A. Leaflet 161. 3 pp.

- Roland, J. 1986. Parasitism of winter moth in British Columbia during build-up of its parasitoid *Cyzenis albicans*: attack rate on oak vs. apple. *Journal of Animal Ecology*, 55: 215–234.
- Roland, J. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature*, 386: 710–713.
- Segarra-Carmona, A. and P. Barbosa. 1983. Nutrient content of four rosaceous hosts and their effects on development and fecundity of the eastern tent caterpillar, *Malacosoma americanum* (Fab.) (Lepidoptera: Lasiocampidae). *Canadian Journal of Zoology*, 61: 2868–2872.
- Stehr, W.R. and E.F. Cook. 1968. A revision of the genus *Malacosoma* (Hübner) in North America (Lepidoptera: Lasiocampidae): systematics, biology, immatures, and parasites. *Bulletin of the U.S. Natural Museum No. 276*. 15 pp.
- Van Alphen, J.J.M. and L.E.M. Vet. 1986. An evolutionary approach to host finding and selection. pp. 23–62 *In* J. Waage and D. Greathead (eds.) *Insect Parasitoids*. England: Academic Press, Inc. 389 pp.
- Vinson, S.B. 1976. Host selection by insect parasitoids. *Annual Review of Entomology*, 21: 109–133.
- Voelkl, W. 1994. Searching at different spatial scales: the foraging behavior of the aphid parasitoid *Aphidius rosae* in rose bushes. *Oecologia*, 100: 177–183.
- Zar, J.H. 1984. *Biostatistical Analysis*. 2nd edition. Englewood Cliffs: Prentice-Hall, Inc. 718 pp.

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