# Eastern Tent Caterpillars: An Exploration of the Preferred Host Tree Sara Ginzberg, Nick Perri, Erin Skallerup

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### Abstract

Eastern tent caterpillars (*Malacosoma americanum*) are specialist herbivores on the *Rosaceae* family, particularly on black cherry trees (*Prunus serotina*). However, variation in tent occurrence and defoliation exists within populations of black cherry trees. This variation was exemplified in Waldron's Fen in Emmet County, Michigan in the spring of 2010. Black cherry trees were surveyed at the fen to see whether tree size and relative isolation from other trees affected tent occurrence. Additionally, caterpillars from the fen were raised in the lab to track weight gain in three groups each receiving a different food type: leaves from favored black cherry trees, and sweet cherry trees.

It was found that defoliation was higher in densely populated cherry plots and was lower in a plot densely populated with other non-cherry tree species. There were also trends indicating that trees with smaller DBHs and those that were more isolated from other trees had higher tent occurrences. It was also found that the optimal range for height of tent to be between 2 and 2.5m in height. The caterpillars that were fed unfavored black cherry leaves in the first cohort collected had significantly higher growth than the other groups. The caterpillars fed both black cherry leaf types in second cohort collected grew significantly larger than those fed sweet cherry. However, there was not a significant difference between nitrogen and phosphorus levels between the three food categories. All of these results suggest that selection may favor female moths that choose host trees with these characteristics.

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# Introduction

The most widely known species of tent caterpillars in North America is *Malacosoma americanum*, commonly known as the eastern tent caterpillar. During the summer, a female *M. americanum* moth oviposits a clutch of eggs on a host tree. The larvae then hatch from the egg mass in the following spring (Fitzgerald and Willer 1983). The larvae usually can be found on cherry trees as soon as the leaves arrive. If their emergence occurs any later, the leaves they feed on will be too mature for them to grow to an optimal biomass because of the lack in nutritional value in more mature leaves (Travis 2005).

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The siblings then build silken tents in which they grow and develop together during their larval stage, leaving the tent periodically for synchronized foraging. While foraging, tent caterpillars convey information regarding food quality to each other by leaving chemical trails (Bergelson and Waage 1985). A typical tent contains 50 to 300 sibling caterpillars and is expanded upon every day during group spinning periods until the larvae pupate individually (Fitzgerald and Willer 1983).

Although eastern tent caterpillars can survive on over 50 different species of tree (Bergelson and Waage 1985), they are specialists on trees in the family *Rosaceae*, particularly cherry (*Prunus*) and apple (*Malus*) trees (Fitzgerald and Willer 1983). This discrimination within the *Rosaceae* family may be the result of differences in nutritional and chemical variation between the tree species. Bergelson and Waage (1985) demonstrated that while larvae can mature on other *Rosaceae* species such as the pin cherry (*Prunus pennsylvanica*), they will switch to black cherry (*Prunus serotina*) when given the choice. This finding suggests that the nutritional and chemical composition of the black cherry species is optimal for the growth of eastern tent caterpillars. In fact, the range of *M. americanum* spans eastern North America from Nova Scotia to Florida, aligning almost exactly with that of black cherry trees (Bergelson and Waage 1985). This relationship between tent caterpillars and black cherry trees has led to the caterpillars' complete immunity to the toxic cyanide produced by black cherry trees, an example of the evolutionary arms race between herbivores and the plants on which they specialize (Fitzgerald 1995). A study by Peterson (1987) suggested that tent caterpillars may even take advantage of the toxin as a defense against predators and parasites. This may indicate that the cyanide content in the black cherry tree leaves has become an attractant for the female moth looking to lay her eggs, as many secondary compounds have for specialist herbivores (Mello and Silva-Filho 2002). The ability of the moth to pick an appropriate host tree in this way is extremely important for its fitness because the caterpillars are relatively immobile and must rely on the environment in which they hatch for feeding and juvenile survivorship (Rausher 1979).

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In years of peak population, eastern tent caterpillars may cause complete denuding, branch dieback, and stunted plant growth on their host trees (USDA 2010). The larvae typically feed on the trees' immature leaves due to the elevated nitrogen and water content (Schroeder 1986), thereby forcing the trees to allocate large amounts of energy into putting out more growth rather than to reproduction (Ruess and McNaughton 1984). The trees' new leaves after caterpillar herbivory are thus smaller and less plentiful, and defoliated host trees may produce less fruit (USDA 2010). As a result, the reproductive fitness of heavily affected trees is greatly decreased; since less energy can be allotted to producing flowers and fruit, denuded trees have less opportunity to pass on their genes.

The population of the eastern tent caterpillar cycles roughly every ten years. This cyclical pattern is not well understood, but it could be influenced by factors such as access to food,

weather, predation, and parasitism (Fitzgerald 1995). In Northern Michigan, the spring of 2010 was a peak year in the population cycle of the caterpillars, and tents proliferated quite noticeably in the area. It was apparent, however, that certain black cherry trees have much higher numbers of tents and defoliation than others. In an attempt to examine this observation further, we formulated a series of questions to explore. Is there a difference in the growth of caterpillars raised on black cherry trees with tents versus growth of those raised on black cherry trees with no tents? What factors—such as location, size, and relationship to neighboring trees—affect the appeal of different black cherry trees for tent caterpillars?

We postulate that larger black cherry trees and trees in more densely populated plots with other black cherries will have a higher number of tents and a higher percentage of defoliation. Because the female *M. americanum* moths find trees on which to oviposit eggs based on the scent of the tree, we believe that the a more dense plots of black cherry trees may emit a stronger, more detectable smell and thus better attract the female moth. We further predict that lower branches will have more tents because of increased protection from predators and parasites. Finally, we hypothesize that caterpillars raised on black cherry leaves from trees with many tents will grow the most, due to higher nutrient content in those leaves.

## **Materials and Methods**

#### Field Observations

In order to establish trends in tent placement and leaf consumption, field observations were taken of the black cherry trees in Waldron's Fen. For observational purposes, the circumference of the fen was divided into six plots based on the natural clumping of black cherry trees around the fen. For each black cherry tree in the plots, the plot number was recorded in

addition to the relative isolation from other trees, the height of the tree, the number of tents in the tree, the height of the tents, the DBH of the tree, and the percentage of defoliation.

Relative isolation was determined by noting the quantity and species of all trees including black cherries within a 5m radius of the tree. Additionally, the quantity of only black cherry trees within a ten meter radius of the tree was noted. Percentage of defoliation was recorded in four categories: 1 = 0.25%; 2 = 26.50%; 3 = 51.75%; and 4 = 76.100%.

#### **Rearing Caterpillars**

Eastern tent caterpillars were collected from Waldron's Fen in Emmet County, Michigan. Tents were cut from black cherry trees and placed into large bags. If more than one tent was taken from an individual tree, they were placed into the same bag, and bags were distinguished by tree number. In addition, leaves were taken from three categories of cherry trees: sweet cherries, black cherries that were favored by tent caterpillars, and black cherries that were untouched by tent caterpillars. Black cherries that were considered heavily denuded contained more than two tents and had a high degree of defoliation.

Caterpillars from the different trees were randomly distributed into petri dishes, each containing two standardized circles of one designation of leaf: favored black cherry, unfavored black cherry, or sweet cherry. Fifty caterpillars were randomly assigned to each food type and were fed *ad libitum*. All caterpillars were kept in an environmental chamber set at 70°F and on a simulated day/night cycle, and food and moisture levels were checked daily. The caterpillars' weight was recorded every other day.

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After three days of weighing, high mortality rates were observed among smaller caterpillars. Because of this high mortality, six more tents were collected to supplement the original 50 caterpillars per food type.

All caterpillars were kept in the petri dishes for a total of nine days, or five weighing sessions. When applicable, date of death or pupation was recorded in addition to weight.

# Statistical Analysis

Analyses of both field observations and caterpillar growth were done using SPSS. First, we ran tests in order to determine if any correlations exist between tree size, isolation, and the density of tents as well as defoliation per tree. For the DBH assessments, DBH measurements were classified into four categories: (1 = 0.15 cm; 2 = 16.30 cm; 3 = 31.45 cm; 4 = 46 + cm). Isolation analyses categorized trees as either in non-dense or dense areas (1 = non-dense, 2 other trees or fewer; 2 = dense, 3 other trees or more). Tent density was calculated using the crosssectional area of the tree trunks and the number of tents per tree, and these densities were then also classified into categories based on the natural breaks in the data. Using these categorizations, a series of Mann-Whitney and Kruskal-Wallis tests compared the mean tent densities and defolation at different DBHs and different isolations. In some cases, two-sample chi-square tests were also performed to obtain clearer results.

Additionally, we examined the distribution of the heights of all tents surveyed on all trees that were at least 5m tall. Frequencies were determined in half-meter ranges from 0 to 6.5m. Shorter trees were disregarded so that the available height ranges could be standardized. A chisquare test was then conducted to determine whether there was a significant preference for particular height ranges. Several tests were also run to interpret the data collected from the reared caterpillars. Chisquare tests were conducted to see whether there was a difference between the frequencies of deaths for caterpillars in each of the food types. Separate tests were run for the two cohorts of caterpillars due to the changing conditions between collections. Additionally, ANOVA tests were run to compare the mean change in weight for each of the food types for Cohort 1. For these tests, Cohort 1 was broken into two groups based on starting weights in order to eliminate the difference in growth rate between small and large caterpillars.

### Results

## Field Observations

A Kruskal-Wallis test was run using the density of tents. We determined densities by using the number of tents per cross sectional area of the trunk. While not significant, a trend demonstrated that smaller DBH trees tended to have a higher density of tents (Figure 2, p-value .138). This data appeared to be in contrast with the original test; therefore, we ran a two-sample chi-square test to clarify any tent density relationships. We grouped the tent densities according to the natural breaks observed in the data. We found that trees with smaller DBH measurements do indeed have significantly greater tent density (p-value<0.001).

Next, a two-sample Mann-Whitney test examined the relationship between the number of tents on a tree and density of other black cherry trees within a 5m radius. The mean number of tents on trees in non-dense areas was 3.34931, and the mean number of tents on trees in dense areas was 2.652174 (Figure 3). While not significant, this difference suggests a slight trend towards an occurrence of more tents on trees that are relatively isolated from other black cherries (p-value .282).

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We ran two more tests to see the effect of black cherries within a 10m radius as well as the effect of other tree species within a 5m radius on the number of tents in a tree. Through use of Mann-Whitney tests, we could not draw any statistical relationship between these isolation variables and the number of tents in a tree (p-value 0.544, 0.818).

Subsequently, we conducted a chi-square test to ascertain the relationship between the density of tents and the percent defoliation on a tree and deterimined whether defoliation was a result of tent caterpillar herbivory. We found that the defoliation was directly correlated with the number of tents (p-value<0.001). Based on this result, we tested to see if percent defoliation was correlated with isolation.

We ran chi-square tests to compare the defoliation of each tree with the density of black cherries in a 5m radius, the density of black cherries in a 10m radius, and the density of other trees in a 5m radius. We found that more defoliation occurred in trees that grew in plots densely populated by other black cherries within 5m (Figure 4, p-value 0.015). However, we did not find a correlation between density of black cherries within 10m of a tree and the amount defoliation (p-value 0.747). Furthermore, lower densities of other, non-cherry trees yielded higher levels of defoliation (Figure 5, p-value 0.045).

Lastly, we analyzed the heights of all the tents surveyed on the trees that were 5m tall or more. When a frequency chart was created, the distribution of tents was nearly a normal curve. The highest frequencies of tents were centered around the 2-2.5m range. The chi-square test indicated that the preference for certain height ranges was very significant (Figure 6, p-value<.001).

Rearing Caterpillars

When chi-square tests were conducted for both Cohort 1 and Cohort 2 to determine whether there was a significant difference in death rate for each food treatment, no statistically significant result was found ( $\chi^2 = .311$  and .052, respectively, df = 2). The survivorship curves showed nearly identically slopes (Figures 8 and 9).

In the analysis of the caterpillars' total change in weight over the course of treatment, Cohort 2 could not be used due to an inadequate sample size for each food type. For Cohort 1, the caterpillars were split into two groups based on starting weight before statistical tests were run. Those in Group 1, with starting weights up to 0.069g, displayed significantly different changes in weight in the ANOVA test (p-value 0.042). Caterpillars fed unfavored black cherry leaves grew a mean 0.045g, while those fed favored black cherry leaves grew a mean 0.015g and those fed sweet cherry leaves grew a mean 0.002g (Figure 9). Thus, caterpillars in the unfavored black cherry treatment grew significantly more than those in the other two treatments, and caterpillars in the favored black cherry treatment grew significantly more than those in the sweet cherry treatment.

Additionally, caterpillars in Group 2, with starting weights greater than 0.069g, also showed significantly different changes in weight in the ANOVA test (p-value 0.001). Caterpillars fed unfavored black cherry leaves grew a mean 0.089g, and those fed favored cherry leaves grew a mean 0.083, but those fed sweet cherry leaves lost a mean 0.019g. Therefore caterpillars fed both unfavored and favored black cherry leaves grew significantly more than those fed sweet cherry leaves (Figure 10).

#### Discussion

Selection favors moths that elect host trees that lead to the maximum survivorship and growth of their clutches. Because *M. americanum* caterpillars are precocial, larval

survivorship and growth is dependent on female moth choice of oviposition. The results of this experiment demonstrate characteristics that contribute to optimal oviposition for the female moth. We examined four different potential juvenile survivorship and growth determinants: host tree isolation, size of host tree, tent height, and host tree nutrient content.

We first analyzed the role of host tree isolation in moth fitness. To begin, we found that the number of tents placed on a tree does not significantly depend on the presence or absence of other black cherry trees within a 5m radius, despite a slight trend of more tents on more isolated cherry trees. Since M. americanum moths use scent to locate host trees on which to lay, we expected to see denser tent formation in densely packed black cherry stands (Travis 2005); however, this was not the case. Our finding could likely be explained through further investigation of female M. americanum moth oviposition. Previous studies found that female moths show no preference towards larger or more densely packed trees and that the density of previously deposited egg hatches in a tree does not influence oviposition (Fitzgerald 1983). If female moths do not display any preference in egg placement amongst P. serotina, we would expect to see an equal distribution between numbers of tents in all black cherry trees. Thus, the slight trend of more tents in trees isolated from other cherry trees could possibly be attributed merely to the availability of space for egg-laying. That is, if a group of black cherry trees attracts a female moth, she may lay her eggs on any of the trees in that area. Yet if just one tree is in the direct vicinity, that tree would be more likely to have more tents simply because it is the only viable habitat in the area.

In contrast, we found that host trees in areas with more other black cherry trees within 5m showed significantly higher levels of defoliation than host trees that were isolated. Given that there was no significance between the number of black cherry trees in a 5m radius and the

number of tents—and a trend in fact showed that trees more isolated from other black cherry trees tended to have more tents—this result was surprising. A possible explanation for this finding is that tents of the eastern tent caterpillar have been known to form from multiple clutches when conditions are permitting (Fitzgerald 1983). Because more caterpillars would be foraging from fewer tents, higher defoliation would occur even with a lower numbers of tents.

Another potential reason for this finding could be the eastern tent caterpillar's ability to forage on more than one tree (Fitzgerald 1983). Often as caterpillars grow, they will forage on other trees in close proximity to continue eating the younger, more nutritious leaves from less denuded trees (Rausher 1980). Thus, if caterpillars can move between trees, a tree without a significantly higher number of tents can still be favored and therefore have a greater amount of defoliation.

Conversely, it was found that host trees surrounded by many trees of other species in a 5m radius showed significantly less defoliation. It is known that polycultures typically attract fewer pests than do monocultures due to the possible scent masking and visual obstruction of the target host. Perhaps caterpillars are practicing optimal foraging in that a plot that is more densely populated with cherry trees has a better cost-benefit ratio than a plot in which a single cherry tree is found with densely growing trees of other species.

No relationship was found regarding cherry trees within 10m and the number of tents or the amount defoliation. This could be due to the fact that trees between 5m and 10m away from the host tree are outside of the browsing range of the caterpillars. While caterpillars do forage in multiple trees, their range is rather short due to vulnerability to predation and mechanical inhibitions (Rausher 1979). Therefore trees more than 5m away from the host tree are most likely unaffected by the caterpillars from that host. Consequently, we can infer that trees more than 5m do not have a role in the choice of oviposition for the female moth since they do not affect the survivorship of her offspring nor, as a result, her fitness.

The second determinant of moth fitness we examined was the size of the host tree. Using density of tents, we found a higher mean number of tents on trees with smaller DBHs. This result could be due to predation. Birds account for 66% of the predators of the eastern tent caterpillar (Fitzgerald 1995). A smaller DBH usually results in a shorter tree. Smaller trees may be less prone to predation by birds because they are not as easily seen when a bird is in flight and their thinner branches may be harder to land on. It was previously observed that eastern tent caterpillar moths do not show a preference towards tree size (Fitzgerald 1983), so these observations may be an object of interest in future studies.

We next examined the distribution of tent height as an characteristic of optimal oviposition. We found that the distribution of the heights of all the tents surveyed was nearly normal. The curve was centered around a height range of 2 to 2.5m with a very high level of significance. This finding suggests that the height ranges with the highest frequencies of tents are optimal for moth oviposition. This preferred range could be due to multiple factors related to selection. Tents in higher branches may be more susceptible to predation and parasitism from the birds and parasites that fly overhead. This range could also be influenced by temperature. Higher branches will have less shade and therefore heat up the most during the day. To avoid reaching the upper-critical limit on the hottest day of the year, lower branches may be preferred.

Lastly, we examined leaf nutrient content as a determinant of moth fitness. Caterpillars that were fed unfavored black cherry leaves had a significantly higher weight gain than both the favored black cherry and sweet cherry groups. This result is quite counterintuitive. However, several problems exist with this weight data set. Firstly, preferred trees may have been labeled

unfavorable and vice versa because one tent does not necessarily correlate to one clutch. Because the food we fed the caterpillars in the two black cherry food categories was based on the number of tents found on the black cherry trees, this error would cause a considerable change in our study.

Secondly, we did not control for leaf maturity when feeding the caterpillars, potentially creating another issue for an accurate comparison of weight gain between food treatments. Since the nutrient content of leaves changes with age, each caterpillar group may have been getting a different level of cyanide as well as of nitrogen and water (Peterson 1987; Schroeder 1986). Thus, the different treatment groups' changes in weight could have been more influenced by leaf maturity than by the actual variation in nutrient content between trees.

Had the leaf maturity been standardized, we would at least expect to see a difference in growth rate between the black cherry groups overall and the sweet cherry group, for the eastern tent caterpillar is considered a black cherry specialist. A similar study comparing growth of caterpillars on black cherry to pin cherry (*Prunus pensylvanica*), another closely related species like sweet cherry, showed that caterpillars raised on pin cherries had lower growth rates (Bergelson and Waage 1985).

The confounding variable of leaf maturity may have also skewed the survivorship curve of the caterpillars. For both cohorts, there was no significant difference in survivorship between any of the three categories, yet in the Bergelson and Waage study (1987), survivorship was higher among caterpillars raised on black cherry. Furthermore, the extreme temperature variation may have been a more influential factor than nutrient content in our experiment. This would mean that we could not link the mortality to nutrient content because of temperature. The spring of 2010 was considerably warmer than normal. We collected the caterpillars in 90°F weather. The specimens were then moved to environmental chambers controlled at 70°F, the typical temperature for that time of year. The extreme temperature change may have caused much of the initial mortality. There may have also been high mortality due to temperature because of the capture process. The caterpillars were kept in plastic bags on an extremely hot day, and the bags were in the sun for approximately two hours. This may have created lethal conditions for the caterpillars.

Because of the limitation of our laboratory, we were unable to test the cyanide content of the leaves. However, this may be a topic of interest for future research. It is known that members of the *Rosaceae* family like black cherry and sweet cherry produce cyanide (HCN) as a secondary compound (Peterson 1987). The Peterson (1987) study suggests that eastern tent caterpillars actually digest the secondary compound and use it as a deterrent against predators. Additionally Mello and Silva-Filho (2002) suggest that secondary compounds initially created as deterrents may eventually act as attractants for the herbivore specialists. Testing to see if favored black cherry trees contain more cyanide than unfavored black cherry trees may be an interesting topic for future study.

Based upon our findings and previous studies on the eastern tent caterpillar, we suggest that the observed tent placement preference may be due to a selective pressure for moths to lay their larvae on trees that will provide maximum larval growth and the most protection from predators. Additionally, our results suggest that caterpillars will forage more in areas of plentiful cherry trees than where cherry trees are masked by the presence of other tree species. Certainly, the factors that we analyzed are not the only determining characteristics for optimal oviposition. It would be interesting to test the effect of sunlight and wind on tent placement. This data could

be further studied to help prevent caterpillar infestations on cherry trees for personal use in

gardens and for aesthetics.

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Figure 1. Locations surveyed for field observations at Waldron's Fen based on natural clumping of *P. serotina*.



Figure 2. The Effect of *P. serotina* Diameter at Breast Height on *M. americanum* Tent Density. DBH was categorized into classes (1 = 0.15 cm; 2 = 16.30 cm; 3 = 31.45 cm; 4 = 46+ cm). There is a trend showing greater density in the smallest DBH class than in all other classes (P=.138).



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Figure 3. The Effect of the Denseness of *P. serotina* Within a 5m Radius on the Number of *M. americanum* Tents. Trees were categorized as in a non-dense or a dense area (1 = non-dense, 2 other trees or fewer; 2 = dense, 3 other trees or more). There is a trend showing a somewhat higher mean number of tents for trees in less dense areas (P=.282).



Figure 4. The Effect of the Denseness of *P. serotina* Within a 5m Radius on Defoliation. Trees were categorized as in a non-dense or a dense area (1 = non-dense, 2 other trees or fewer; 2 = dense, 3 other trees or more). Trees in denser areas had significantly higher percent defoliation (P=.015).



Figure 5. The Effect of the Denseness of Other Tree Species Within a 5m Radius on Defoliation. Trees were categorized as in a non-dense or a dense area (1 = non-dense, 2 other trees or fewer; 2 = dense, 3 other trees or more). Trees in less dense areas had significantly higher percent defoliation (P=.045).



Figure 6. Frequency of Caterpillar Tents at Different Heights on *P. serotina*. Only trees 5m or taller were included. Tents occurred significantly more frequently at heights between 2 and 2.5m. Distribution is nearly normal ( $X^2=95.7$ , df=6).



Figure 7. Survivorship Curve for Cohort 1 Based on Food Type. Day number represents day in weigh schedule. No significant difference exists between the amounts of death in each food treatment ( $X^2$ =.311, df=2)



Figure 8. Survivorship Curve for Cohort 2 Based on Food Type. Day number represents day in weigh schedule. No significant difference exists between the amounts of death in each food treatment ( $X^2$ =.052, df=2).



Figure 9. Mean Change in Weight for Caterpillars Fed Each Food Type in Cohort 1, Group 1. Calculated based on weights from last weighing period compared to first weighing period. Caterpillars in the Unfavored Black Cherry treatment grew significantly more than the others, and caterpillars in the Favored Black Cherry treatment grew significantly more than those fed Sweet Cherry (P=.042).



Figure 10. Total Change in Weight for Caterpillars Fed Each Food Type in Cohort 1, Group 2. Calculated based on weights from last weighing period compared to first weighing period. Caterpillars in the Favored Black Cherry and the Unfavored Black Cherry treatments grew significantly more than those in the Sweet Cherry treatment (P=.001).

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