The effects of parasitism and temperature on growth rates of eastern caterpillars

(*Malacosoma americanum*)

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Abstract

Malacasoma americanum, commonly known as the eastern tent caterpillar, makes tents on black cherry trees and is parasitized by flies from the family Tachinidae. Past studies have shown that increased temperature in the tents speeds up caterpillar development. In this experiment we tested the effects of parasitism and increased temperature on the growth rate of eastern tent caterpillars from Waldren's Fen in Alanson, MI. We also collected field data at the fen that examined tent isolation and tree size in relation to a tree's degree of parasitism. We found that the greater the number of tents on a tree, the more likely the tree was to have a high degree of parasitism. This is likely due to heightened scent of tents. Also, after a two-day period, caterpillars in the higher temperatures had higher mortality than those in the lower temperatures and parasitized caterpillars had lower mortality than those unparasitized at the same temperature. We attributed the latter results to a smaller mean weight of unparasitized caterpillars in our sample. However, we cannot conclude that parasitism is a deciding factor in the mortality of eastern tent caterpillars.

I. Introduction

Anyone driving on a highway in northern Michigan recently has to have wondered at the proliferation of large web-like tents covering trees on the side of the road. These structures are home to the eastern tent caterpillar (*Malacosoma americanum*), an insect found throughout the eastern half of the United States and southeastern Canada. These tiny creatures are especially conspicuous because of the tents they build on black cherry trees (*Prunus serotina*), which they also defoliate (Fitzgerald 1995). The tents, usually spun on the fork of two or more branches, protect the caterpillars from predators and regulate their body temperatures. Joos et al. (2004) found that tent interiors are 4 °C warmer than the outside air temperature. A possible explanation is that increased body temperature shortens development time by accelerating a caterpillar's metabolism, thereby reducing exposure to parasitoids and predators (Wagner 2005).

As in many other caterpillar populations, upswings in eastern tent caterpillar populations are periodic. Outbreaks, which occur every nine to twelve years, also lead to an increase in bird predation, parasitoid breeding and virulence of caterpillar pathogens. Eventually, the caterpillar population crashes as a result of these factors (Stacey 1975). The eastern tent caterpillar serves as a host for a number of species of parasitic flies and wasps; however, tachinid flies are the most predominant. These flies are often highly specialized to eastern tent caterpillars and because of this, caterpillar outbreaks are usually followed by an outbreak in fly populations (Fitzgerald 1995). Mondor and Rolen (1998) found that flies are attracted to the scent of *M. americanum* caterpillar frass, which is abundant in the tents. Alternately, Bess (1936) found that that *Leschenaultia exul*, a parasitic species of tachinid fly, oviposited when forest tent caterpillars were nearby or when presented with clipped leaves. When ready to breed, flies target tents and, depending on the species, lay eggs either on caterpillars' food sources or on the caterpillars themselves. Eggs from endoparasitoids, which oviposit on their hosts' food, hatch once they are ingested and develop inside the caterpillar. In contrast, ectoparasitoids develop outside their hosts' bodies (Fitzgerald 1995). In this study we focus on ectoparasitoids.

We expect parasitized caterpillars to have lower growth rates and higher mortality than unparasitized caterpillars, because fly eggs draw necessary nutrients from the host. We also tested the effects of temperature on caterpillar growth rates. We postulate that caterpillars kept at 26 °C will have higher growth rates and lower mortality than those kept at 21 °C, because the higher temperature mimics conditions inside of the tent and increased body temperature will result in higher metabolic rate (Wagner 2005). On a broader scale, tree characteristics and tent density may play a role in determining the degree of parasitism on trees. We expect trees with a greater number of tents to have a higher degree of parasitism, because higher concentrations of caterpillar frass will attract more flies (Mondor and Rolen 1998). We also believe that the more neighboring black cherry trees present, the higher the degree of parasitism on a tree, because flies will be better able to locate a cluster of trees. If this is the case, flies might be attracted to the smell or sight of black cherry trees in addition to caterpillar frass.

I. Materials and Methods

The caterpillars for the experiment were collected at Waldren's Fen in Alanson, MI on May 26, 2010. We took tents from ten different black cherry trees. We stored them in plastic bags, taking care to leave individual bags in the shade while collecting more tents. In the lab, we sorted the caterpillars into two groups: 100 parasitized and 100 unparasitized. We identified parasitized caterpillars by the small white eggs located on their bodies and then recorded the number of eggs on each parasitized animal. Also, we tried to choose relatively small caterpillars so that they would not metamorphose during the course of the experiment. We placed each individual caterpillar in a 9 cm petri-dish with black cherry tree leaves and filter paper hydrated with water.

We further divided the caterpillars into different temperature treatments. We stored fifty parasitized and fifty unparasitized caterpillars in an environmental chamber set at 21 °C. The remaining fifty parasitized and fifty unparasitized were kept in a second chamber set at 26 °C. We carried the experiment out for twelve days. We checked the caterpillars for food and water once a day, supplying food as necessary, and weighed and recorded any mortality on alternate days. The death rate in the warmer treatment was high, and by the fourth day of the experiment, only 22% of the caterpillars in the chamber had survived. We concluded this aspect of the experiment and moved all remaining caterpillars to the 21°C chamber. Due to a large overall loss in sample size, we also revisited the fen and collected four tents for an addition of twenty-three caterpillars total to our previously collected sample, of which, seventeen were unparasitized and six were parasitized.

We visited Waldren's Fen a third time to collect field data. We surveyed eighty trees, recording the following variables for each tree: degree of isolation, height, number of tents, DBH, degree of defoliation, and degree of parasitism. We determined the degree of isolation by counting the number of black cherry trees within a ten-meter radius of the tree. We also counted the number of other tree species within a five-meter radius of the tree. We classified defoliation on a numerical scale based on the percentage of leaves foraged: 0% to 25%, 26% to 50%, 51% to 75% or 76% to 100%. We determined the degree of parasitism based on the number of parasitized tents on a tree. If dead caterpillar skin was present on the outside of a tent, we considered the tent parasitized and recorded the number of parasitized tents per tree. We classified the degree of parasitism as high if greater than half of the tents on a tree were parasitized and low if less than half were parasitized.

We performed a Chi-square test of homogeneity to compare growth rates of parasitized and unparasitized caterpillars at 21˚C, using the initial and final weights of the individual caterpillars to calculate growth rate. We repeated the same test for the samples from the warmer treatment. We then counted the number of deaths over the course of the experiment, and used the data to construct two separate survivorship curves for parasitized and unparasitized caterpillars. We used a Chi- square test of homogeneity to analyze the frequency of dead caterpillars with regards to the difference in temperature. We divided the data into the number of dead and alive caterpillars at each time interval and temperature. In addition, we used a Mann-Whitney test to analyze tree isolation and number of tents on a tree versus the degree of parasitism. A T-test was used to analyze tree height versus degree of parasitism.

II. Results

There was a significant difference between mean mortality rates in the four treatments after the first weighing period. The mean mortality rate was 0.32 for unparasitized caterpillars in the 21°C treatments, 0.12 for parasitized caterpillars in the 21°C treatment, 0.50 for unparasitized caterpillars in the 26°C treatment and 0.48 for parasitized caterpillars in the 26°C treatment. The number of dead and alive caterpillars under each treatment after the first weighing period is shown (Figure 1). We also used survivorship curves to see trends in mortality of parasitized and unparasitized caterpillars (Figures 2 and 3).

Though there was no significant difference between mean growth rates of parasitized and unparasitized caterpillars, we observed a trend of lower growth rates of parasitized caterpillars than those unparasitized at both temperatures over the first two weighing periods (Figure 4). We also saw a trend of lower mean weights of parasitized caterpillars than unparasitized caterpillars kept at the same temperature after the first weighing period (Figure 5). After the second weighing period, mean weights of caterpillars were more uniform (Figure 6).

A Mann-Whitney test indicated a significant difference between the mean number of tents on trees with high and low degrees of parasitism. Trees with high degrees of parasitism had more tents on average(Figure 7). There was no significant relationship between the number of neighboring cherry trees a tree had and its degree of parasitism.

III. Discussion

We expected parasitized caterpillars to have higher mortality than unparasitized caterpillars; however, in the 21°C chamber, significantly more parasitized caterpillars survived after the first weighing period than unparasitized caterpillars. We observed a trend of a smaller mean weight for unparasitized caterpillars was less than the mean weight of than parasitized caterpillars in our sample. Younger or smaller caterpillars may have been less capable of handling the disturbance of the transfer from the fen to the lab. After the second weighing period, we noticed that caterpillars in different treatments had more similar mean weights because many smaller caterpillars had died by the second weighing period. Growth rates then followed the trend we expected, with parasitized caterpillars having lower growth rates than those unparasitized. However, from our results we cannot conclude that that egg parasitoids are a deciding factor in the survival of eastern tent caterpillars.

We expected caterpillars kept in the 26°C chamber to have lower mortality rates than those kept in the 21°C chamber. However, after two days, mortality rates were highest among caterpillars kept at 26°C. Past studies have shown that higher temperatures speed up caterpillar development, which suggests that caterpillars would be well adapted to warmer temperatures.

Knapp and Casey (1986) found that eastern tent caterpillars grew fastest at 30°C. The authors also found that younger caterpillars had a lower optimum temperature than later instars. Because our caterpillars were smaller, we may have exceeded their upper critical limit. Furthermore, it might not be viable for caterpillars to have as high an optimum temperature in northern Michigan as in New Jersey, where Knapp and Casey's study took place. Also, high mortality in our experiment after the first two days may have also been a result of extremely high temperatures on the day we collected the caterpillars. The high for that day was 30°C, 8°C greater than the region's average high of 22°C for May 26th (NOAA). Though we kept tents in the shade, we stored them in plastic bags without ventilation, which may have caused caterpillars to overheat.

We also found that trees with more tents were more likely to be highly parasitized. This supports the idea that tachinid flies are attracted to trees with more tents because higher concentrations of caterpillar frass are easier to smell (Mondor and Rolen 1998). We did not find a significant relationship between degree of parasitism on a tree and the number of black cherry trees surrounding it which also supports Mondor and Rolen's findings that eastern tent caterpillars parasitoids locate their hosts by their scent rather than the scent of their habitat and food source. Witter and Kulman (1979) found that parasitism of forest tent caterpillars (*Malacasoma disstria*) was most prevalent in cocoons at ground level, and decreased as cocoon height increased. This suggests that the ease at which parasitic flies choose and locate caterpillar tents is related to a variety of factors, including tent height, which we did not test, and tent density. Therefore, it is reasonable to expect that, in order to avoid tachinid flies, eastern tent moths oviposit high in trees and on trees that contain few other egg masses. To test the latter hypothesis, one could see if the number of tents per tree is higher in areas where there are historically less parasitoids than in areas where parasitoids are common.

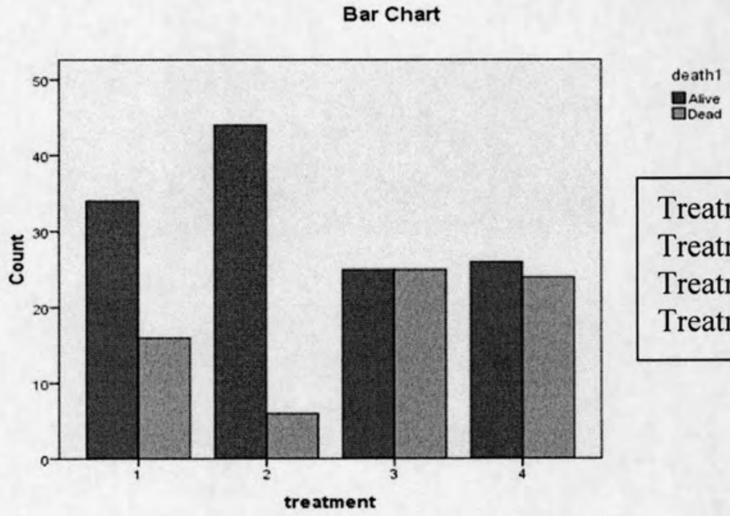
Despite differences in initial mortality rates, parasitized and unparasitized caterpillars had similar survivorship curves. Both treatments had characteristics of type II and type III survivorship. According to Schowalter (2006), insects, with the exception of the order *Drosopilia,* exhibit type III survivorship. We postulate that the reason we did not observe strictly type III survivorship in our sample because we did not follow the caterpillars from birth and only measured mortality during a twelve-day period at short time intervals. Also, because caterpillars generally exhibit type III survival, the highest mortality is usually in young caterpillars, which made up most of our sample. To improve our results, we could have collected caterpillars that were large enough to have already escaped juvenile mortality.

One unanticipated phenomenon that may have affected our results was molting by parasitized caterpillars. We observed a number of parasitized caterpillars that shed their outer chitin layer and subsequently lost the eggs on their bodies. We included these caterpillars in our data under the treatment for which they were originally classified, though the parasitoid may not yet have entered the body. This may be a caterpillar defense against the parasitism and the main reason that later instars are more affected by parasitism (Choate and Rieske 2005). As a caterpillar prepares for pupation and stops molting, the eggs remain on the body. The cost to the fly larvae of ovipositing on older caterpillars is that the egg may not be present long enough to siphon adequate amounts of nutrients from the host. For this reason, eggs ingested by the caterpillars have a higher fecundity (Stireman et al. 2006). In our experiment we assumed that caterpillars without eggs on their bodies were unparasitized; however, endoparasitic eggs are not visible and as a result, we may have counted parasitized caterpillars as unparasitized. Lastly, growth rates may not be the best measurement of caterpillar fitness for parasitized caterpillars because any nutrients lost from the caterpillar may be transferred to the parasitoid.

In this study we could not conclude that parasitoids significantly affect the mortality of eastern tent caterpillars. However, our experiment raises a number of questions. Future studies could focus on the relationship between a caterpillar's size or age and its ability to handle high temperatures and disturbance. Also, our experiment focuses primarily on parasitoid choice in tents, rather than on caterpillar defense and avoidance. Future experiments could examine where eastern tent moths lay eggs to minimize the risk of parasitism. Lastly, more research can be done on whether molting eliminates parasitoids from a caterpillar's body; if so, frequent molting might be evolutionarily advantageous for eastern tent caterpillars. There is still much to learn about the parasitic relationship between caterpillars and tachinid flies.

IV. Acknowledgements

We would like to thank Dr. Joel Heinen for his mentorship and for providing logistical guidance in the field. We would also like to thank Luke Dereske and Marshall McMunn for answering questions and helping with statistics. Lastly, we would like to thank the Waldrens for letting us use their property in this study.



Treatment 1: Unparasitized 21°C
Treatment 2: Parasitized 21°C
Treatment 3: Unparasitized 26°C
Treatment 4: Parasitized 26°C

Figure 1:Number of caterpillars dead and alive after first weighing period.
The number of dead caterpillars was significantly higher in unparasitized and parasitized treatments at 26°C than parasitized and unparasitized caterpillars at 21°C. In both temperatures the number of dead parasitized caterpillars was less than the number of unparasitized caterpillars at the same temperature. The Chi-square test of homogeneity was significant (df=3 and $p<0.000$).

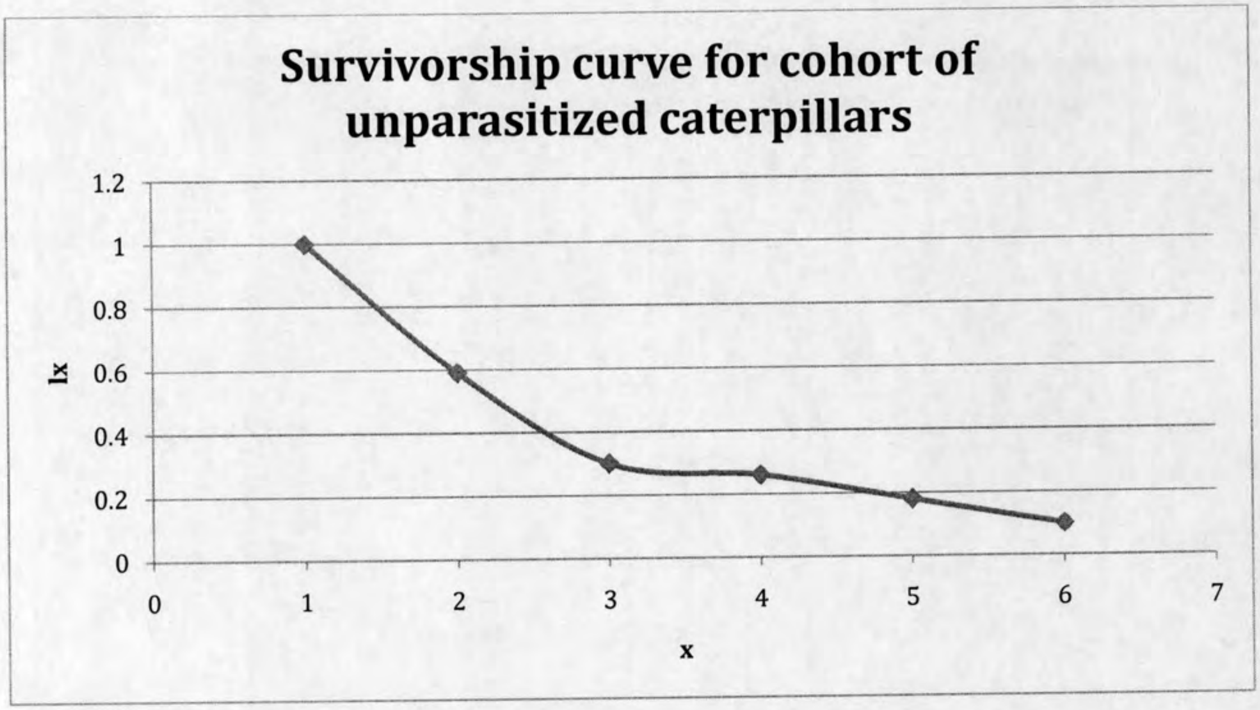


Figure 2: Survivorship curve for the cohort of unparasitized caterpillars.
The graph represents a cohort of unparasitized caterpillars over 6 time intervals.

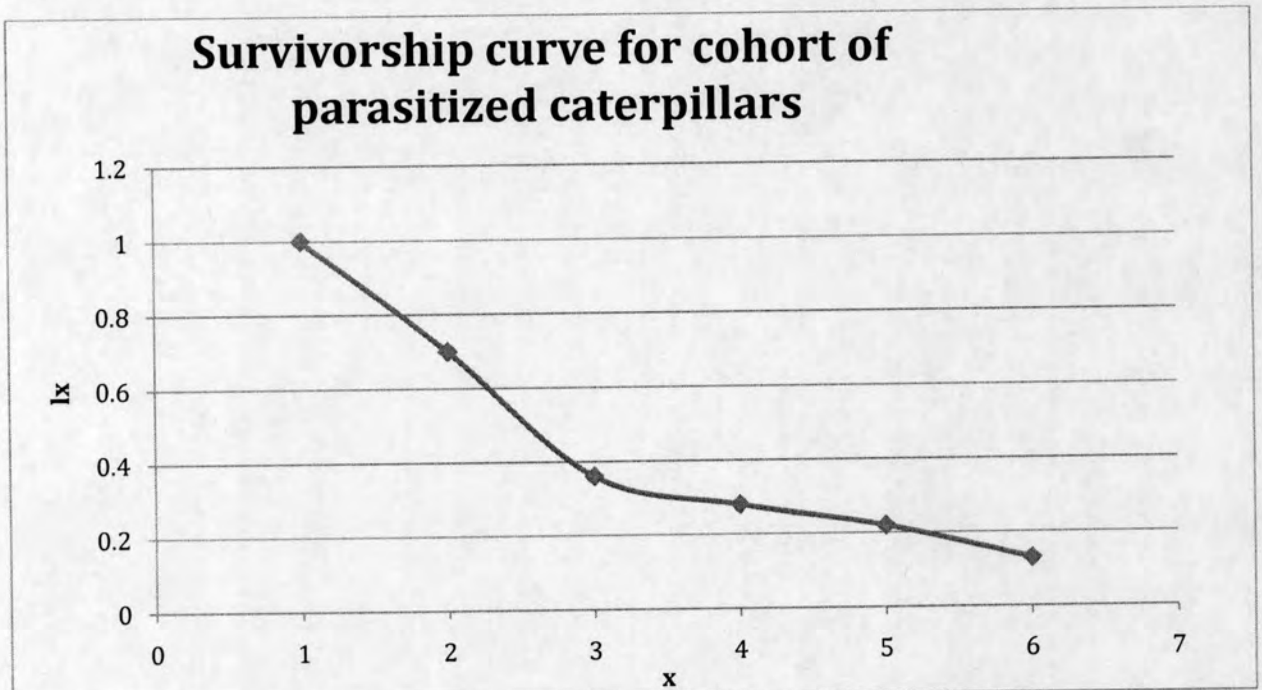


Figure 3: Survivorship curve for parasitized caterpillars.

The graph represents a cohort of parasitized caterpillars over 6 time intervals.

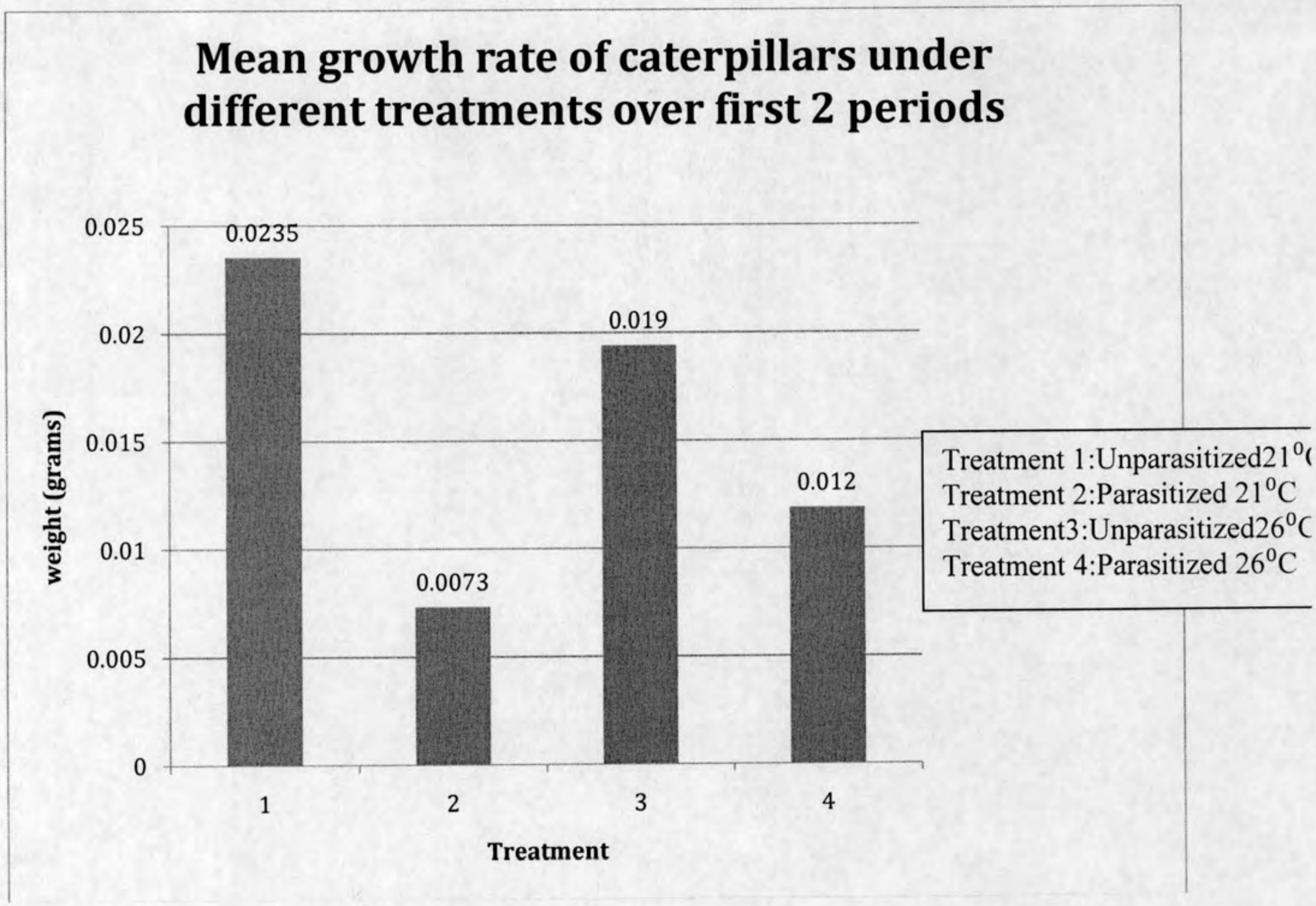


Figure 4: The mean growth rates of caterpillars under different treatments over first 2 periods.
A trend shows that the mean growth rates of caterpillars in both unparasitized treatments were higher than in the parasitized treatments after two weighing periods.

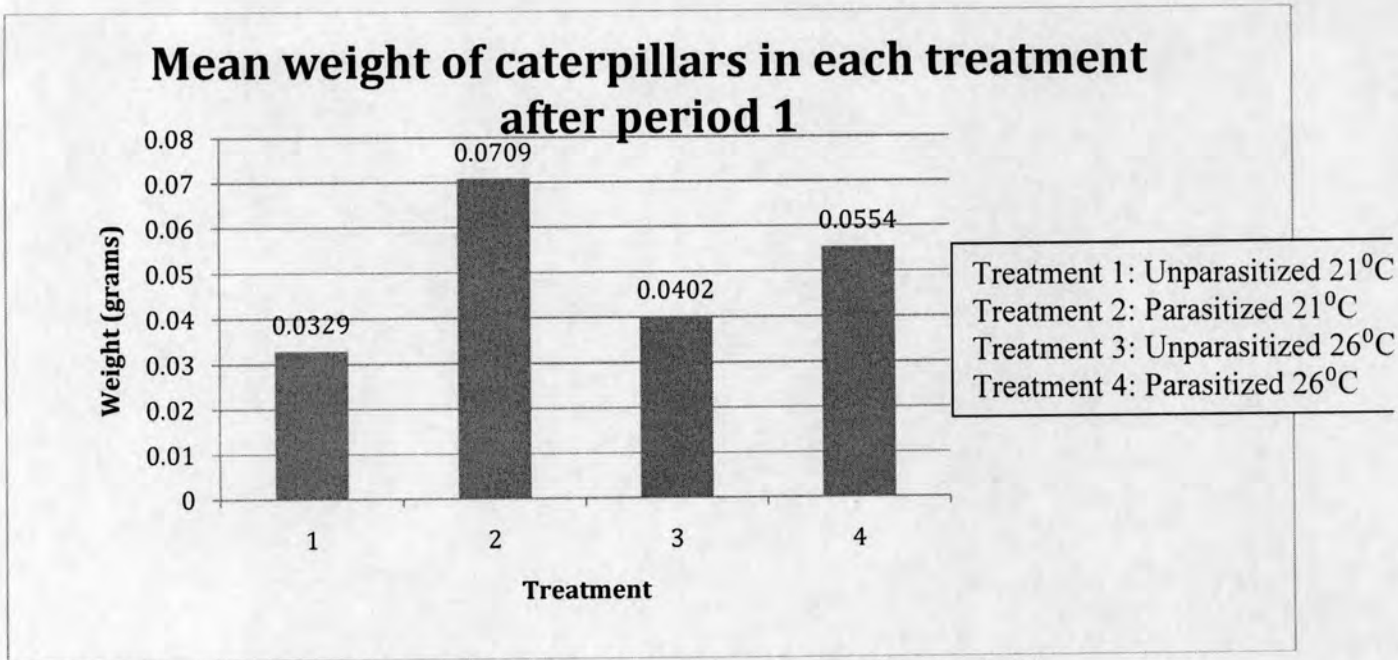


Figure 5: The average weight of caterpillars in each treatment after period 1.
A trend showed that the average weight of parasitized caterpillars in both temperature treatments was lower than the average weight of unparasitized caterpillars.

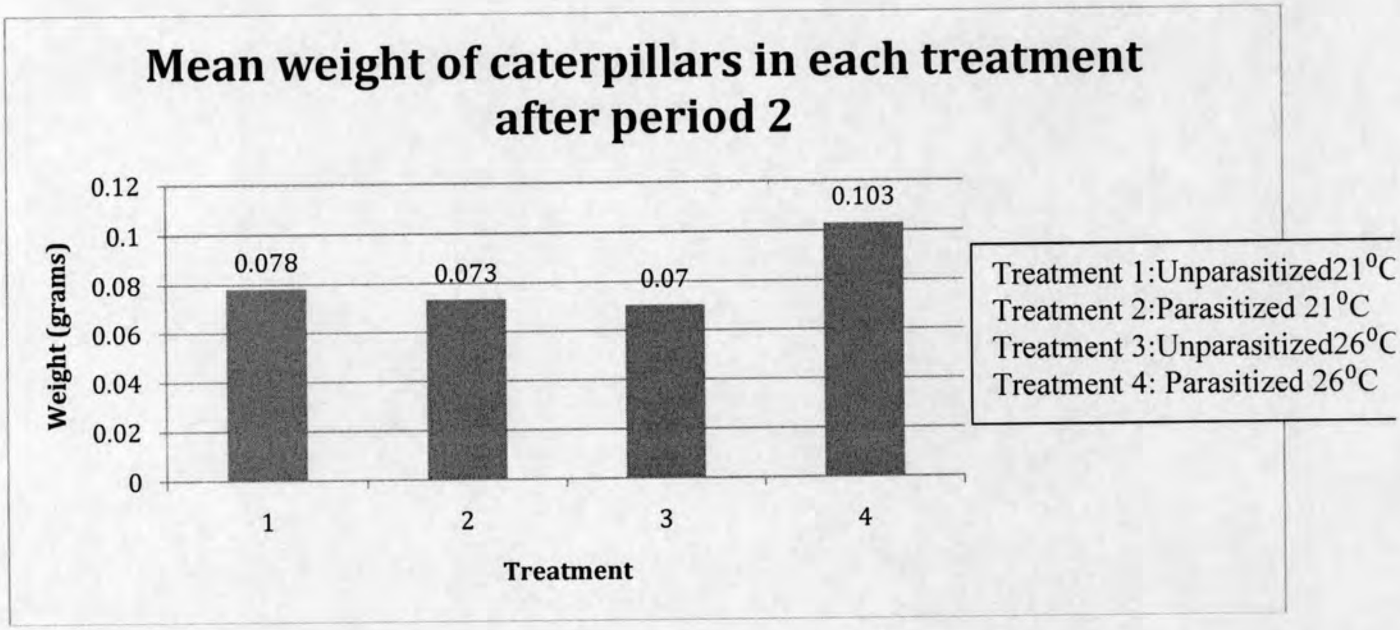


Figure 6: The average weight of caterpillars in each treatment after period 2.
A trend shows that the average weight of the caterpillars after the second weighing period was more uniform across the different treatments.

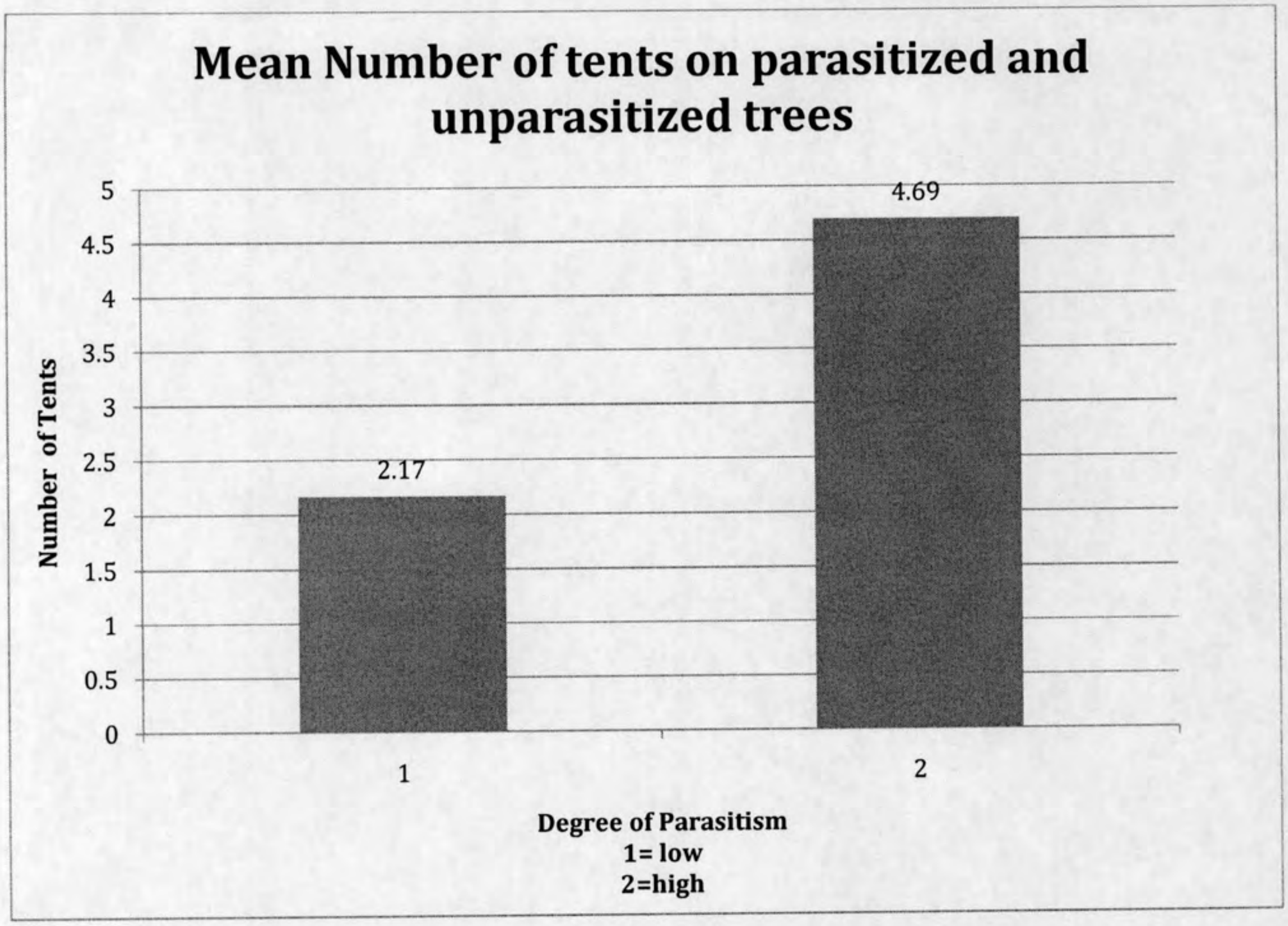


Figure 7: The mean number of tents on parasitized and unparasitized trees.

The graph shows a direct relationship between the number of tents on a tree and degree of parasitism ($p<0.000$).

References

Bess, H. A. The biology of *Leschenaultia exul* Townsend, a tachinid parasite of *Malacosoma americana* Fabricius and *Malacosoma disstria* Hubner. Annals of the Entomological Society of America 29: 593–613.

Choate, B. A., L. K. Rieske. 2005. Life History and age-specific mortality of eastern tent Caterpillars. Entomological Society of America 98:496-502.

Colasurdo, N., and E. Despland. 2005. Social Cues and Following Behavior in the Forest Tent Caterpillar. Journal of Insect Behavior 18:77-87.

Fitzgerald, T.D. *The Tent Caterpillars*. Ithaca, NY: Cornell University, 1995. 182-186, 206.

Joos, B., T. M. Casey, T. D. Fitzgerald, and W. A. Buttemer. 1988. Roles of the Tent in Behavioral Thermoregulation of Eastern Tent Caterpillars. Ecology 69:2004-2011.

Knapp, R and T. M. Casey. 1986. Thermal Ecology, Behavior, and Gowth of Gypsy Moth and Eastern Tent Caterpillars. Ecology 67:598-608.

Mondor, E. B. and J. Roland. 1998. Host Searching and Oviposition by *Leschenaultia exul*, a Tachinid Parasitoid of the Forest Tent Caterpillar, *Malacosoma disstria*. Journal of Insect Behavior 11:583-592

National Oceanic and Atmospheric Administration. Web. 17 June 2010. <http://www.noaa.gov>.

Schowalter, T. D. *Insect Ecology: An Ecosystem Approach*. Burlington, MA: Elsevier, 2006. 140.

Stacey, L., R. Roe, and K. Williams. 1975. Mortality of Eggs and Pharate Larvae of the Eastern Tent Caterpillar, Malacosoma americana (F.) (Lepidoptera: Lasiocampidae*)*. Journal of the Kansas Entomological Society 48:521-523.

Stireman, J. O., J. E. O'Hara, and D. M. Wood. 2006. Tachinidae: Evolution, Behavior, and

Ecology. Annual Review of Entomology 51:525-555.

Wagner, D.L. *Caterpillars of Eastern North America: A Guide to identification and natural history.* Princeton, NJ: Princeton University Press, 2005. 206.

Witter, J.A. and H.M. Kulman. 1979. The Parasite Complex of the Forest Tent Caterpillar in Northern Minnesota. Environmental Entomology 4: 723 – 731.