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NYS DEC Forest Tent Caterpillar Defoliator Report 2005

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This report focuses on forest tent caterpillar, though gypsy moth information is frequently included. The following sections are covered:

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1. Forest Tent Caterpillar Life Stages

Forest Tent Caterpillar (*Malacosoma disstria* Hübner) is a <u>native</u> insect found in hardwood forests throughout North America and is especially abundant in eastern North America. Their preferred food tree hosts vary by region. In New York they prefer to eat sugar maple, aspen,



cherry, apple, oaks, birch, ash, alder, elm and basswood. They never eat red maple, sycamore & conifers. The active part of the life cycle occurs from early spring to July, the rest of the year is spent overwintering in the egg stage (Table 1). A brief review of the life stages is provided below, for a more in-depth life stage overview see Appendix 1.

Table 1. Forest tent cate	rpillar life stages						
Life stage	Length of time per individual	dividual Time of year					
Larva (Caterpillar)	\sim 5-6 weeks	Early spring – June					
Pupa (Cocoon)	\sim 3 weeks	June					
Adult (Moth)	$\sim 5 \text{ days}$	July					
Egg (Egg mass)	~ 10 months	July - early spring					

Table 1. Forest tent caterpillar life stages

The larvae hatch near the time of host tree bud break and feed through May & June for 5-6 weeks. They will first feed on growing flower and leaf buds in the host tree crown and will next feed on foliage, usually one branch at a time. They are gregarious in early instars and use silk to form a trail. They will rest and molt on silken mats; they do not form tents! The fifth instars are responsible for most of the defoliation and will often move to new and distant locations.

The pupal stage occurs in June when larvae form solitary cocoons of pale yellow silk in folded leaves or protected areas. They are not host specific about which leaves they use; red maple leaves are often used in outbreak situations as the leaves were not defoliated. It takes 24 hours for a caterpillar to construct their cocoon; the adults emerge about 3 weeks later.



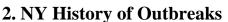
Moths emerge in July and individuals will live roughly 5 days; the adult stage lasts approximately 2 weeks. Their main purpose is to mate, locate hosts and lay eggs. They are strongly attracted to light and do not eat or drink during this time. Females secrete a pheromone within ½ hour of emergence and males will use odor and visual cues to find the females. After mating, the female will oviposit all her eggs in one batch; thus the size of egg mass can be correlated with size of female.



The egg masses are covered with spumaline, a lacquer-like substance, and are deposited on small twigs <8mm (average is 5-8mm) of host trees (sugar maple, aspen, oak, cherry) in July. Within three weeks the embryos develop to fully

formed pharate larvae and will overwinter in

this stage. Most egg masses are deposited in upper $\frac{1}{3}$ or $\frac{1}{4}$ of tree crown though during outbreak conditions they may also be laid in the understory. An average size egg mass is $\frac{1}{2}$ -inch long and contains about 150 eggs per egg mass.

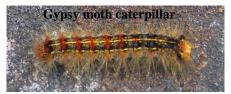




Outbreaks of forest tent caterpillars (FTC) are episodic and typically last 3 years in northern populations, though they may last from 2-9 years (Fitzgerald 1995). In New York State, outbreaks of varying severity tend to occur at 10 year intervals (Hodson 1941). Heavy defoliation will rarely occur for more than two or three years at a given site (Allen 1994). Prior known outbreaks in New York occurred in 1887, 1896-1901, 1923-24, 1935-1940 (Hodson 1941), 1951-1955, 1980-1982, 1991-1993 (Allen, personal conversation). The 1951-1955 outbreak in northern NY, which peaked three years later in 1954, began with 110,000 acres and ultimately damaged more than 15 million acres (Connola et al. 1957). The current forest tent caterpillar outbreak began in St. Lawrence county in 2002 (See figure 1 –aerial defoliation polygons) and areas which have experienced two to three years of heavy defoliation should soon be experiencing a decrease in FTC population numbers.

The first Gypsy Moth (GM) outbreak occurred in New York between 1953 and 1957. Caterpillar numbers and defoliation levels are highest during the initial infestation of this non-native insect.

Once they become "naturalized" outbreaks alternate between few to many years with little defoliation followed by 2-4 years of visible defoliation. Heavy defoliation typically lasts no more than 2 years. Prior known outbreaks in New York occurred in 1959, 1969, 1971-73, 1980's and 1990's (peaking



between 1989-91). From the 90s to date gypsy moth populations have generally subsided and when defoliation does occur it is restricted to relatively small areas; such as the oak type in the Catskill region, the Thousand Islands, and the vicinity of Lake George. It may be that gypsy moth population numbers are currently reaching outbreak levels in some of these areas of NY.

3. Effects of Defoliation

Light defoliation (<30%) has little effect on tree health. Moderate defoliation (31-50%) causes loss of foliage but little mortality is expected. Heavy defoliation (>50%) may cause tree mortality to hemlock, pine and spruce, whereas deciduous trees can usually withstand one year of defoliation. Trees that are defoliated early in the season often flush a new, smaller set of leaves in July (Dodds and Seybold 2005). Defoliated trees have decreased wood production, decreased food storage, and may have less photosynthetic area due to branch dieback (Gregory and Wargo 1986 and references therein). Defoliation of susceptible trees can result in reduced

tree growth and vigor, which in combination with other stress factors (e.g. drought) and secondary organisms (i.e. disease organisms, insects) can result in tree mortality (Fleischer et al. 1992). According to Johnson and Lyon (1991), large and seriously injurious populations of the two-lined chestnut borer (*Agrilus bilineatus*), a pest of *Quercus, Castanea*, and sometimes *Fagus* species, almost always follow outbreaks of defoliators. If a tree is weakened (i.e. by defoliation) and supports *A. bilineatus* for 2-3 years in succession, gradual death of the tree occurs from the top down.



Forest tent caterpillar typically does not cause mortality to host trees, though mortality can occur when concurrent with other disturbances (i.e. drought or insect outbreaks) (Dodds and Seybold 2005). During an outbreak in northern NY in the early 1950's repeated defoliation resulted in dieback of twigs and branches and, in many cases, death of trees (Connola et al. 1957). Sugar maple tree sap flow and sugar content may decrease in the year following defoliation. A report from The North American Maple Project in 1997 stated that "sugar maple trees in areas defoliated by forest tent caterpillar for 1-3 consecutive years, and areas experiencing drought conditions for 2 years, had significantly thinner crowns, but normal foliage returned after 1-2 years. In these types of situations, where trees were exposed to a stress agent for a short duration, tree recovery is expected to be good."

Oaks suffer from gypsy moth attack more than other species. Sustained multiple year defoliation may result in tree decline or mortality (Johnson and Lyon 1991, Witter et al. 1992) and weakened trees are vulnerable to attack by disease organisms, such as *Armillaria*, and insects, such as the two-lined chestnut borer (McManus et al. 1989). Conifers will die after one year of complete defoliation (Johnson and Lyon 1991).

4. Natural Factors Contributing to Outbreak Collapse

Environmental conditions as well as natural predators help regulate forest tent caterpillar populations after only a few years (Dodds and Seybold 2005). Parasites are often abundant in FTC populations which likely accounts for the cyclic nature of outbreaks (Johnson and Lyon 1991). Pupal parasitoids appear to have a greater effect on population numbers than egg or larval parasitoids (Fitzgerald 1995). The main factors contributing to or causing collapse of FTC outbreaks are low spring temperatures, adverse weather conditions, disease/pathogens (i.e. Nuclear Polyhedrosis Virus (NPV) and *Entomopthera* fungi), pupal parasitoids, and starvation of larva (Fitzgerald 1995). See Appendix 2 for more in-depth information.

The factors contributing to the collapse of Gypsy Moth outbreaks are similar to that of forest tent caterpillars and include: low spring temperatures, adverse weather conditions, starvation of larva, disease/pathogens (such as Nuclear Polyhedrosis Virus (NPV) and *Entomophaga maimaiga* fungus), and predation by insects, birds and mammals.

5. Management/Control Options for Forest Tent Caterpillar

- 1. Do nothing as trees usually survive defoliation (Dodds and Seybold 2005).
- 2. Mechanical options: place barriers on trees, remove egg masses before they hatch, and remove larvae when they are congregated (Dodds and Seybold 2005).
- 3. Formulations based on the bacterium *Bacillus thuringiensis (B.t.)* can be used to protect weakened trees or to cover large areas where populations have remained high for consecutive years (Dodds and Seybold 2005). It is not a contact insecticide and needs to be swallowed to be effective. Bt is registered for use against FTC and is commonly used to suppress small infestations (Fitzgerald 1995). Cost of aerial spraying Bt costs about \$25 per acre and is most effective when sprayed in the springtime when caterpillars are still small.

6. Harvesting Recommendations

We recommend delaying timber harvests in defoliated areas for two or three years after an outbreak to minimize additional stress on trees. Time will also allow you to see which trees remain healthy and alter harvesting plans if necessary. If forest tent caterpillar numbers have not been high locally but there is a statewide outbreak, be flexible when scheduling timber sales, so harvesting can be postponed if populations build in your area. Historically, outbreaks last 1-3 years in one region, but 2-9 years statewide, as new regions are defoliated.

Vermont Department of Forests, Parks & Recreation surveyed for forest tent defoliation effects on sugar maples in 2004. They found heavier defoliation present where sugar maples were exposed to light: sugarbushes, recently thinned stands, and roadsides.

Harvesting your stands during an outbreak can do the following:

- Cause the outbreak to last longer, as parasites of the forest tent caterpillar are more successful in closed stands (i.e. parasites will not help to manage forest tent populations as well in your recently thinned stand).
- > Create a situation where there are fewer trees for about the same number of caterpillars, thus concentrating the associated defoliation on the remaining trees.
- Damage and/or further stress the remaining already defoliation-stressed trees. It is not a good idea to add unnecessary stressors to a forest stand as trees usually die from multiple causal agents.

- > Give root rot fungi many new stumps to spread from, with stressed trees nearby.
- > Temporarily provide you with some positive cash flow. However this may leave poor trees to act as parent trees and ultimately can affect your long-term investment .

Nutrient-rich sites may allow for more management flexibility. Following a forest tent caterpillar outbreak in Pennsylvania, trees growing on nutrient-rich soils were found to be more tolerant of defoliation. In Vermont, starch tested in the roots of defoliated maples during the fall, showed there was plenty of starch in most trees that had been leafless all summer if they were growing on good sites; this was not necessarily the case for trees on shallow or nutrient-poor sites. Sites in Pennsylvania with lower levels of calcium and magnesium, usually those with acidic soils, had more sugar maple decline and mortality. This was also the case after Vermont's last outbreak, when most of the maple decline occurred in the more acidic Green Mountain biophysical regions.

7. Egg Mass Sampling Protocol

In the past couple of years, defoliators have come again to the public eye and questions have been asked as to how to predict defoliator population numbers and defoliation for future years. There was no current NYSDEC protocol for egg mass sampling so sampling protocols were created for forest tent caterpillars and gypsy moths in order that a survey could be conducted in fall 2005 to predict 2006 populations and defoliation levels for NY.



The 2005 NYSDEC forest tent caterpillar egg mass sampling protocol is based on methodology from the Field Protocol for Sampling Forest Tent Caterpillar Egg Masses in NY (Allen 1994) and the methodology and sequential sampling tables from The

Development of a Sequential Sampling Plan for Forest Tent Caterpillar in New York (Connola et al. 1957) which studied a 1951-1955 forest tent caterpillar outbreak in northern NY. Additional survey procedures were added to reduce survey technician bias in choosing the trees to sample and the direction to walk to additional plots. Further clarification, from personal experiences of technicians and other studies, was added to the protocol methodology as well. Other studies reviewed provided good background sample method information but did not provide relevant sequential sampling tables for New York as they were designed for Vermont (Walker and Waters 1954. Kelley, R.S. 2004) or based on a study in Alberta, Canada (Shepherd and Brown 1971).

In future surveys, decreasing the binocular multiplier from a 4 to a 2 may want to be considered as numbers seem to be similar when using binoculars and spotting scopes. Perhaps egg masses missed when using binoculars are compensated for as old egg masses may be counted as new.

The 2005 NYSDEC gypsy moth egg mass sampling protocol was based largely on the following two USDA forest service publications: Sequential Sampling Plans for Estimating Gyspy Moth Egg Mass Density (Fleischer et al. 1992) and Gypsy Moth Egg Mass Sampling for Decision Making: a User's Guide (Leibhold et al. 1994). As with the forest tent caterpillar protocol, additional survey procedures were added to reduce survey technician bias in choosing the trees to sample and the direction to walk to additional plots; further clarification, from personal experiences of technicians and other studies, was added to the protocol methodology as well.

8. Defoliator Educational Materials

The following documents have been created and/or compiled to provide background information (i.e. defoliator life history, host trees, control) and methodology for sampling egg masses. Paper and electronic copies are available for interested persons.

Forest Tent Caterpillar

- 1. **Field Protocol** for Sampling Forest Tent Caterpillar Egg Masses. Includes data sheets and necessary sampling tables.
- 2. Forest Tent Caterpillar **Training Presentation** (PowerPoint) with FTC background information and the egg mass survey protocol description.
- 3. Forest Tent Caterpillar Additional Information (PDF versions) of the following:
 - a. Forest Tent Caterpillar Pest Alert- USDA Forest Service
 - b. Forest Tent Caterpillar Insect & Disease Leaflet 9- USDA Forest Service
 - c. Tent Caterpillars Information Sheet- H.C. Miller & D.C. Allen

Gypsy Moth

- 1. **Field Protocol** for Sampling Gypsy Moth Egg Masses. Includes data sheets and necessary sampling tables.
- 2. Gypsy Moth **Training Presentation** (PowerPoint) with gypsy moth background information and the egg mass survey protocol description.
- 3. Gypsy Moth Additional Information (PDF versions) of the following:
 - a. Gypsy Moth Pest Alert- USDA Forest Service
 - b. Gypsy Moth Insect & Disease Leaflet 162- USDA Forest Service
 - c. Gyspy moth egg mass sampling for decision making: a user's guide- Liebhold et al. 1994
 - d. Sequential sampling plans for estimating gypsy moth egg mass density-Fleischer et al. 1992

9. Trainings for NYSDEC regional offices

Forest Tent Caterpillar and/or Gypsy Moth Information and Egg Mass Sampling Trainings were offered to regions 3, 4, 5, 6, and 7 for forestry staff, consulting foresters and private landowners. These trainings had multiple functions; to provide information and training to attendees, to supply offices with handouts/electronic forms for people who request forest tent caterpillar and/or gypsy moth information, and to encourage staff to survey within their regions, especially those areas where spraying is being considered. Trainings consisted of a 1 hour PowerPoint presentation and a field component for practicing viewing egg masses and survey methodology. Training folders were handed out with relevant background information, survey protocols, data sheets, and necessary survey tables. Three trainings were requested. Region 3 New Paltz received a Gypsy Moth training, Region 5 Stamford and Region 6 Potsdam received a Forest Tent Caterpillar Training. Approximately 60 people were trained (30 DEC staff, 15 consulting foresters, 15 private landowners). Attendees were requested to email or mail any surveys done to NYSDEC Forest Health and Protection so that their data could be added to defoliation prediction maps for New York.

10. Choosing Sample Sites for 2005 FTC Egg Mass Survey

Forest tent caterpillar sample sites were chosen from within areas that met the following criteria: on state land, forest type containing a sugar maple component, aerial and ground survey polygons (including a 500 foot buffer) of observed defoliation noted during 2002-2005, and between 100 feet and one-half mile from a road. Additionally included were areas submitted by regional foresters as places that were hit heavily this past year or that were being considered for spraying. A 50 acre grid was placed over areas that met the above criteria and one site plot was randomly placed within each 50 acre area. Order of sampling priority was as follows: 3 years of prior defoliation, 2 years of prior defoliation, 1 year of defoliation in 2005, 1 year defoliation in 2004.

Gypsy moth sample sites were chosen more informally. Field technicians were given maps showing aerial and ground survey polygons of observed defoliation noted during 2002-2005, state land boundaries and forest type containing a major oak component. They were told to choose sites that met all three criteria.

11. Field Crews

3 field crews, of 2 people each, were hired to conduct 8 weeks of forest tent caterpillar egg mass sampling from October 24-December 16. Training for forest tent caterpillar egg mass surveys occurred in Potsdam October 18-21. Actual field days were considerably less due to holidays and inadequate sampling weather. Sampling cannot occur on rainy, snowy, extremely windy days or under low light conditions. Each field crew worked out of a different office in northern NY, and was responsible for the sites in that area. Matthew Manning and Will McGee worked out of the Potsdam office, Tom Colarusso and Ryan Houghton worked out of the Raybrook office, and Naja Kraus and Jason Hiller worked out of the Warrensburg office. All three field crews with the addition of Jason Denham and Jerry Carlson spent one week surveying sites in the Catskills.

To survey for gypsy moth egg masses, two technician positions were extended from the summer forest health crews. Training for gypsy moth egg mass surveys occurred at the Saratoga Tree

Nursery on September 8th. A one week survey for gypsy moth egg masses was done by Tom Colarusso in Region 5 and Matt Manning in Region 6. Both technicians sampled in the Catskill region for one week as well. Of the 17 sites surveyed, none predicted defoliation for 2006. The low number of sites and locations surveyed keep this from being a good prediction of gypsy moth defoliation for 2006. There are a number of areas reported by private landowners and regional foresters in Regions 3 & 4 that contained very high number of egg masses that were not surveyed by NYSDEC field technicians. During forest tent caterpillar surveys, high numbers of gypsy moth egg masses were noted if present.



gypsy moth egg masses

12. Egg Mass Surveying & Predicted Defoliation

159 sites were surveyed for forest tent caterpillar egg masses between October 24 and December 14 in regions 3, 4, 5, 6 & 7 (Figure 1). Although 202 sites were originally visited, some sites were unable to be sampled: 27 sites had inadequate levels of sugar maple, 12 sites were surrounded by or on private land, and 4 sites were inaccessible. Defoliation from FTC was predicted for 2006 on 111 of the sites surveyed, and 48 sites predicted no FTC defoliation (Table 1). Ten of the sites surveyed for FTC noted gypsy moth egg masses present at the site (4 of

which also predicted defoliation for FTC). These survey sites paint a broad picture of what New York State forests can expect next year in regard to FTC defoliation (Figure 1) if weather and parasites do not cause significant egg or larval mortality. If you want to have a better picture of what to expect at a smaller scale (i.e. your woodlot, specific state land area) additional survey plots will need to be done. It is recommended that for areas larger than 100 acres, 1 plot per 50 acres should be sampled; as you consider smaller scales additional plots are needed (i.e. <10 acres, 2 sites per 5 acres).

All FTC sites surveyed in Northwestern NY (i.e. St. Lawrence County) and in the northern Catskill region predicted noticeable defoliation for next year. The northeastern portion of the Adirondacks mostly predicted NO defoliation for next year. The southeastern Adirondacks and adjoining area as well as the southern Catskills show a patchier outcome. Even if 2006 noticeable defoliation was predicted for a site, this does not mean that heavy (e.g., 60% or more) defoliation will definitely occur as weather and parasites may cause significant egg and larval mortality before defoliation occurs. Other factors to consider that will also influence actual defoliation and may temper egg mass survey predictions are: level of defoliation (heavy defoliation usually does not occur for more than 3 years at a given site), extent of defoliation in adjacent areas (if adjacent areas are heavily defoliated it may spread to nearby areas), and size of egg masses (small egg masses may indicate decreasing population). For sites where defoliation is predicted and heavy defoliation has occurred for the past three years the cycle may be nearing an end.

NYSDEC Region		Defoliation edicted	FTC Defoliation Predicted		No Sugar Maple	Private Property or No	Number of Sites Surveyed
		GM present		GM present	Present	Access	Surveyed
3	2	5	12	4	2		25
4	0		15			2	17
5	40	1	20		25	14	98
6	0		51				51
7	0		9				9
Total # of sites	42	6	107	4	27	16	202

Table 2. Number of sites, by region, predicting forest tent caterpillar (FTC) defoliation.

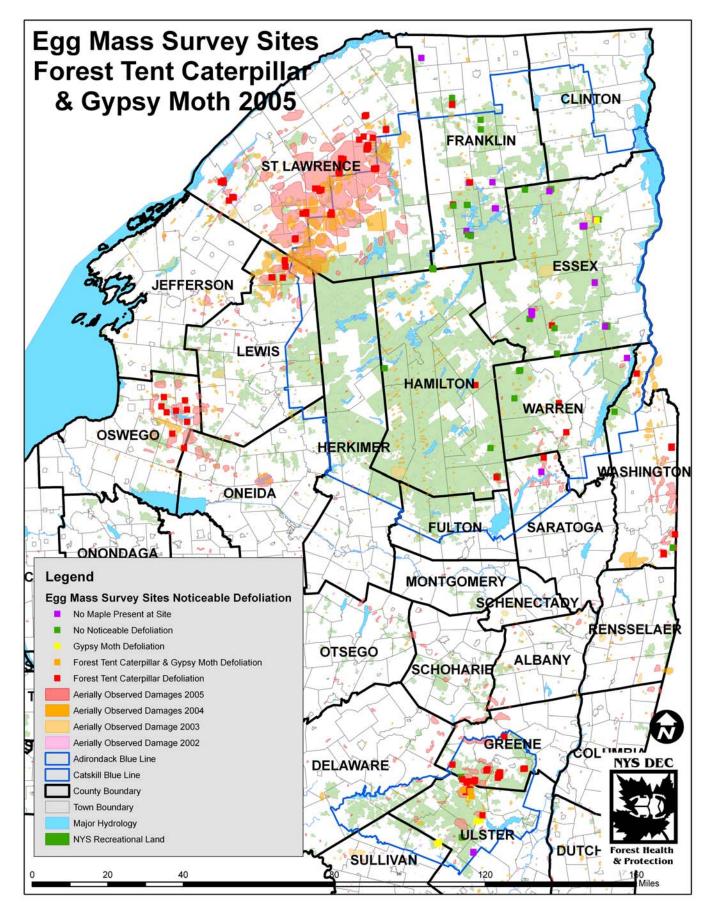


Figure 1. Aerial defoliation polygons and predicted 2006 defoliation from Forest Tent Caterpillar Egg Mass Surveys in 2005.

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Appendix. 1. Forest Tent Caterpillar Description/Life History

There is one generation per year. Larvae do not construct tents!

Eggs (July-spring, ~ 10 months)

Dark compact, cylindrical egg masses, 25-37 mm wide, with square ends (Eastern tent caterpillars have spindle shaped egg masses), covered with spumaline (varnish-like substance), are deposited in July around small twigs, of host trees, hatch in the spring (Dodds and Seybold 2005, Shepherd and Brown 1971) and are often concentrated on trees near well-lit urban areas (Dodds and Seybold 2005). A greater proportion of egg masses are deposited in the middle and upper crowns of trees (Batzer et al. 1995). In a study by Cooke and Roland (2003) they found that current year egg masses had substantial spumaline and older egg masses did not. In a study in Minnesota from 1936-38 almost all egg bands oviposited on dead twigs remained for three years, those on smaller twigs persisted from one to three years, and those deposited on succulent, growing terminals were nearly all gone by the end of the first summer (Hodson 1941).

The egg masses may contain up to 350 eggs (Dodds and Seybold 2005), though average number of eggs per mass is lower: 121 to 228 in central Canada in 1952-53 (Blais et al. 1955), 97 to 200 - average ~150 in MN (Hodson 1941), 46 to 368 in MN & MI (Batzer et al. 1995) and 170 eggs was considered normal during outbreak in northern NY in the early 1950's (Connola et al. 1957). Within about three weeks of oviposition the embryos develop to fully formed pharate larvae within the eggs; morphological development is arrested while larvae undergo an obligatory diapause throughout autumn and winter (Fitzgerald 1995, Shepherd and Brown 1971); i.e. overwinter as a fully developed embryo inside the egg shell (Johnson and Lyon).

Larvae – five instars (early spring-June, ~5-6 weeks)

Larvae hatch near budbreak in the spring and feed through May and June. Larvae feed on new foliage on host trees, if they emerge a few days before budbreak they may face starvation, if they emerge late they struggle with decreasing foliar quality as the season progresses, low temperatures can cause mortality as well (Blais et al. 1955, Parry et al. 1998, Raske 1975).

Newly hatched larvae are 3 mm in length, black and have noticeable hairs. As larvae grow and become more brownish in color, pale bluish lines form along the margins of the larvae and white spots (often described as keyholes or footprints) form along the back (Eastern tent caterpillar have a white stripe down their back). Full-grown larvae are about 50 mm in length.

After they hatch they tend to migrate to the tops of the trees to feed on growing flower and leaf buds. Next, FTC feed on foliage, concentrating on one branch at a time. Larval feeding is usually completed in 5 or 6 weeks (Ives 1973). A study in Minnesota found that the feeding capacity of an individual FTC is about 8 ½ aspen leaves, most of which are eaten during the later instars (Hodson 1941). During the early instars they are gregarious, use silk to form a trail, and form silken mats, on a tree trunk, branch, or leaves where they will gather, rest and molt (ETC reside in elaborate silken tents in branch forks) (Johnson and Lyon, Fitzgerald 1995, Shepherd and Brown 1971). During the fourth instar the caterpillars will feed more independently but still gather when resting or molting. Fifth instar larvae may travel many yards to search for food (Hodson 1941) and are responsible for most of the defoliation (Fitzgerald 1995, Parry et al. 1998). FTC are the only tent caterpillars to use a nomadic foraging strategy and will often move to new and distant locations even after only partially defoliating a feeding site (Fitzgerald 1995).

Pupa (June, ~ 3 weeks)

In June larvae pupate in solitary cocoons spun from pale yellow silk (ETC cocoons are white) in folded leaves or protected areas (Dodds and Seybold 2005) and adults emerge a few weeks later. Caterpillars take about 24 hours to construct a cocoon, once completed they remain inactive in the prepupal stage for 2 days, and as pupae for 8 to 12 days (Hodson 1941).

Adults (July, ~5 days) As a community the adult stage may last 2 weeks

Adult moths are about 40 mm long, light brown with two narrow dark bands/stripes on the forewings (ETC are reddish brown with two white stripes) and have a wingspan between 25-28 mm. Adults emerge in July (ETC emerge in late June/early July), locate hosts, mate and lay eggs. The moths are strongly attracted to light (Dodds and Seybold 2005).

Flight and mating activities begin in late afternoon and continue through the night (Johnson and Lyon), though they are not active for long after sunset in the northern part of their range (Fitzgerald 1995). The female moths secrete a sex pheromone within the first half-hour of emergence; the males use the odor and visual cues (drawn to cocoons and brown objects resembling moths) to find the females.

After mating, the females fly to a different location (a study by Hodson (1941) found they were attracted to light 2 to 3 miles from known infestations) and oviposit all of their eggs in one batch completely encircling a branch ("helical" masses); the size of the egg mass is positively correlated with the mass of the female. Female fecundity can be determined by egg masses, as each mass contains all the eggs produced by the female that laid it (Batzer et al. 1995).

Appendix 2. Natural Factors Contributing to Forest Tent Caterpillar Outbreak Collapse

- Although tolerant to cold, FTC are susceptible to freezing by extreme cold; -41.8° F is cited commonly as the mid-winter cold tolerance threshold of FTC eggs, in addition this threshold changes with the insect's seasonal biology and mortality varies seasonally with changes in temperature and physiology (Hanec 1966, Wetzel et al. 1973). Wetzel et. al. (1973) found cold temperatures 1 to 4 days before hatch caused mortality of pharate larvae; temperatures of 14° F caused low mortality, -4° F caused moderate mortality and -22°F caused high mortality. Newly hatched larvae, in eastern Manitoba, had low survival rates below 30.2° F and above 59° F (Hanec 1966).
- Low spring temperatures can cause larval mortality through starvation, as development of larvae may not be synchronized with that of host leaves (Fitzgerald 1995), e.g. host foliage may be killed, bud development delayed, or low temperatures cause prolonged immobilization of larvae before they feed so that leaves develop faster than larvae and thus when the temperatures are high enough for the larvae to try and eat the leaves are too tough for them (Blais et al. 1955, Hanec 1966).
- > High temperatures during the period of mating and oviposition may decrease female fecundity and high temperatures during the following three weeks may interfere with embryonic development (Hodson 1941).
- Larvae are preyed upon by ants (1st to 4th instar) (Green and Sullivan 1950) spiders, beetles, pentatomids (stink bugs), birds, parasitized by many species of wasps and tachinid flies, nematodes, microsporidians, and act as hosts to Dipteran parisitoids (Fitzgerald 1995).
- Parasites include Sarcophaga aldrichi Parker (superficially resembles a large housefly) that can be so abundant that it is almost as much of a nuisance as the caterpillar (Johnson and Lyon 1991). The adult fly oviposits on the cocoon of a FTC and the maggot burrows into the pupa reducing the FTC pupa to a liquefied mass upon which the maggot feeds. The population of the fly increases during successive years of outbreaks and is often very abundant in the year preceding a FTC collapse (Fitzgerald 1995).
- Nuclear polyhedrosis virus (NPV) also occurs in nature and can reduce FTC populations (Johnson and Lyon 1991). NPV is spread through caterpillar to caterpillar interactions and also carried over into following generations. Larvae that are infected early enough are completely overrun by the pathogen, the body contents turn into a liquid mass of viruses that will spill from dead larvae when the cuticle ruptures (Fitzgerald 1995). On tree boles one can often see these FTC, which look like melted, stretched out, empty caterpillars.
- Fungi in the genus *Entomopthera* are also pathogens of the FTC (Johnson and Lyon 1991). FTC typically disperse in the fifth instar and come into contact on the ground with the fungal conidia while moving from one tree to another. Germ tubes, produced by germinating spores, penetrate the FTC and the mycelium grows to eventually fill the body cavity. Once the FTC is infected through contacting the conidia, it typically dies four to five days after. After death of the FTC, the hyphae emerge and the mycelium will grow over the outside of the caterpillar, eventually covering it with a light to dark brown, crustose coating. The disease can now also be spread from the conidia on the dead caterpillar to other caterpillars and Sarcophagid flies also help to spread the conidia (Fitzgerald 1995).
- > Adult moths are occasionally eaten by sapsuckers (Johnson and Lyon 1991). Many species of birds, of which the cuckoo is the most important predator, have been observed eating FTC larvae; some eat only the FTC insides, (Fitzgerald 1995).