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Fluctuation in tent caterpillar abundance and some of the factors influencing it.

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FLUCTUATION IN TENT CATERPILLAR ABUNDANCE AND SOME OF THE FACTORS INFLUENCING IT

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William E. Tomlinson, Jr.

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Contents

Purpose of Investigation

Alternate periods of abundance and scarcity, known as cycles, are of common occurrence in nature among numerous species of animals. No phylum of animals is more rich in examples of this phenomenon than the insects. We are all familiar with the grasshopper outbreaks of the middle west, which occur from time to time. Within recent years interest has grown considerably in the study of these cycles and their causes.

The cyclic nature of insect abundance is only partially understood. Tent caterpillars, *Malacosoma americana* Fabricius and *Malacosoma disstria* Hübner, were chosen for this study because they are now near the peak of abundance in this region and are probably better known than most of the other species that exhibit cyclic phenomena. Some other insect, however, such as the fall webworm, *Hyphantria cunea* Drury, could have been used perhaps as advantageously to illustrate cycles of insect abundance, but at present it is at the bottom of its cycle.

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There have been many guesses and a few studies of the cyclic nature of tent caterpillars, yet little of it is conclusive. Is it due to predators, parasites, disease, or weather, or all four?

This is a report of an investigation concerning the causes of these cycles of tent caterpillars through an analysis of the available literature, and observation and experiment on their eggs and larvae.

From a more practical standpoint there is the economic importance of these insects to be considered. If a weak spot can be found in their life history by this study, it may perhaps aid us in lengthening the time between rises in abundance of these insects even if not making it possible to eradicate the entire cycle. Finally an understanding of this phenomenon is important if for no other reason than to clear up much of the guesswork centering around it.

General Importance.

From time to time tent caterpillars become very abundant, doing considerable damage to fruit, shade, and forest trees in the United States and Canada. These cycles of abundance appear to follow a rather definite course, the peak occurring about every ten or twelve years. The peak lasts usually from two to four years, then subsides for several years, only to reappear about ten years later.

It is only natural that these caterpillars which cause such widespread defoliation of our forests and orchards should have received considerable attention even from the earliest days. A very small proportion of this literature deals with the cyclic phenomena, however, most of it being concerned with control and abundance during certain years.

Species to be Considered and Distribution.

The two insects to be studied in this paper are the eastern tent caterpillar - *Malacosoma americana* Fabricius, and the forest tent caterpillar - *Malacosoma disstria* Hübner. These two species are the only members of this genus in the eastern part of the United States where this study was carried out.

Both of these insects are native to the North American continent and are distributed over most of the United States and Canada where their food plants occur (Fig. 1). The host plants of *M. americana* Fabricius are chiefly wild cherry and apple (Britton, 1935.) *M. disstria* Hübner is a more general feeder, feeding on most deciduous forest and fruit trees, though it does show a preference for maple, oak, poplar, willow, and apple (Felt, 1905; Tothill, 1923).

Taxonomic Relationships.

The tent caterpillars belong to a small family of moths, the Lasiocampidae. The genus *Malacosoma* Hübner

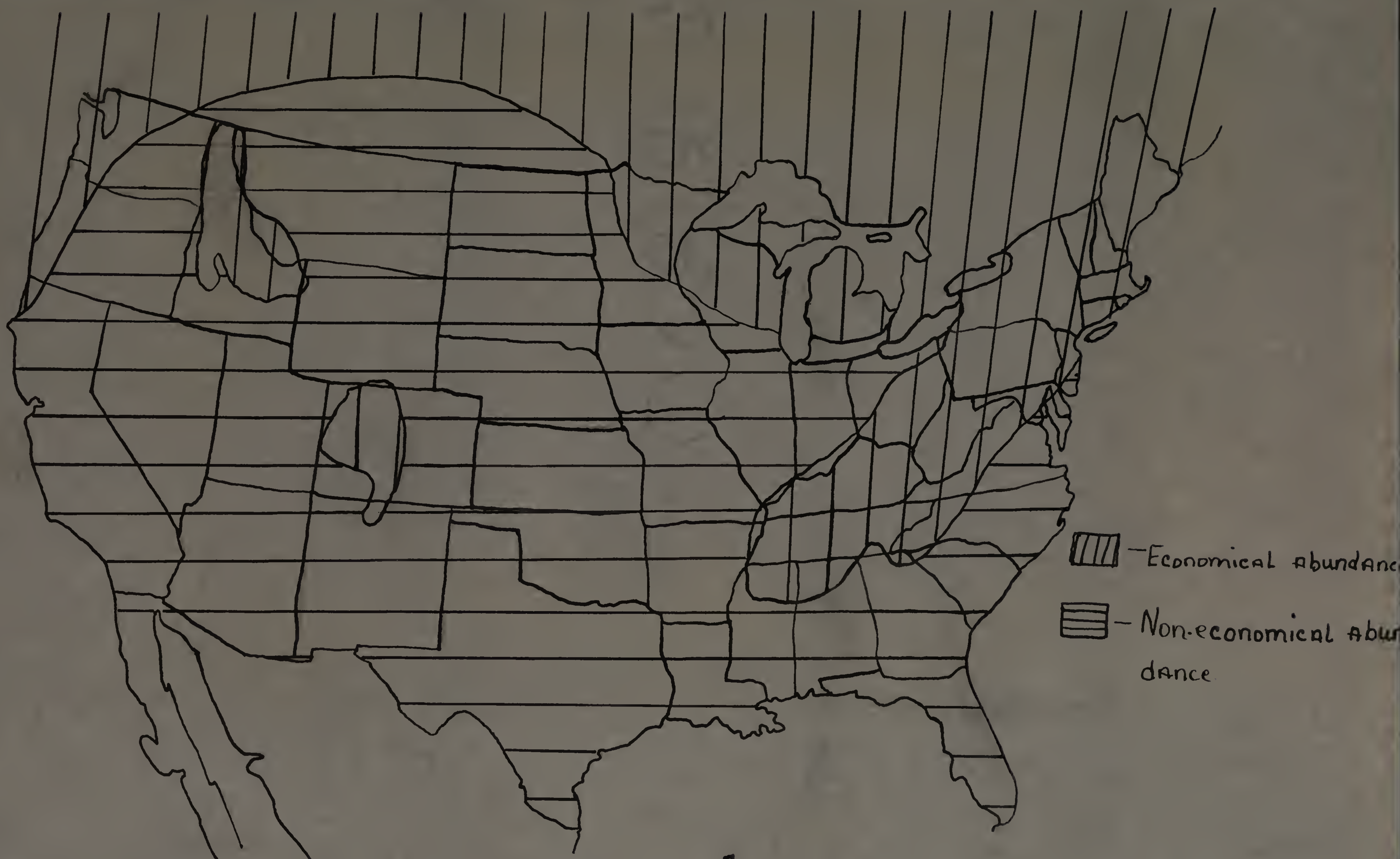

Figure 1

Distribution of Tent Caterpillars in
United States and Canada

is the largest and most important economically of the seven North American genera (Dyar, 1902). The two species *M. americana* Fabricius and *M. disstria* Hübner are the most widespread, the other species being limited mainly to the Pacific Coast area where they occasionally do considerable damage to fruit, shade, and forest trees in a cyclic nature similar to the two species discussed in this paper.

The synonomy is as follows (Dyar, 1902):

Malacosoma Hübner

Synonym: *Clisiocampa* Harris

Malacosoma americana Fabricius

Synonyms: *decipiens* Walker

frutetorum Boisduval

Malacosoma disstria Hübner

Synonyms: *drupacearum* Boisduval

sylvatica Harris

thoracicoides Neumogen and Dyar

sylvaticoides Neumogen and Dyar

peversa Neumogen and Dyar

thoracica Stretch

Life Cycles of Species.

The life cycles of both of these species are practically the same. They both have but one generation a year throughout their range. They overwinter as larvae in the egg masses, appearing in the early spring about the time leaves appear on their host trees. Here they feed for a month or more, pupating in the latter part of June and early July. The adults are short lived, the females living only long enough to copulate and lay their eggs. The egg masses contain 200-300 eggs and are laid in more or less regular cylindrical masses near the ends of twigs or small branches of the host trees where they are near food when they emerge from the eggs the following spring (Lowe, 1899). The length of time spent in each stage is: egg - 10 months, larva - 1½ months, pupa - 10 days to 2 weeks, adult - 4 to 5 days.

Analysis of Literature

Forest tent caterpillar (Fig. 2).

The first authentic report of the forest tent caterpillar was made by Smith and Abbot in 1797 in Virginia. In 1791 there was an outbreak of an insect in Vermont that was probably this same species (Baird, 1917).

There is no record of this insect again until 1820 by Harris in Massachusetts in his Entomological Correspondence. This appears to indicate that the insect was common if not abundant at that time, and had not been especially troublesome before that for several years. Harris again mentions the forest tent caterpillar in his Treatise on Insects in 1841, and in 1844 states that it was abundant at Kennebec in Maine (Harris, 1841, 1844).

According to "Acer" in the Country Gentleman the in-

Figure 2

Tent Caterpillar Cycles since 1790

sect has appeared three times in the past thirty years or about 1830, 1844 and 1855. The first date corresponds to the report in Harris' Entomoligical Correspondence of July 3, 1826. The second date corresponds to an account by Harris in 1844, while the third date corresponds with that of Fitch, 1855, of New York, and with Eaton in New Hampshire in 1854-55 (Baird, 1917).

From the foregoing it may be inferred that this insect has had cycles of abundance at least as far back as 1791. Records are infrequent, but any mention of them in early papers indicates that the insect, when mentioned at all, was more prevalent that usual.

The next outbreak that occurred was fairly general over the eastern United States and Canada as far west as Missouri, and since records are more abundant it is easier to follow this outbreak which occurred between 1866-1870. Walsh notes it in Maine in 1866 and in Virginia and New York the following year. Riley says that the forest tent caterpillar was destructive in the eastern states in 1867-1868. Again he reports it from western New York, and Missouri, the following year (1869). In 1872 Saunders says "we have not met with a single full grown specimen this year though they have swarmed on our trees and fences in the years past." The only notice of its abundance that year was near Memphis, Tennessee (Riley, 1872).

The following outbreak, only four years after the preceding one, began in 1874 and extended through 1878. Fernald reports "very serious ravages in Maine during the past two years." By 1880 it had almost completely disappeared (Baird, 1917).

The next outbreak, first noted in 1883 and 1884 in Illinois and several other states, may have been the forerunner of the more widespread outbreak that followed in the next few years between 1886 and 1889. In 1886 it was attracting attention in orchards in Vermont and in 1887 the outbreak had spread practically over its entire range (Baird, 1917). Riley and Howard (1889) say that they were so abundant in Maine on railroad tracks that trains were held up on several occasions for two or three hours at a time by innumerable caterpillars crossing the tracks. By 1890 this outbreak had subsided, for Bethune states that "the forest tent caterpillars have been remarkable for their absence or rarity in all parts of Ontario."

Local outbreaks were recorded in Maine and New York in 1890 and in Carolina in 1891 (Riley and Howard, 1891). It also was abundant in Nebraska and Minnesota in 1890 and 1891, but all of these were sporadic, probably being left from the last general outbreak (Baird, 1917).

The insect is noted in 1895 in Vermont where it had begun to attract attention again (Perkins, 1900). By 1897 we find frequent mention of the insect over the entire eastern United States and Canada. It appeared in great abundance extending even as far west at Minnesota, Nebraska, Saskatchewan, and Alberta. The outbreak in the east subsided in 1901, while the outbreak in the mid-west did not decline until about 1905 (Baird, 1917).

The forest tent caterpillar again became numerous all over the East beginning in 1910 and extending to 1915, in which year it was markedly on the decline. This outbreak seems to have been worse in Canada than in the eastern United States, and did not spread to western Canada as did the 1897 outbreak (Baird, 1917).

The next outbreak was first noted in the West, being reported in Alberta by Hewitt (1920) in 1917 and 1918. This same outbreak was noteworthy in the midwestern United States for it did enormous damage in Minnesota, North Dakota, and Idaho in 1921 and 1922 (Ruggles, 1921; Evendon, 1922; Webster, 1922). In the latter year the insect again reappeared in outbreak proportions in the east, where it was reported to be extremely abundant by Peirson (1922) in Northern Maine. In 1923 it was in outbreak proportions in Maine, Vermont, New Brunswick, Nova Scotia and Ontario, and in more that usual numbers in Massachusetts, Connecticut, New York, and New Jersey, though not in outbreak proportions in these latter places. In 1924 it was again abundant in the east, but had subsided in 1925. It continued in the west until 1926, subsiding finally in

1927 (I. P. S., Vols. 3-7, 1923-1927). In 1927 it was abundant in one area only in the East, North Carolina (I. P. S., Vol. 7, 1927).

In 1928 it was again abundant in Canada from British Columbia eastward to New Brunswick, but especially so in Alberta and Saskatchewan, subsiding finally in 1930. The same year it was becoming abundant in Minnesota and in one isolated spot in Virginia (I. P. S., Vol.10, 1930).

The beginning of a new outbreak was reported from Hancock County, Maine, in 1931 by Peirson and in the same year one of the worst outbreaks on record in Virginia was reported (I. P. S., Vol.11, 1931). In 1932 the Maine outbreak covered considerably more territory, causing complete defoliation of poplar and white birch. Again in 1933 the caterpillar did severe damage in Maine. The same year the Virginia outbreak continued severe and the insect was reported in Pennsylvania. By 1934 the outbreak area included Maine, New Hampshire and eastern Canada where conspicuous defoliation took place. Reports during the same year show their increase in Minnesota, Mississippi and Wisconsin, so that Felt (1934) stated that these restricted outbreaks may be the forerunner of a general outbreak. This prediction was borne out the following year (1935) for the insect was universally abundant from New England westward to Minnesota, as well as in eastern Canada. It also did extensive damage in Louisiana and Mississippi. Again in 1936 "unprecedented outbreaks" occurred throughout New England, New York and extending northward over Michigan into Minnesota. At the same time in Canada extensive defoliation is noted from the Maritime provinces, Quebec, north and northwest Ontario, and in Saskatchewan and local areas in Manitoba and Alberta (I. P. S., Vols. 11 to 16, 1931-1936).

The abundance of the insect continued almost undiminished in 1937 over the same areas as in 1936, though a slight decline was generally noted. It was on the increase in North Carolina. Thus our most recent outbreak began in 1934, and may be expected to continue for another year or two unless controlling factors come into effect (I. P. S., Vols. 16 to 18, 1936, 1937, 1938).

The Eastern Tent Caterpillar.

One of the first insects discussed in the entomological literature of the United States was the eastern tent caterpillar, *Malacosoma americana* Fabricius. In 1646, 1649 and 1658 it was reported as a serious pest on fruit trees in Massachusetts. Such years of abundance were known as "caterpillar years" by the early settlers, attesting to the cyclic nature of this insect even then (Britton, 1935). The next report of this insect was in 1796 by Peck in Massachusetts, and by Smith and Abbot in Georgia in 1797 (Harris, 1842). Neither of these reports, however, mention abundance, though that is the probable reason the species received notice by these authors. The eastern tent caterpillar was noted as abundant by Harris in 1826 at Framingham, Massachusetts. Beginning with this report by Harris there have been fairly continuous reports of its appearing and disappearing at quite regular intervals to the present day; a period of 112 years of continuous record (Fig. 2).

Harris discussed the eastern tent caterpillar in his Treatise on Insects in 1841, stating that they "have been abundant in years past." In 1843 Gaylord stated that they were extremely abundant in New York. In 1855 and 1856 Asa Fitch said that he "had not known them to be as abundant for 25 years in New York."

Ten years later, in 1865, Warder reported the caterpillar as rare in Ohio, implying that it had been abundant at some previous date. It was noted as abundant in Missouri in 1866, and in Kentucky between 1864 and 1867 by Walsh (1868). Hartwell (1870) mentions that it was scarce in Massachusetts in 1869 or 1870, implying that it had been abundant at some previous date in that region. Cook (1875) reported it as abundant in Michigan in 1873, while Saunders (1876) states that it was not abundant in Ontario in 1875 but had been in years past. This is probably the end of the outbreak noted in Michigan by Cook (1875). In 1877 they were abundant in Illinois according to Thomas (1878), while they were conspicuous by their absence in Ontario according to Saunders (1878).

The first serious and general outbreak of M. americana Fabricius was noted by Lintner (1889) in New York in 1888 when he stated that "there is no record of its having appeared before in such enormous numbers over as extended a territory." The records of this outbreak, which began in 1888, are a little more extensive than those for any of the preceding outbreaks when it was noted as very destructive in Massachusetts by Fernald (1893), in Vermont by Perkins (1888), and in New York by Lintner (1888). This outbreak had completely subsided by 1892 (Fernald, 1893).

The eastern tent caterpillar again attained outbreak proportions in 1897. It was noticed to be on the increase in Vermont (Perkins, 1899) and Ontario (Bethune, 1897) in 1896 but was not unusually abundant at any place. From 1897 through 1899, however, it was extremely abundant all over the northeastern United States and Canada, where it did considerable damage to fruit trees (Felt, 1898). By 1900 it was on the decrease and was almost lacking in 1901 and 1902, except in scattered areas in Delaware, Michigan, Maryland, Connecticut, Rhode Island, and parts of New York (Chittenden, 1903; Felt, 1903).

Between 1903 and 1911 there are almost no records of its being abundant except in scattered points in Virginia, Maryland, Delaware, and Ohio (Anon., 1905). About 1909 the eastern tent caterpillar was definitely on the increase in the northeast and by 1912 was again in outbreak proportions in that area (Lochhead, 1909; Felt, 1913). By 1916 the outbreak was on the wane and by 1917 had almost completely subsided except in very limited areas (Felt, 1916; Caesar, 1917).

Between 1923 and 1927 another outbreak covered most of northeastern America as far south as Maryland and as far west as Illinois, probably being as extensive, if not more so, than any outbreak previously recorded in the literature (I. P. S., Vols. 3-7, 1923-1927).

From 1928-1930 a period of general relative scarcity prevailed in the north, though the insect was more than usually abundant in Virginia southward to South Carolina (I. P. S., Vols. 8-10, 1928-1930).

In 1931 and 1932 it was again becoming fairly numerous in Maine, and by 1933 and 1934 was in outbreak proportions once again over the whole of eastern North America as far south as South Carolina, through Kentucky and Tennessee. It was on the decrease in 1936 and 1937 and, though still abundant in many areas, it seemed to be definitely less serious than a few years previous (I. P. S., Vols. 11-18, 1931-1938).

Coincidence of the Outbreaks of both Species.

There is a marked coincidence in the outbreaks of both of these species since 1897. Beginning with that outbreak they have become abundant and subsided at almost exactly the same period each time since then, implying common limiting factors.

That they appeared and subsided together before that time seems more than probable. Preceding 1897 there is a scarcity of exact records. Both species were often confused with one another. Even though there is an increase in the number of records in the literature beginning with Harris about 1820, these are still too few for complete confidence until around 1890 when there was a great increase in interest in entomology, especially pest control.

According to Peirson (1927) the forest tent caterpillar is not necessarily sporadic over an entire region, but may start in a small area within a large poplar stand, and each year spread out further until the entire stand is infested. In this manner we have an isolated outbreak. When numerous areas subject to similar conditions attain outbreak proportions at the same time we have a general outbreak over a whole region, such as has been experienced around 1900, 1912, 1922 and 1935.

But what makes this condition come about? According to Uvarov (1931) an organism is not kept in stable equilibrium by its natural enemies and quantity of food alone. "No one will deny the controlling value of these factors, but the key to the problem of balance in nature is to be looked for in the influence of climatic factors on living organisms. These factors (climatic) cause a regular elimination of an enormous percentage of individuals under so-called normal conditions, which in fact are such that insects survive them not because they are perfectly adapted to them, but only owing to their often fantastically high reproductive abilities. Any temporary deviations in the climatic factors, however slight they may be, affect the percentage of survival, either directly or indirectly, and thus influence abundance."

Tothill (1920, 1923) believes that these outbreaks are due to absence of parasites and relaxing of the food pressure. Pure stands of poplar which are becoming more and more plentiful are ideal breeding grounds for the caterpillars. Therefore distribution of parasites and planting of mixed conifers in burnt areas would help materially in extending the periods between outbreaks, though he states that this would not entirely eliminate them.

The literature has frequent references to the controlling effect of parasites on these two species, yet very little confidence can be placed in these claims. The few workers that have gone into this phase by actually rearing parasites from larvae and pupae in no case record over 28 per cent parasitism, which is far from sufficient to hold the insects in check (Tothill, 1923). Fiske (1903) says that a very reasonable estimate of parasitism of M. americana Fabricius larvae and pupae would be from 15 to 20 per cent, year in and year out.

Tothill (1923) claims that a Rogas sp. is an important factor in keeping the forest tent caterpillar in equilibrium, although Schaffner and Griswold (1934) do not mention this species as a parasite of M. disstria over a fifteen year period, and only a .96 percent parasitism of M. americana in the same time by it.

In the same paper Tothill (1923) passes lightly over the effect of spring weather on the caterpillars. That the spring weather might be one of the important limiting factors was not noted by him. Because of killing of the caterpillars "by spring frost" Rogas sp. was unable to reproduce and was reduced to a low ebb. However, even at the peak of its parasitism, 28 per cent according to his figures, it was far from sufficient to act as a check without other factors or parasites aiding.

According to records compiled by Schaffner and Griswold (1934) over a period of fifteen years on the larval and pupal parasites of both of the tent caterpillars, none of the species of parasites averaged over 15 per cent for the whole fifteen years. The highest possible parasitism from their figures for any of the fifteen years is 50 per cent for M. disstria Hübner and 45 per cent for M. americana Fabricius. Thus the total parasitism of eggs, larvae and pupae at the greatest would be in the vicinity of 57 per cent only for M. disstria and about 53 per cent for *M. americana*. These percentages were derived from Schaffner and Griswold (1934) and study of egg parasitism during 1938. That parasitism is generally much lower is indicated by Fiske (1903). Thus a more conservative estimate of *M. americana* parasitism is in the vicinity of 25-30 per cent and possibly slightly higher for *M. disstria*.

The key to this problem appears to be in the physical environment rather than in the action of parasites, as so many authors have stated. Parasitism undoubtedly plays its part, but the total effect is gained through multiple factors working together.

Weather varies considerably from year to year, season to season, and even from day to day and from place to place. The analysis of the effect of weather is difficult for this reason. There seems to be a correlation between abundance and yearly rainfall, but to check this in many places is impossible due to lack of records on the weather or on actual distribution of the caterpillars during the outbreak. Even though an outbreak is recorded, the occurrence of insects is usually scattered. They may be abundant in one place and a short distance away, under outwardly similar conditions, be almost entirely lacking and for reasons which give no clue.

We do have a few definite records of the effect of temperature as a controlling agent of both tent caterpillars. Blackman (1918) records the almost complete extermination of M. americana at Syracuse, New York, in 1917 due to adverse weather conditions. There caterpillars hatched during the last week in April in a week of warm weather. The following five weeks were unusually cold and wet so that the leaves of wild cherry did not develop, and when the nests were examined at the end of this period they were found to be filled with first instar larvae that had died of starvation or effects of cold.

A similar instance is noted by Tothill (1923) with M. disstria in New Brunswick. In the spring of 1915, April was unusually warm over all of eastern North America; thus the eggs hatched. During May, on the other hand, it was cool with frequent frosts; thus the insects probably starved or were gradually weakened until death resulted.

Methods and Equipment

During the winter and spring months of 1937 and 1938 several hundred egg masses of M. americana Fabricius were collected in Massachusetts in order to rear parasites from the eggs. Late in March, 1938, about 150 egg masses of M. disstria Hübner were collected at Walpole, New Hampshire; Grafton, Vermont; and Amherst, Massachusetts, for the same purpose.

Rearing cages consisted of gallon battery jars with window glass for covers, and pint "Ball" preserve jars. Egg masses were kept at constant humidities of 75 per cent (saturated sodium chloride solution) and 100 per cent (tap water). These humidities were maintained by placing the saturated salt solution or tap water in wide mouthed bottles (2 inches high by 2½ inches wide). These bottles were then covered with fine mesh cloth to prevent entry of insects. The bottles and solution were placed on the bottom of the battery or preserve jars. The resulting rearing cage was held at the required humidity by placing a cover on it to keep the moisture from escaping.

While rearing parasites the temperature was allowed to fluctuate with the temperature of the laboratory or greenhouse. The experiments with the effect of cold on developing larvae were carried on under greenhouse temperatures, during warm intervals when they fed, and under controlled cold temperatures in the cold storage plant during cold exposures, when they failed to feed. The temperature of the cool periods varied from 32° to 38° F. for periods of varying length.

Nests of M. americana Fabricius were placed in pint preserve jars, sealed, and placed in the cold room. The nests were disturbed as little as possible to avoid injury to the larvae within. At the end of the desired period the larvae were brought into the greenhouse and allowed to feed on wild cherry and apple leaves, then returned to cold storage after the required feeding time.

Natural Parasitism of Eggs

The percentage of natural parasitism of the eggs was determined by gathering egg masses in the early spring at various places in Massachusetts, New Hampshire, and Vermont. This was done to obtain a representative cross-section of conditions in different regions. Eggs. of *M. americana* Fabricius were collected from numerous cities and towns in central and eastern Massachusetts, and of *M. disstria* Hübner from Walpole, New Hampshire; Grafton, Vermont; and Amherst, Massachusetts.

These were placed in battery jars with a humidity of 100 per cent. The caterpillars were allowed to hatch in these jars in the greenhouse. When hatching was complete the egg masses were transferred to preserve jars and left there until the emergence of parasites was complete.

The parasites were then counted, and percentage of parasitism calculated taking the average number of eggs per mass of *M. americana* Fabricius as 275 (Lowe, 1899, Perkins, 1901, et al). The number of eggs per mass of *M. disstria* Hübner was 220 (Peirson, 1927; Schaffner, 1936; Swaine, 1918).

Parasitism of *M. americana* Fabricius was as follows:

Locality	No. of masses	Percentage of parasitism
Waltham, Mass	12	8.65
Amherst, Mass.	11	6.08
Hubbardston, Mass.	26	2.57
Acton, Mass.	23	2.91
Littleton, Mass.	9	2.32
Lunenberg, Mass.	11	2.66
Ipswich, Mass.	27	1.37
Gloucester, Mass.	21	7.50
Danvers, Mass.	15	2.72
Lynnfield, Mass.	18	4.19
Total - - -	173	Average - 4.09

Parasitism of M. disstria Hübner was as follows:

Locality	No. of masses	Percentage of parasitism
Walpole, New Hampshire	44	1.322
Grafton, Vermont	57	0.488
Amherst, Mass.	4	0.113
Total - - -	105	Average - 0.641

Action of Winter Predators

During the winter and spring months more than 400 egg masses of both species of tent caterpillars were collected or observed in various sections of Massachusetts, Vermont, and New Hampshire. An effort was made to determine if any of the eggs had been disturbed in any manner by birds or other animals. In no case was it observed that predators had materially reduced the number of eggs per mass. In many cases the masses and their cover were intact when collected. On numerous other masses this frothy material had been removed in some manner, but in almost no instances were the egg masses broken into or eggs removed. The covering was probably removed through rubbing against an adjacent twig, rather than by predators.

Effects of Various Exposures on Eggs

Several egg masses were found and observed at several places in Amherst in various sites during the fall and winter months. This was done to find if different exposure, such as distance from the ground, north and south slopes, bottom land or hill top, affected survival.

Six masses on top of a hill were exposed to the wind on all sides, as well as to the heating effects of the sun's rays. Hatching was normal in this location.

Twelve egg masses on an eastern slope, sheltered from the north but exposed from other directions, were observed. Hatching was normal.

Hatching was normal on five masses on a western exposure, sheltered from the south, east and north.

Hatching at all of these sites was on approximately the same days, beginning about the first week in April, which is unusually early for Amherst.

No egg masses were observed close to the ground where the snow might cover them, so that the effect of snow and ice covering masses could not be observed in nature. At Newton, Massachusetts, however, about twenty-five masses were placed on the ground in a shady spot for storage and were covered with snow and ice for a period of two weeks. These same masses were allowed to hatch later in the spring and hatching was apparently normal in every respect.

Effects of Various Artificial Exposures on Larvae

A duplication of what might happen in nature was attempted. Several tents of the eastern tent caterpillar were alternated between cold room temperatures of 32° - 38° F. and natural feeding conditions in the Fernald Hall outer greenhouse which is unheated. The combinations and results of exposure were as follows:

Days in cold exposure	Days in warm exposure	Survival	
		Days	Per cent
1	1	24	15
1	3	"	20
3	1	"	50
3	7	"	75
4	4	"	15

Weeks in cold exposure	Per cent Survival
1	95
2	65
3	0
4	0
5	0

Three nests were used for each set of exposures except in the four and five week exposures where only two were used. The latter four masses were collected on April 20 on or near the college campus. Most of the larvae were in the second instar. The other 24 masses were collected on or near the campus also, but on April 26. Most of the larvae were in the second instar, though a few were already in the third instar.

The one day exposures to cold temperature were the most detrimental to the larvae. There was a slight difference only between those that were allowed to feed one day and those allowed to feed three days.

The three day warm exposures were slightly more favorable, size increase and survival being slightly greater. The four day exposures to cold were the least favorable of all. Larvae from one nest were dead at the end of eight days, while those from the second survived only twelve. Those in the last nest, though weakened, were not completely killed and were able to grow and to feed.

All of the three day cold exposures, whether one day out or seven, were more favorable than the one or four day exposures to cold. There was a difference between the one and seven day warm exposure, however. None of the larvae in the nests were completely killed, but a greater mortality was noted among the nests exposed to the warmth one day only. Their size increase was much slower also.

In the second series of experiments quite definite results were obtained with different periods of cold exposure. Larvae exposed to cold for one week only showed no apparent ill effects after being placed on trees and allowed to feed and to construct a new nest. The two week exposures were definitely less favorable to the larvae although the per cent of survival was still quite great. Two of the colonies were able to construct a new nest on the tree, while in the third nest there were only a few survivors which were unable to do so and soon died. Colonies exposed to the cold for three weeks or longer were not able to survive in any instance; all of the larvae were dead when removed from cold storage.

Economic Abundance.

The economic abundance of both species of tent caterpillars is limited by their preferred food plants. *M. americana* Fabricius prefers wild cherry and apple and does not become abundant in their absence, though it may feed on other trees such as peach, plum, and prune during periods of abundance (Britton, 1935). The distribution of wild cherry, according to Gray's Manual, is from Georgia westward and northwards.

M. disstria Hübner, although a more general feeder, has rather definite host preferences and seldom attains outbreak proportions where its food plants are scarce or do not grow. Sugar maple, quaking aspen, large toothed aspen, yellow birch, and white oak are preferred to all other trees (Tothill, 1923; Felt, 1905). It is for this reason that outbreaks are limited almost entirely to the natural vegetation areas known as the "northeastern hardwoods" where these host plants are naturally abundant, and to the "spruce - fir" and "northeastern pine forest" where extensive cutting and burning have caused almost pure stands of poplar and yellow birch to replace the natural forest (Tothill, 1923).

There is slight correlation between abundance and the area occupied by Merriam's (1898) "Life Zones". Both species do occur in all of the life zones in North America, except the tropical, but they become economically abundant outside of the boreal and transitional zones only at rare intervals.

Economic abundance does not agree with any of the "Climatic Provinces" of Thornthwaite (1931). Tent caterpillars are more abundant in the "microthermal provinces" than elsewhere. This is not always true, however, and the insects do become abundant in portions of the "mesothermal provinces" bordering the "microthermal provinces."

There is little correlation of abundance and yearly precipitation in the north. A tendency appears for the peak to follow years of sub-normal precipitation and to end during years of above normal precipitation (Fig. 3). During the months of larval activity of these insects, April, May, and June, precipitation is not the limiting factor as is noted in Figure 4.

Deviations from the average annual temperature do not correspond to abundance. Peaks of abundance follow periods of high or low average temperature (Fig. 5).

Extreme winter cold has been mentioned as an important limiting factor of tent caterpillars through killing of unhatched larvae. Temperatures of 45° below zero were reported as having killed eggs in one area in New Brunswick by Gorham (1923). Another instance is given by Patch in Maine (1907), but the caterpillars were in a period of relative scarcity at that time so that there is no way to check the effects of this low temperature from the literature. Bailey (1935) reports a similar effect in the Montpelier section of Vermont.

It is almost impossible to determine if these low temperatures killed the eggs as reported. It is evident

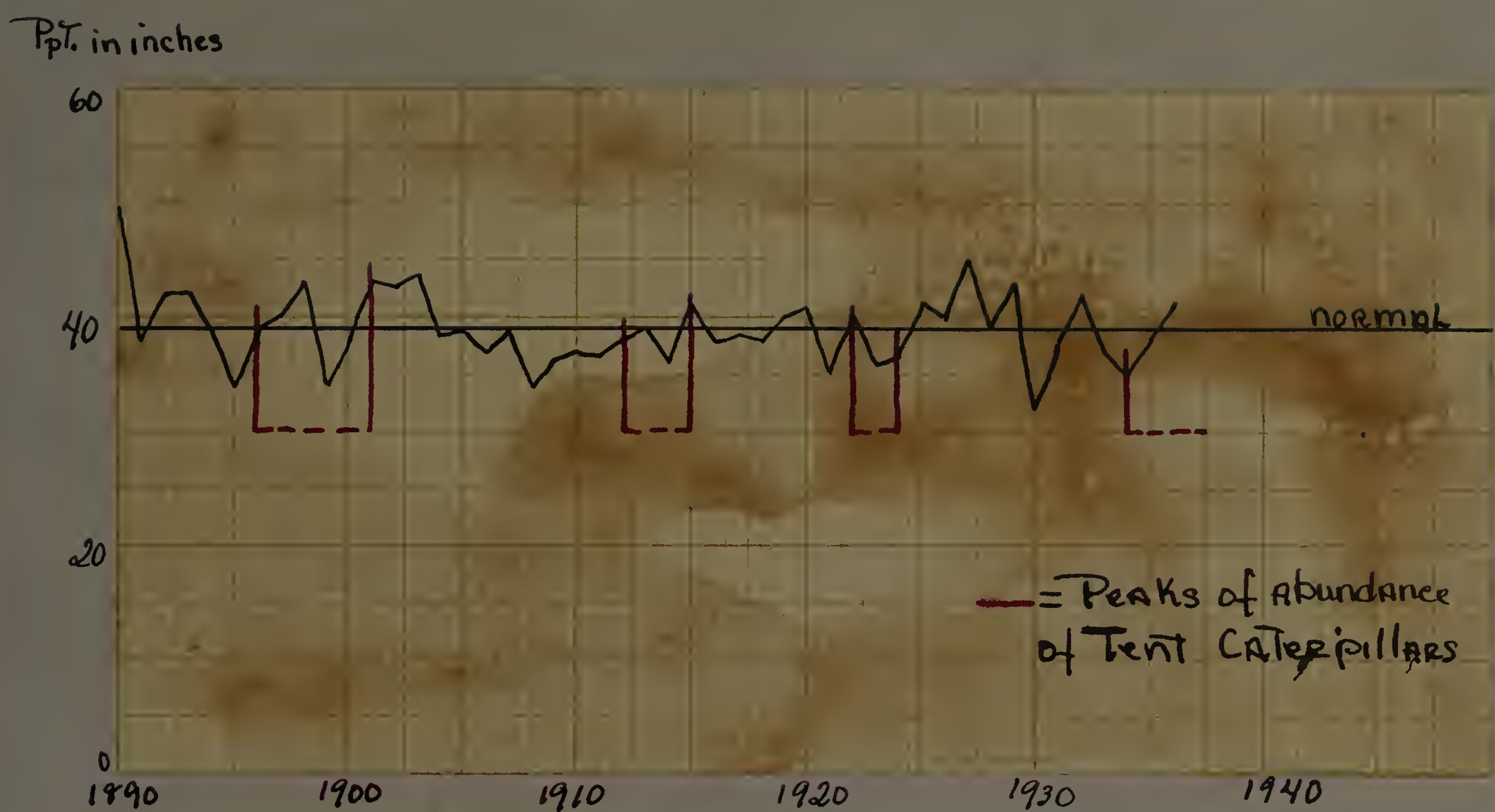

Figure 3

Yearly Precipitation in The New York Area since 1890.

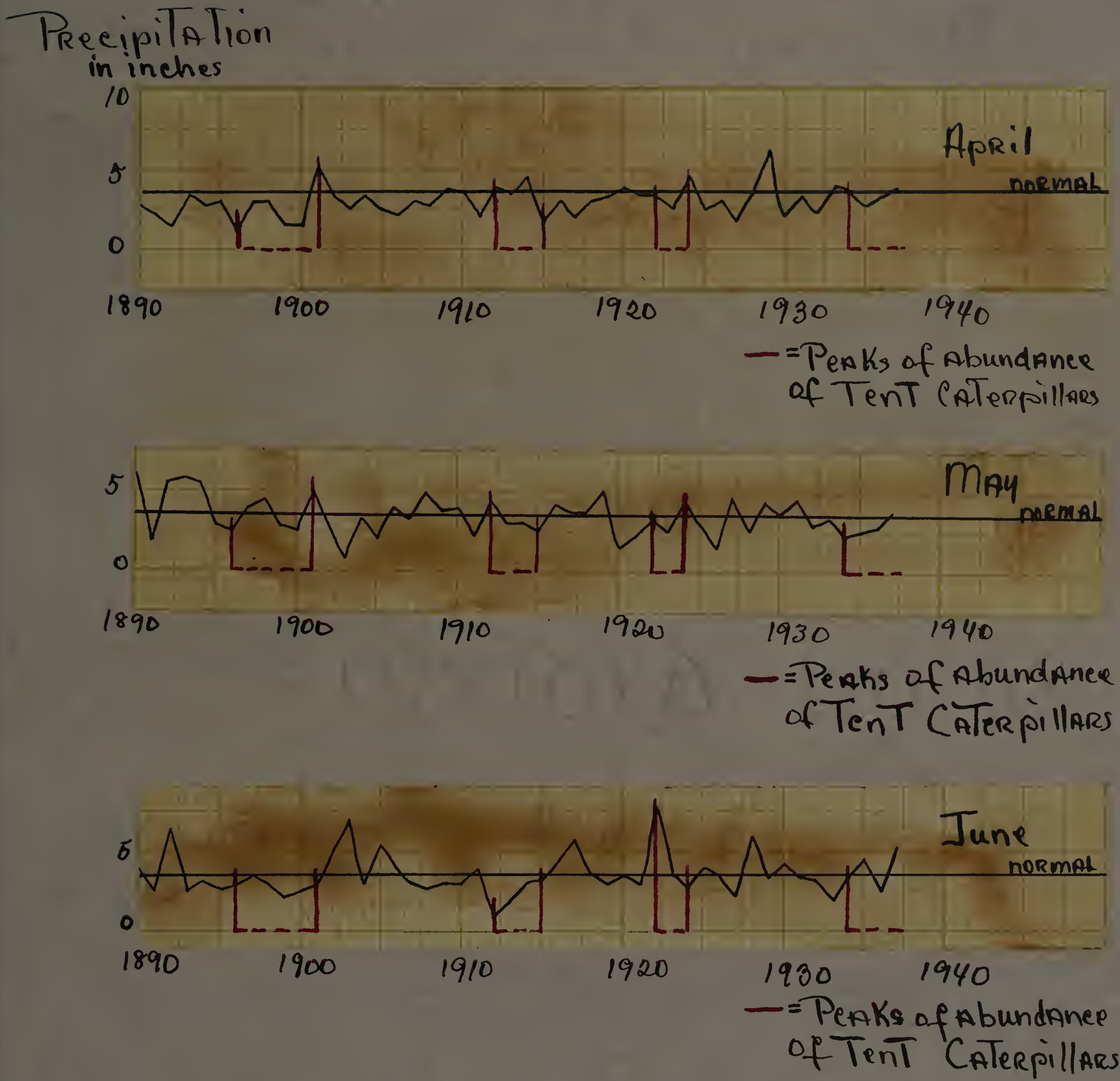

Figure 4

Precipitation for April, May, and June in the New York Area since 1890.

Figure 5
Yearly Temperature in the New York Area since 1890.

that tent caterpillar eggs do withstand much colder temperatures than in any of the above localities, for they are able to survive the winters in Manitoba, Alberta and Saskatchewan where temperature extremes are from 10° to 15° F. lower than the above during an average winter.

In spite of the relatively long period, August through April, as eggs and unhatched larvae within the egg, tent caterpillars appear to be quite unaffected by outside disturbances during this time. Extreme winter temperatures in central Canada do not suppress them, nor is there any known record of extreme heat killing the eggs in nature.

Parasites of the egg stage are of little importance as a controlling factor. As has been demonstrated earlier in this paper, parasitism is not higher than 4 per cent in nature. Predatory birds and animals are unimportant during this stage except in rare instances.

The feeding stage of the larvae, though only about eight weeks long, appears to be the critical period for the survival of the caterpillars. It is during this stage that the caterpillars are subject to the attacks of numerous hymenopterous and dipterous parasites, many insect and bird predators, virus, fungous and bacterial diseases to say nothing of overcrowding and its consequent ill effects, such as starvation and epidemics of disease. None of the above destructive agencies are limiting factors over large areas. However, in a few cases such as was noted by Chapman and Glaser at Lunenburg, Massachusetts, in 1915, the eastern tent caterpillar was almost exterminated in that town by a virus disease.

With the two instances by Blackman (1918) and Tothill (1923) as a clue to what might be one of the more important limiting factors of tent caterpillar abundance, substantiation was looked for in weather records. It is usual for the larvae to hatch from the egg masses in the latter part of April or early May in the New England and New York areas. From the above instances it is noted that cold weather is adverse to the tent caterpillars, and particularly a cold month of May. A few warm days are usually sufficient to hatch the larvae. If the weather changes and stays cold after this time the caterpillars become weakened from cold and starvation and death results.

The graph for May temperatures (Fig. 6) for the New York area substantiates this hypothesis for the most part. The caterpillars were unusually abundant from 1896 to 1901, 1912 to 1915, 1922 to 1924 and 1935 to date. It is evident from the graph of May temperatures (Fig. 6) that each period of abundance follows a year in which May has above normal temperature, and the average temperature of the four years preceding the outbreak are above the normal temperature for the month of May. Such years are 1893 to 1896, 1909 to 1912, 1919 to 1922, and 1930 to

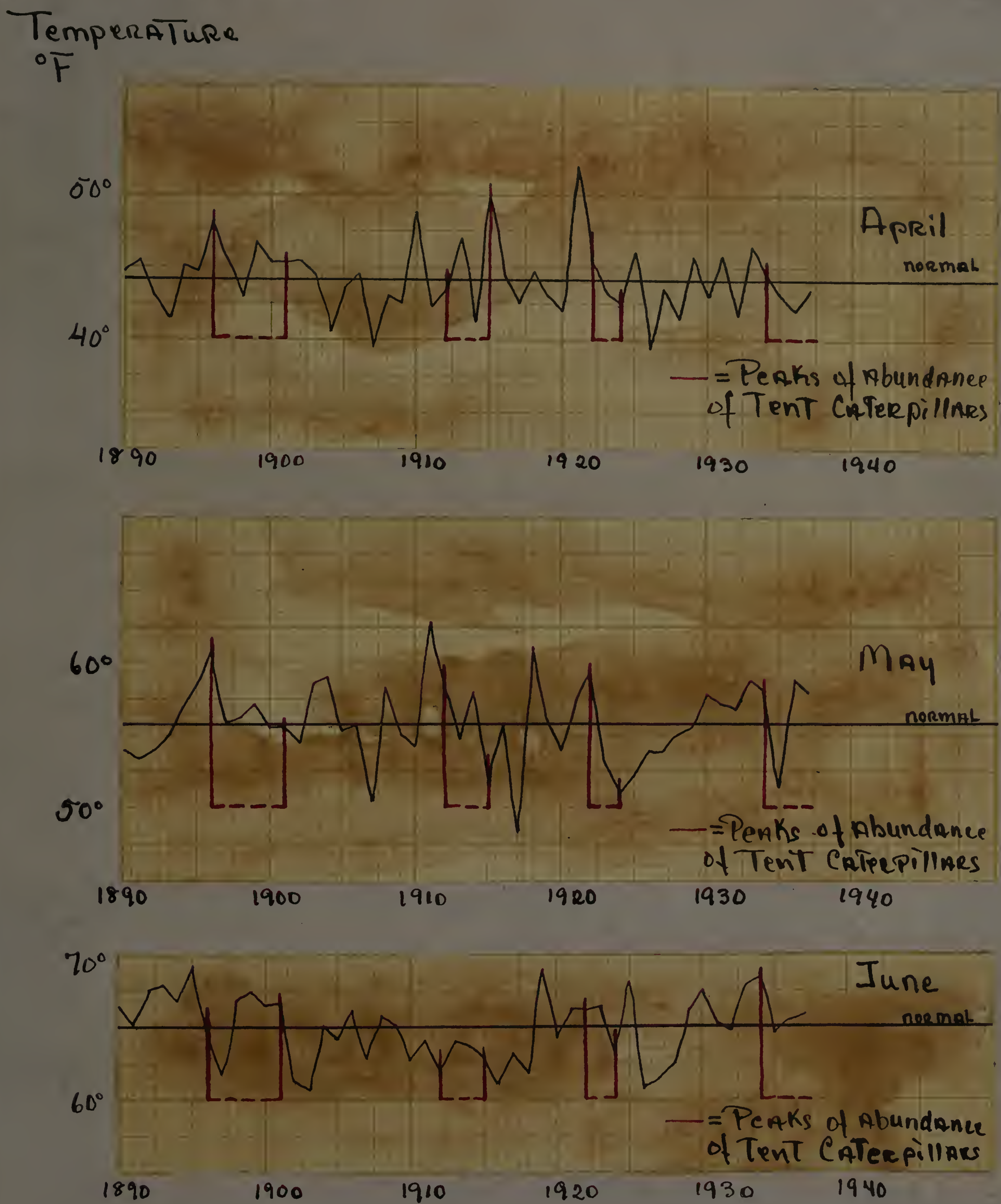

Figure 6

Temperature for April, May, and June in the New York Area since 1890.

1934. It is noted from the above that more than one year is necessary to build up an outbreak. There is one period, 1930 to 1934, when more than four were necessary to build the population to outbreak proportions. These years, however, followed an exceptionally long series of years with cold May weather, 1923 to 1929, which reduced the population to such an extent that a longer period was necessary to build up an outbreak.

The ending of each of the outbreaks on the other hand is noted to take place during a period of normal or below normal May temperatures. More than one year of unfavorable May temperature is necessary to end an outbreak, just as more than one year of favorable May temperature is necessary for an outbreak to follow. Thus the average low temperatures of the years 1900 to 1902, 1915 to 1918, and 1923 to 1929 brought about the end of the 1896 to 1901, 1912 to 1915 and 1922 to 1924 outbreaks respectively, though the single cold Mays of 1913, 1923 and 1935 were unable to do so. The otherwise detrimental effects of the cold May lf 1935 may have been offset by the cold April of the same year which retarded the hatch of the caterpillars until more favorable weather prevailed (Fig. 6).

That these caterpillars become destructively abundant in the southern United States and possibly Mexico appears to be a contradiction to the theory of a cold month of May being the limiting factor. Such peaks occurred in Mississippi and Louisiana in 1934, 1935 and 1936 (I. P. S., Vols. 14-16, 1934-1936). The season in considerably advanced there in comparison to that of the north. The tent caterpillars hatch the last of February or the first of March rather than the last of April or first of May as they do in the north. This exposes the growing larvae to temperature conditions similar to those experienced in the north, except that in the south these corresponding temperatures occur in March instead of May.

There are inadequate records of abundance of these moths in the south previous to the 1934 outbreak, which makes it difficult to correlate weather with abundance there. It appears that outbreaks build up more rapidly there when conditions are favorable than is the case in the north. March, 1933, was favorable for their increase and during the following year, in spite of slightly unfavorable March temperatures, the insects were able to maintain their numbers which had been built up the previous year. March temperatures in 1935 and 1936 were very favorable and the insects were in outbreak numbers both years in Mississippi and Louisiana. The outbreak subsided in 1937 when March temperatures were decidedly below normal and unfavorable to the caterpillars (Fig. 7).

The pupae are subject to the attacks of several parasites which are generally unimportant (Fiske, 1903).

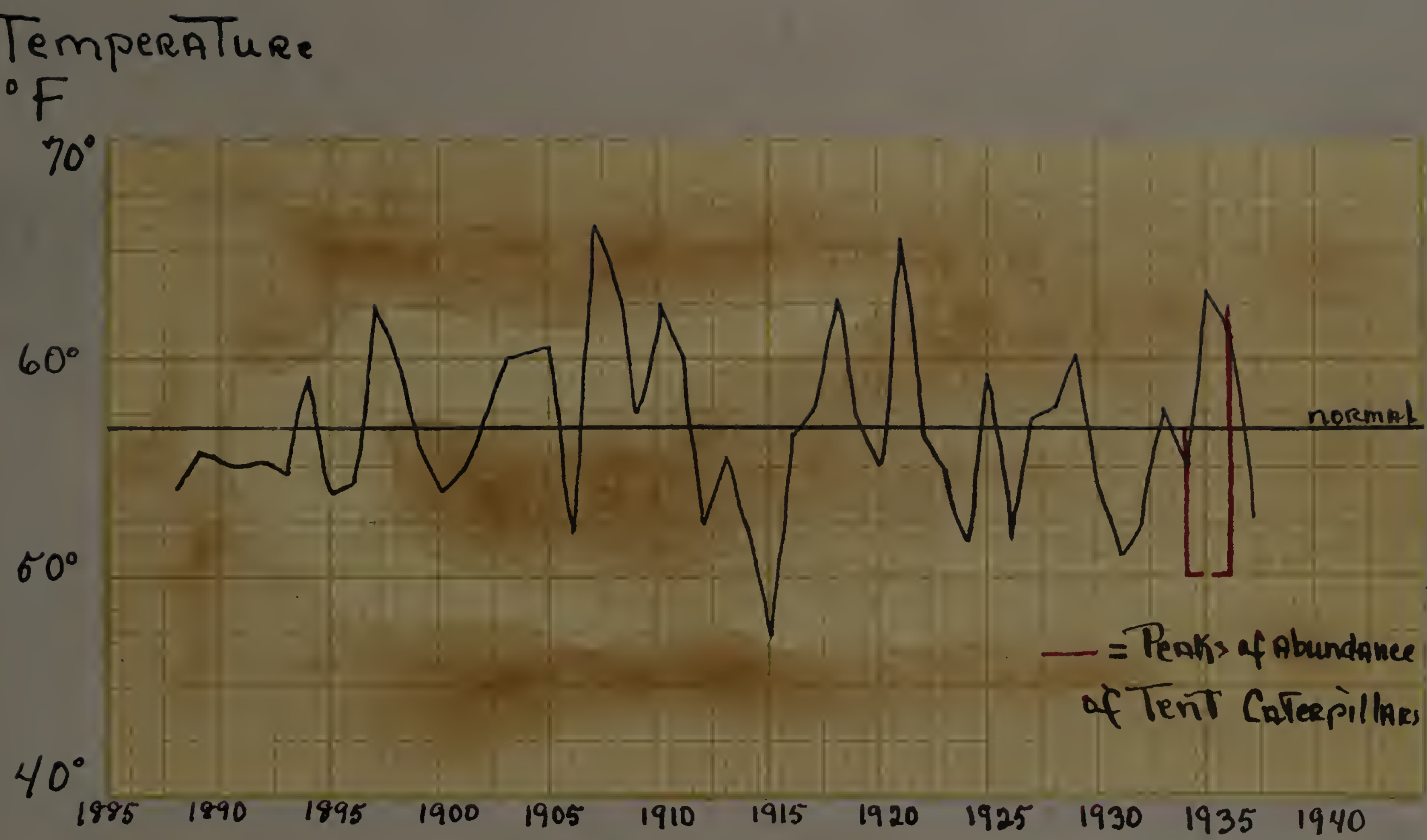

Figure 7

Temperature for March in the Louisiana Area since 1888.

Their habit of pupating in sheltered places in addition to their thick cocoons protect them from many parasites and predators, and the effects of weather.

The adult insects are relatively free from parasites. They fly only at night during their short life, which reduces the attacks of predators to some extent. A few birds have been recorded as feeding on them (Felt, 1905). There is no record in the literature of the effect of temperature or precipitation on the adults during the period of mating, flight and oviposition. Apparently dispersal by flight is comparatively slight.

Peaks of tent caterpillar abundance correspond rather closely to sunspot minima. This fact would seem to conflict with, rather than substantiate, the idea that cold May temperature is the limiting factor of abundance, for precipitation increases during sunspot minima. According to Stetson (1937) this cools the surface of the earth and the air. These effects are for the yearly average, however. There is apparently a certain correlation between these minima and favorable May temperatures which appear to be the chief limiting factor (Fig. 6 and below).

During the last hundred years sunspot minima and peaks of abundance have occurred as follows:

Sunspot minima	Peaks of abundance
1833-34	1830
1843-44	1844
1855-56	1855
1866-67	1866-70
1878-79	1874-78
1888-90	1887-90
1901-02	1896-1901
1911-13	1912-15
1922-23	1921-24
1933-34	1935-

Summary

The tent caterpillars, *Malacosoma disstria* Hübner and *Malacosoma americana* Fabricius, are both native insects occurring in the United States wherever their food plants are available. These moths are the most important species economically in the small family Lasiocampidae. The life cycle of both species is the same, with one generation per year throughout its range.

Cycles of abundance follow a rather definite course, occurring every ten to twelve years. The peaks of these cycles last two to four years, then subside. Since 1820 there have been regular reports of abundance of the forest tent caterpillar. The same is true of the eastern

tent caterpillar beginning in 1826. The peaks of abundance of these two species have coincided rather closely in the same areas in the Northeast implying a common limiting factor or factors for both.

It has been stated many times in the literature that tent caterpillar abundance is dependent upon relaxing of the food or parasite pressure. Little attention has been given to the possible effect of the physical environment.

Natural parasitism of 173 egg masses of Malacosoma americana Fabricius was found to be in the vicinity of 4 per cent, while that of 105 masses of Malacosoma disstria Hübner was less than one per cent.

Winter predators were found to be unimportant limiting factors. Eggs laid at several different sites and distances from the ground showed no variation in hatching. Short alternations between cold and natural feeding temperatures were found to be more detrimental to the larvae than long ones for the most part. Cold exposures of one week did not kill many larvae in the nests. A two week exposure was survived by about two-thirds of the larvae in the nests, while exposures of three or more weeks killed the caterpillars in every instance.

Economic abundance is limited by the favored food plants in both species. The caterpillars occur in all of the North American faunal zones of Merriam except the tropical and arctic Alpine. Greater abundance occurs in the microthermal provinces of Thornthwaite.

Effects of yearly precipitation and temperature are an unimportant factor in limiting abundance. Extreme winter temperatures, though reported to limit abundance, apparently do not do so to any extent. Weather conditions do not affect tent caterpillar eggs in any season. Parasites and predators of this stage are unimportant.

Weather conditions are the true limiting factor of abundance as they affect newly hatched larvae. A warm period to hatch the larvae, followed by a cold period, is apparently the most important limiting factor. Several years of favorable springs are necessary to build up a population to outbreak proportions, while more than one spring with adverse weather is necessary to reduce an outbreak.

Neither weather conditions, parasites nor predators are limiting factors as they affect the pupae and adults.

Peaks of tent caterpillar abundance have corresponded quite closely to sunspot minima since 1830, both occurring at periods of approximately ten to twelve years.

Conclusions

Both the eastern and forest tent caterpillars have cycles of abundance in the Northeast that occur at quite regular intervals. Peaks and hollows in abundance coincide quite closely in both species.

The total parasitism and predatism for all stages is inadequate to explain this phenomenon as far as can be ascertained from the literature, in spite of numerous statements to the contrary.

Cycles of abundance are not dependant upon precipitation at any season. They are dependant, however, upon temperatures after hatching in the spring months. Cold temperatures after hatching are more important limiting factors than parasites and predators.

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