THE ROLE OF SMALL MAMMALS AS PREDATORS
OF THE LARCH SAWFLY
PRISTIPHORA ERICHSONII (HARTIG)
IN EASTERN MANITOBA
(1952 and 1953)

By

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CONTENTS

1. ABSTRACT

The problem presented in this thesis was approached from a predator-prey population standpoint. Population sampling techniques were developed for the host insect in stages relevant to the study and for the predator species, and population trends were studied using these techniques. Coactions of the larch sawfly and small mammals were investigated in a restricted universe and it was found that small mammals, particularly shrews, can discriminate between sound, parasitized, diseased, and dead prey insects. Predation in the field was estimated utilizing a modification of an earlier cocoon planting technique and by this means the relative importance of mice and shrews as predators of the larch sawfly was clarified. The method also indicated that the time of predation on this insect is more limited than was previously supposed and that predation in this case may not be a simple density dependent factor. It was further demonstrated that predation upon larch sawfly cocoons by small mammals constitutes one of the largest natural control factors operating against populations of this insect.

2. INTRODUCTION

The larch sawfly, Pristiphora erichsonii (Htg.), is probably the chief suppressive agent in stands of tamarack, Larix laricina (Du Roi) (K. Koch.) (21,38). The insect was probably introduced from Europe, and appears to have been present in North America since about the beginning of the nineteenth century (15, 21, 31). A number of serious outbreaks of the larch sawfly have been recorded on this continent since 1882, causing such severe mortality to the host tree that it has fallen from high economic importance to relative insignificance (32). A recent outbreak began in Manitoba about 1938 and the insect now occurs in epidemic proportions over extensive areas of Manitoba, Saskatchewan, Ontario, and the Lake States (38). Lejeune (39) has pointed out that soil moisture , parasites, predators, and the growth habits of the tamarack itself are important ecological factors governing populations of the larch sawfly.

Although chemical control has achieved remarkable success in the control of some forest insect pests, the larch sawfly has received little attention in this respect. There are two main reasons for this situation; firstly, tamarack usually grows in isolated pockets on boggy sites, thus affording a poor target for aircraft treatment; secondly, the larval stage of the insect is staggered over such a long period that a single application, even if it destroyed all the exposed insects, would only partially reduce the population (14). Thus it appears that control by use of natural factors offers greater promise than the use of insecticides.

The effect of soil moisture appears to be the most important physical factor governing larch sawfly abundance. Insects in post-diapause and pre-diapause stages are rapidly killed by flooding, but this control is limited to two short and well defined periods in the development of the insect. Furthermore, where only partial control of the insect occurs during flooding, an adverse effect may be exerted upon the resident parasite and predator populations (39).

Apparently the principal control agency of the larch sawfly in early outbreaks was the introduced ichneumonid parasite, Mesoleius tenthredinis Morley, which has been credited with ultimately decimating outbreak populations (15, 31). In the present infestation, however, Muldrew (52) has shown that the host has developed a natural immunity to the parasite in central Canada, thus dramatically reducing its control value. Unpublished results of Lejeune and Hildahl (40) suggest that the only other important parasite of the insect, the tachinid, Bessa harveyi (T.T.), has not been able to reach population levels to an extent where the host population is appreciably affected. Parasite releases of these two and other species of parasites have been largely unsuccessful in the present outbreak.

The growth habits of the host tree also tend to discourage the maintenance of high insect populations over a period of years. As defoliation progresses the vigor of the tamarack is reduced with an accompanying drop in foliage production. This causes servere competition amongst the larvae, but at the same time it imperils the life of the tree.

Small mammal predation of larch sawfly cocoons has been shown to be a major controlling factor in the present outbreak, having almost exterminated the insect from some stands (21). Early work indicates that these animals usually account for about 50 per cent of the total mortality, and occasionally 100 per cent of the cocoons have been destroyed by small mammals. Despite their importance, little research has been carried out to determine in more than general terms, the role of mammalian insect predators. Isolated notes appear to be the only references available in this field (21,22,50).

This project was initiated in order to determine more precisely the effect of mammalian predators on the population of the larch sawfly. Field research was conducted in the Whiteshell Forest Reserve in eastern Manitoba. The study may be conveniently subdivided into three phases as follows:

(1) studies on small mammal populations

(2) studies on larch sawfly populations

(3) studies on the coactions of mammals and larch sawfly

3. REVIEW OF THE LITERATURE

3.1 Small Mammal Populations.

A fundamental problem in ecological investigations is the enumeration of the organism in its natural habitat. Allee et al (2) have advanced seven categories by means of which animals may be censused, but in dealing with small mammals this can be reduced to four:-

1. Direct counts
2. Line censusing
3. Trapping
4. Indirect methods

The direct count is the most simple of all techniques of animal census, but since most small mammals are either nocturnal or secretive in their habits, the method is of limited use. Similarly the strip or line census (28, 41) is only practical in censusing such diurnal animals as squirrels, chipmunks, gophers, and hares.

In determining small mammal populations, the most widely used methods are those utilizing traps, although indirect methods have been used to a limited degree (41).

3.1.1 Home ranges and cruising radii.

Before the merits of the trapping methods can be properly discussed, the methods of measuring home range should be reviewed. The significance of home range will be apparent when trapping for population assessment is discussed.

Although indirect methods have also been used (16, 63), the conventional way of determining the home range of an animal is through recapture data. Live traps are set in a regular pattern, and the animals are marked and released in an attempt to catch them at various points in their range. Manville (46) has reviewed the methods used in marking small mammals.

Once the data have been collected, there remains the problem of treating them. Several techniques have been advanced to measure ranges from recapture data (60, 27, 13), but these make no correction for animals extending beyond the "trap revealed" home range, or are influenced by human judgment. Blair's method (8) appears to be the most discriminating technique advanced, largely overcoming these objections, and it has been shown to give the most accurate results on experimental populations (61).

3.1.2 Use of dead traps.

In most early population studies concerning small mammals, the dead trap has been used. Dice (17) suggested that snap-back traps could be used to indicate the relative abundance of any one species in various habitats and in different seasons or years, whereas Bole (9) set snap-backs in a grid and concluded that the number of individuals divided by the area gave an absolute population figure. Stickle (60) however, pointed out that in either live trapping or grid trapping the home range of the animals being studied would influence the results. Animals other than those living on the plot would also be trapped and this would greatly increase the population estimate. Stickle furthermore suggested that the home range of many animals varied with population density, season, and habitat. Trap design and arrangement also appear to influence trap-revealed populations (18, 30, 46). Saunderson (58) gives evidence that small mammals cannot be trapped out of an area, but most other authors suggest that the "levelling off" effect after three trapping nights is due to influx from other places. Hayne (29) has advanced a method of plotting the results in order to determine when this occurs.

The method of dead trapping as a measure of animal populations is crude. Only vague relative figures can be derived until the home range problem has been settled.

3.1.3 Use of live traps.

The method of small-mammal census that has been exploited to considerable extent recently is the use of live trapping experiments. Manville (47) has reviewed the literature and lists the qualities that a good live trap should possess; effectiveness, portability, durability and economy.

Animals captured in live traps for the purpose of population studies are marked and returned to the population. The traps are usually laid in grid fashion and the individuals captured are numbered so that they can be recognized when they are recaptured. Petersen (54, 55) working on fish populations, and Lincoln (42) studying water fowl populations independently derived a method for estimating the population utilizing the ratio of marked to unmarked individuals in the recapture sample. The formula is

$$T = m \frac{n}{x}$$

where T = total population
m = number originally marked
n = number in the sample
x = number marked in the sample

Ricker (57) advanced the following stipulations on the use of the Lincoln or Petersen Index:

"(1) The marked animals must suffer the same natural mortality as the unmarked;

(2) The marked animals must not lose their marks;

(3) Marked and unmarked animals must be equally subject to sampling;

(4) The marked animals must become randomly mixed with the unmarked, <u>or</u>, the distribution of sampling effort must be proportional to the number of animals in different parts of the habitat being studied;

(5) All marked animals must be recognized and reported on recovery.

(6) There can be only a negligible amount of recruitment to the population being sampled during the sampling period."

Using this method, natural migration can be accounted for (5), and in instances involving large samples corrections can be made for birth and death rates in natural populations (33, 34, 35, 36, 42). Adams (1) has pointed out that the method is subject to statistical errors of probablility and has published graphs from which the confidence limits at the 95 and 99 per cent levels can be readily obtained. An excellent review of the techniques involved in the use of recapture data has been published by Bailey (6).

In work on small plots, many of the animals captured in the outside lines of traps are living only on a portion of the plot and these animals will increase the population estimate manifold (60). Blair (8) suggests that where no natural barrier occurs around the plot, a boundary strip be included equal to the cruising radius of the experimental animal. The "area trapped" is thus the area encompassed by the traps whilst the "effective trapping area" is the area trapped plus the boundary strip. Stickle (60) makes a similar correction for circular plots.

The live trapping method overcomes many of the difficulties experienced in dead trapping, since ranges can be calculated for each species, sex, age, habitat and season studied at the time the population is being assessed. It is, however, more expensive and laborious, and is impractical where only general trends are required.

3.2 Mammalian Predators of Forest Insects.

The role of small mammals as predators of forest insects has received varied attention in ecological investigations. Hewitt (31) mentions mammalian predators of the larch sawfly as does Graham (23) and several other authors. Bess, Spurr, and Littlefield (7) suggest that mammals are important in controlling the gypsy moth, Hardy (25) mentions their importance as predators of Diprion similis in Poland, Schumanov (59) considers them effective in controlling cicada outbreaks in Russia, and Morris (48) has shown them to be important predators of the European spruce sawfly. The list of North America mammalian species known to prey upon forest insects now numbers 20, including two moles, seven shrews, one chipmunk, one flying squirrel, two deer mice, five voles, and two jumping mice. In addition to these there are 14 species that are suspected of preying upon insects, including two lemmings, one chipmunk, one flying squirrel, three ground squirrels, three squirrels, one skunk, and three weasels, as determined by laboratory and field observations.

The effect of small mammal predation on forest insect populations has received attention from several authors with varying conclusions. Hewitt (31) in 1912 noted that small mammals feed upon cocooned larch sawfly larvae but placed little value in this predation as a natural control. Graham (21) using cocoon collections and planted cocoons suggested that small mammals exert considerable control on larch sawfly populations, often consuming 50% of the overwintering population and occasionally taking 80 - 100%. He considered mice to be more important than shrews by virtue of the higher populations exhibited by mice. This view is supported by Hamilton and Cook (24) who suggest that small mammals often hold in check insects which would otherwise become an economic problem. Hardy (25) using cocoon collections has shown that 46% of Diprion similis in Poland were opened by small mammals during 1936. He points out that there is often considerable overlapping of control factors, since small mammals will prey upon parasitized and diseased cocoons. He suggests that this overlapping occurs randomly. Morris (50) on the other hand disagrees with this assumption since he has shown that mammals can differentiate between sound and unsound cocoons to varying degrees depending upon their insectivorous nature.

It is difficult at the present time to define the importance of small mammals as forest insect predators, since Graham (22) Hamilton and Cook (24), and Morris (50), suggest that these animals exert considerable control on sawflies, whereas Hewitt (31), Hardy (25), Balch (4), and Bess, Spurr and Littlefield (7) consider them as a relatively minor natural control factor.

The role of small mammal predation on forest insects is received with mixed opinions by entomologists. It seems evident that small mammals do exert some control on insect populations and it appears from the literature that at times this may be considerable. Previous investigations have not examined the problem from a predator-prey population viewpoint, and at present this seems to be the most promising approach. Once the role of mammalian predation on forest insects has been established, a better idea of the control that might be expected from this source will be gained, and in developing management plans the utilization of small mammals as well as other natural control factors should be considered. In addition to this, small mammals might aid in spray controls by consuming insects that are knocked down by the spray but are not affected strongly enough to be killed.

4. THE STUDY AREA AND PLOT DESCRIPTIONS

During the spring and early summer of 1952, four small-mammal plots were established in the Whiteshell Forest Reserve in eastern Manitoba. All plots are square, enclosing an area of 4.9 acres (i.e. 7 chains square). Trap positions are at one chain intervals and are located by a four-sided blaze on the nearest tree. This gives eight trap positions per line, or 64 per plot. The one chain interval was arbitrarily chosen by Dr. R.F. Morris (49) and it was deemed appropriate to adhere to this spacing in order to make data of this experiment comparable, especially since Hayne (30) has shown a variation in the apparent home range (of *Microtus*) in relation to the interval between the traps.

Tables I and II give the detailed ecological description of the plots.

Plot 1.

This plot is situated 2½ miles south of Red Rock Lake and may be described as tall trees on a dry site. The tamarack in this bog are 30-40 feet in height. Black spruce, of the same general height as the tamarack, occurs throughout the plot and is the predominant species in the southwest corner of the plot. The plot is bounded on the east side by a road, on the north by a drainage ditch, and on the west by a rock ridge. The understory is chiefly alder on the east side, changing to labrador tea towards the west.

Plot 2.

This plot is situated near the Trans-Canada Highway, approximately five miles east of Rennie, Manitoba. The site is dry and open with intermingled tamarack and black spruce about 6-12 feet high. Ground cover is mainly labrador tea, and pitcher plants are common throughout.

Plot 2A.

During the spring of 1953 one additional plot was established. This plot is 10 chains west of Plot 2 and is similar to it.

Plot 3.

This plot is located near the north end of Red Rock Lake in an extensive, pure tamarack stand. The trees are tall (about 40 feet in height) and the site is wet. Understory is chiefly alder.

TABLE I

Per Cent Ground Cover on Small Mammal Plots.

Component	Plot 1	Plot 2	Plot 2A	Plot 3	Plot 3A
Moss	36.0 ± 4.6	21.3 ± 7.2	19.4 ± 4.2	16.8 ± 3.5	11.6 ± 2.9
Fern	.4	--	--	.8 ± .1	--
Herbacious plants					
Grass	4.0 ± 1.2	16.3 ± 3.9	18.2 ± 4.1	16.7 ± 10.5	16.8 ± 3.5
Sedge	1.2 ± .3	6.9 ± 2.0	5.6 ± 1.0	3.2 ± .9	2.4 ± 1.1
Smilacina	2.0 ± .1	--	--	2.8 ± 1.3	1.2 ± .3
Viola	.4	--	--	1.6 ± 1.0	3.9 ± .9
Fragilus	.8 ± .1	--	--	.8 ± .1	2.4 ± .1
Mianthemum	.4 ± .04	--	--	--	--
Caltha	--	--	--	1.2 ± .12	1.2 ± .25
Sarracenia	--	6.8 ± .1	9.3 ± 2.5	--	--
Unidentified	.8	1.5	.2	1.9	3.5
Woody plants					
Alnus	5.2 ± 1.2	2.5 ± 1.1	4.1 ± 1.6	7.6 ± 1.7	5.2 ± 1.2

(Continued

TABLE I (Cont'd)

Per Cent Ground Cover on Small Mammal Plots.

Component	Plot 1	Plot 2	Plot 2A	Plot 3	Plot 3A
Ledum	26.0 ± 5.3	17.7 ± 3.5	10.3 ± 2.8	11.6 ± 2.9	10.6 ± 3.2
Vaccinium	.4	7.2 ± 2.3	4.9 ± 1.8	--	--
Andromeda	2.8 ± 1.7	6.2 ± 1.8	8.4 ± 1.8	2.4 ± 1.1	2.0 ± .1
Prunus	2.4 ± .1	--	--	--	--
Saplings					
Betula	2.0 ± .1	1.5 ± .2	1.9 ± .8	--	--
Picea	.4	3.1 ± 1.6	4.8 ± 1.7	--	--
Surface water	7.2 ± 3.7	8.6 ± 2.0	12.1 ± 3.6	28.6 ± 13.5	36.0 ± 8.3
Litter	6.0 ± 2.4	.4	.4	3.2 ± 1.4	3.2 ± 1.4
Decaying logs	1.6 ± 2.8	--	.4	.8 ± .1	--

TABLE II

Tree Cover on Small Mammal Plots.

Component	Plot 1	Plot 2	Plot 2A	Plot 3	Plot 3A
Tamarack					
Average D.B.H.	5.8	2.2	3.0	5.1	4.9
Stems per acre	312.0	187.0	205.0	260.0	283.0
Black Spruce					
Average D.B.H.	5.4	3.6	3.9	--	--
Stems per acre	156.0	128.0	217.0	--	--
Jack Pine					
Average D.B.H.	5.1	--	--	--	--
Stems per acre	2.0	--	--	--	--
% Crown closure	48.5 ± 5.4	11.3 ± 3.5	13.1 ± 3.6	55.9 ± 5.6	47.0 ± 4.9

Plot 3A.

This plot is about five chains south of Plot 3 and in the same stand. The general description is the same as that of Plot 3, with the exception that in the easterly two chains the tamarack tend to thin out and become somewhat smaller (approximately 20-30 feet).

5. SMALL MAMMAL POPULATIONS

5.1 Field Techniques.

In order to study the populations of small mammals, a supply of 75 Sherman traps was obtained (see Figure 1), as it was found that they meet the desirable characters outlined by Manville (46).

The trap is constructed entirely of metal and is set by pressing the door, which is hinged at the bottom, into a horizontal position where it is caught by the treadle (see Figures 2 and 3). Animals are attracted by the bait which is placed on a platform at the back of the trap, and are captured when the door is released after the animal has passed to the treadle. Although several baits were tested, a paste of oatmeal and peanut butter was found to be the most effective, and this can be placed in the trap before transporting it to the field.

The traps were placed and set in the morning of the first trapping day of each period, and examined in the morning each day. A tally was made of all animals captured, under the following categories:- trap number, species, small mammal number, sex, age, parasites, whether marked or unmarked, and whether living or dead. Living animals were handled by shaking them into a wide mouthed gallon jar. The numbering system used in 1952 was a modification of that outlined by Burt (13), which utilized ear clipping. Burt numbered his animals by punching a small hole in the edge of the ear, using five positions. Morris (51) found five positions difficult to recognize on small-eared forms such as *Microtus*, and reduced this to three (see Figure 4). Ninety-nine mice can be numbered by this system, and since no plot on which live traps are used is close to any other, the animals of each plot are numbered consecutively, beginning at number one. Each species was numbered separately.

In 1953 the ear-clipping method of numbering was replaced by the use of metal ear tags applied with a pair of pincers, and the handling jar replaced with plastic food bags.

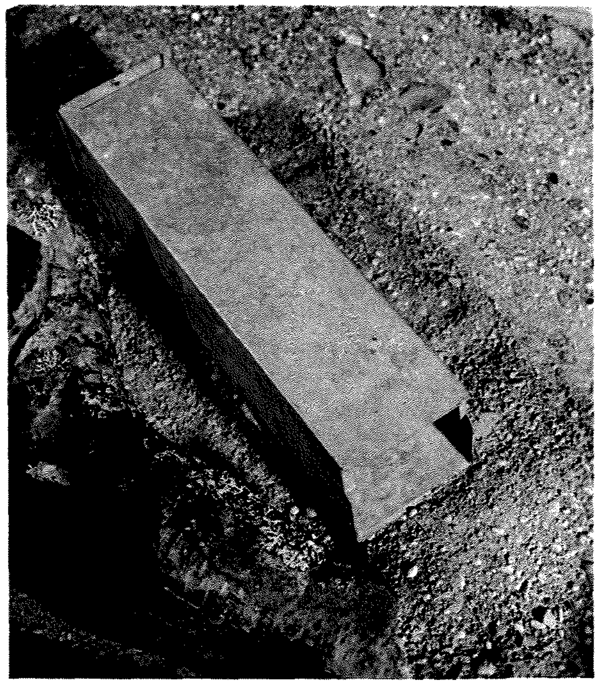


Figure 1. The Sherman Live Trap with Door Open.

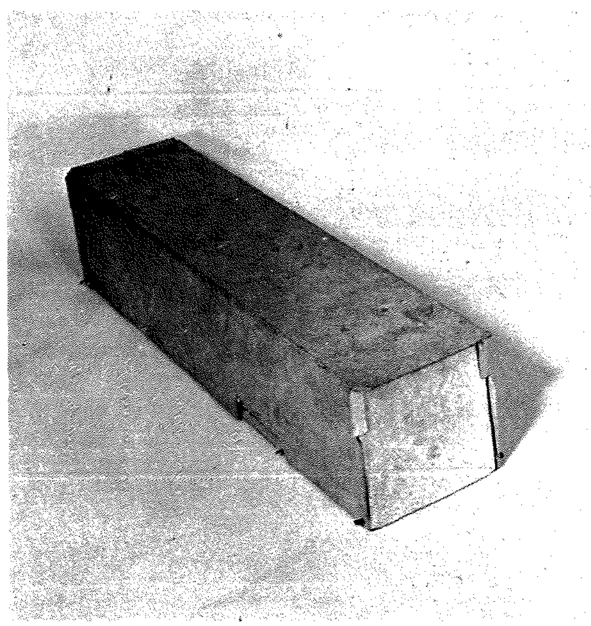


Figure 2. The Sherman Live Trap with Door Closed.

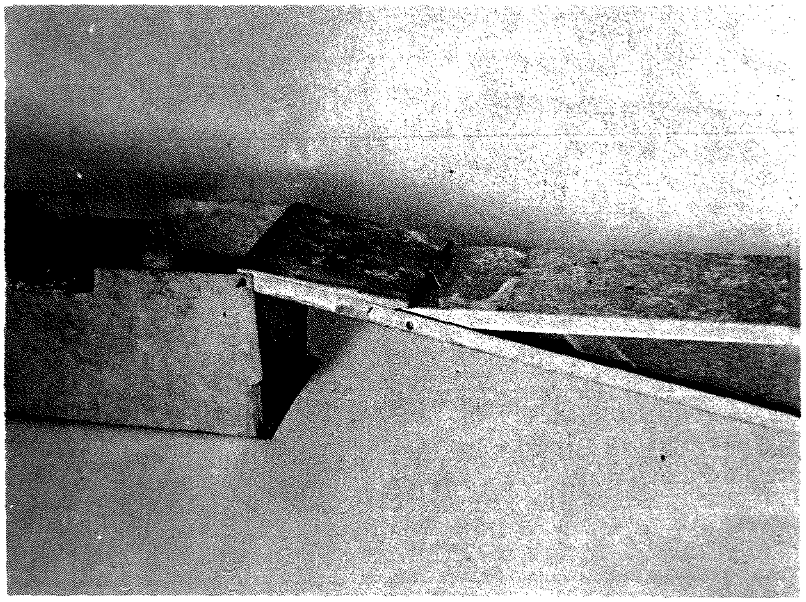


Figure 3. Trip Mechanism of the Sherman Live Trap.

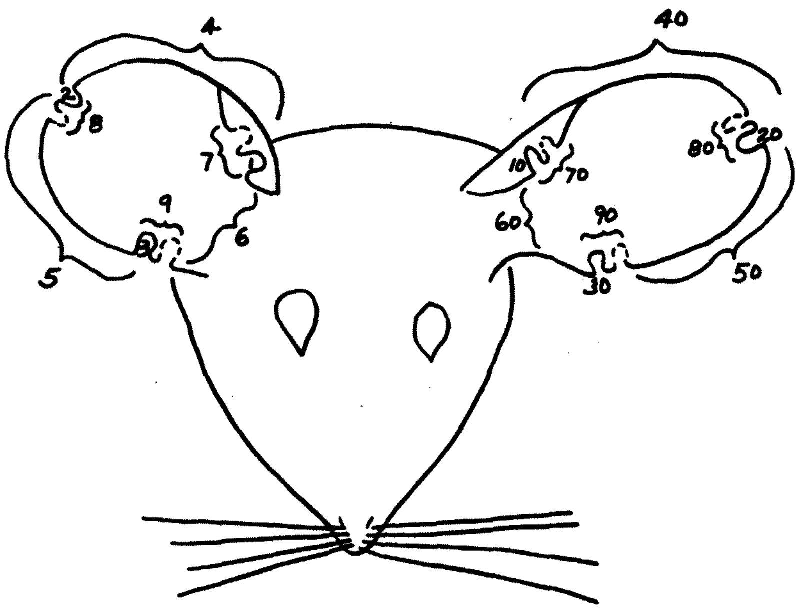


Figure 4. Ear Clip Numbering System Used on Small Mammals During 1952.

In addition to live traps, snap-back traps of the household variety were used on Plot 3A and in bait effectiveness experiments, and on Plots 3A and 2A in refining trapping techniques.

A further problem is keeping animals alive in the traps for periods of from eight to ten hours. Shrews, especially of the genus Sorex, are particularly difficult to keep alive, even in warm weather. Pearson, (53) points out that resting shrews have a higher metabolic rate than mice of the same size, and therefore require a prodigious amount of food. Llewellyn (44) suggests that an abudance of food in the traps will reduce mortality and eliminate the need for cotton bedding in cold weather. A mouse carcass was used as food for shrews in the live traps, but five shrews captured under these conditions were found dead, the carcasses left untouched. Possibly the shrews expend their energy fighting the traps and refuse food. However, a small quantity of oatmeal placed in the traps in November seemed to aid in prolonging life of trapped Microtus and Clethrionomys. During 1953, shrews were successfully live trapped by running the lines hourly during the night.

5.2 Results.

5.2.1 Bait effectiveness.

During the 1952 season the effectiveness of three types of baits was studied. Preliminary experiments indicated that a mixture of peanut butter and oatmeal was superior to bacon rind as a bait. A trapline of 50 snap-back traps baited with bacon rind yielded four Microtus in the first three nights, but when the bait was changed to the oatmeal and peanut butter mixture, the following three nights yielded seven additional Microtus and five Clethrionomys.

An obvious objection to the preliminary experiment is that the effects of the bait were not tested on the same nights. The difference could have been caused by some other factor, such as meteorological changes. In order to overcome this, it was decided to test the bait types simultaneously. During live trapping in early July on Plot 2, two lines of traps (16 traps) were baited with oatmeal and peanut butter and two lines with old cheese. Three nights of trapping captured six Microtus and three Clethrionomys using the peanut butter and oatmeal, while not a single animal was captured in the traps baited with old cheese.

Before the first trapping period on Plot 3A, the three types of bait were used on six lines of snap-back traps. Two lines were set using each bait type, and each bait type was separated by an intervening line. This arrangement was maintained for three nights, giving 48 trap nights for each bait (i.e. one trap for one night is one trap night, hence 16 traps for three nights is 48 trap nights). Table III shows a definite preference for peanut butter and oatmeal.

TABLE III

The Effect of Bait in Trapping Small Mammals.

	No. of captures in 48 trap nights		
Species	Oatmeal and Peanut Butter	Bacon Rind	Old Cheese
Sorex cinereus	10	4	0
S. arcticus	2	0	0
S. fumeus	1	0	0
Clethrionomys gapperi	1	1	0
Microtus pennsylvanicus	2	1	0
Total	16	6	0

5.2.2 Species complement of a tamarack bog.

The following is a list of mammals which were captured or observed on or near permanent plots during the study. Subspecific identification follows Anderson (3).

Sorex cinereus cinereus Kerr. - cinereous shrew
S. arcticus arcticus Kerr. - Saddle-backed shrew
S. fumeus fumeus Miller - Smoky shrew
Blarina brevicauda manitobensis Anderson - Short-tailed shrew
Mustela erminea richardsonii Bonaparte - Richardson's ermine
Peromyscus maniculatus bairdii (Hoy and Kennicot) - Deer mouse
Clethrionomys gapperi loringi (Bailey) - Red-backed vole
Microtus pennsylvanicus drummondii (Audubon & Bachman) - Field vole
Zapus hudsonius hudsonius (Zimmerman) - Meadow jumping mouse
Citellus tridecemlineatus tridecemlineatus (Mitchell) - Thirteen-striped ground squirrel

C. franklinii (Sabine) - Franklin's ground squirrel
Tamias striatus griseus Mearns. - Eastern chipmunk
Eutamias minimus neglectus (Allen) - Western chipmunk
Tamiasciurus hudsonicus hudsonicus (Erxleben) - Red squirrel

Probably few of the above species can be considered important as predators of sawfly cocoons if it is assumed that relative abundance of the various predators determines the extent of predation. The red-backed vole (Clethrionomys gapperi) is universal on the plots examined and is possibly the most important mammalian insect predator in this region. Highest densities of this animal were recorded in the tall, dry stand. The field vole (Microtus pennsylvanicus) is probably of considerable importance in dry, open stands, while the shrews, (Sorex cinereus, S. arcticus, S. fumeus, and Blarina brevicauda), are important predators in dense, wet stands. The deer mouse (Peromyscus maniculatus) and the meadow jumping mouse (Zapus hudsonius) were taken in small numbers on the peripheral regions of two bogs and they are probably of minor importance as predators of the larch sawfly.

5.2.3 Home ranges.

When trapping on small areas it is difficult to derive a true population per acre figure, since many animals which reside immediately outside the trap boundaries, wander onto the plot and are captured. This error can be corrected by adding a boundary strip to include animals living outside the trapping area. Most authors agree that this boundary strip should be the width of the cruising radius of each animal species concerned, and perhaps of each age class and sex as well. In order to calculate the boundary strip therefore, the home ranges of the various species must be known.

The usual procedure in determining the home ranges of small mammals consists of trapping, numbering, releasing and recapturing. However there is considerable disagreement among the various authors as to how the data should be treated.

Buckner (11) adopted a system devised by Morris (51), a modification of Blair's(8) technique, which consists of merely counting the trap units and ignoring the fractions of units. The reasons for the choice are:-

(a) It includes a boundary beyond the trap station.

(b) The boundary is not subject to human error or judgment.

(c) The method can be used in a uniform manner by each person concerned with the data.

(d) The method is both simple and accurate.

Regardless of the method employed, a certain amount of judgment must be exerted, particularly to exclude insufficient data. Animals captured consistently in outside lines should be excluded, and each animal should be captured in at least four different traps before it is included in the calculation of home ranges. Where an animal constantly returns to the same trap, the trap should be kept closed so that the animal will have an opportunity of being captured in other parts of its range. Table IV lists the home ranges of three species.

It is of interest to note that the home range of Clethrionomys is similar on both determinations on Plot 2, but these do not compare with the ranges on Plot 1. Since the population on Plot 2 had approximately doubled by the second determination (see Table X page 24) it suggests that the range of this species varies with habitat, but not with density, for the population levels experienced during the experiment. Table V shows that no significant differences were found in the cruising radii of male and female Microtus, male and female Clethrionomys, and in the ranges of Clethrionomys at two different periods in the year on the same plot. However, the difference in the extent of the ranges of Clethrionomys on closed, dry site (Plot 1) and on open dry site (Plot 2) was highly significant.

5.2.4 Populations.

There are several methods for determining populations of small mammals, most of which give only relative abundance. It is of advantage in work of this nature, however, to derive population per acre figures, and for that reason the Lincoln Index method was adopted (43). Tables VI, VII, and VIII list the populations of Clethrionomys and Microtus and Sorex as determined by the Lincoln Index.

In small mammal population work a Lincoln Index can be derived for each day except the first (no animals are marked until after the first day). This raises the question of accuracy of the various determinations. There are several possibilities to consider when choosing the final population figures. The final determination might be used, an average of all the determinations, the plotting method of Hayne (29) (rejected by the author, 1951) or a method involving the combining of the data of the final three days, suggested to the author by Dr. G.B. Oakland.[1]

[1] Personal communication. G.B. Oakland, Ottawa, May 7,1953.

TABLE IV

Home Range of *Clethrionomys*, *Microtus* and *Sorex*.

Plot	Date	Species	Sex	Range in acres	Cruising radius in feet	Standard deviation	No. of measurements
1	27/VII/52	*Clethrionomys g.*	M.	.60	90	± 17	7
1	27/VII/52	" "	F.	.52	88	± 5	4
2	16/VIII/52	" "	M.	.30	64	No.range	2
2	16/VII/52	" "	F.	.47	77	± 28	5
2	16/VII/52	" "	M.F.	.40	71	± 21	7
2	24/VIII/52	" "	M.	.49	82	± 10	7
2	24/VIII/52	" "	F.	.43	76	± 14	7
2	24/VIII/52	" "	M.F.	.46	79	± 13	14
2	All periods	" "	M.F.	.43	76	± 10	21
1	27/VII/52	" "	M.F.	.34	89	± 14	11
2	16/VII/52	*Microtus p.*	M.	.46	68	± 17	7
2	16/VII/52	" "	F.	.40	78	± 20	5
2	16/VII/52	" "	M.F.	1.40	73	± 19	12
2	19/IX/53	*Sorex c.*	?		139	(range 134-144)	3

TABLE V

t Test For Significant Differences in the Ranges of *Microtus* and *Clethrionomys* on Plots 1 and 2.

Species	Plot	Source	Mean difference	$S_{\bar{x}}$	d.f.	t	$t_{.05}$
Microtus	2	females vs. males	9.7	8.2	11	1.06	2.201
Clethrionomys	2	" " "	.8	7.44	19	1.08	2.093
"	2	period 1 " period 2	6.6	5.35	19	1.23	2.093
"	1 and 2	habitat 1 " habitat 2	15.3	1.74	30	8.8 **	2.042

** Significant at 1% level.

TABLE VI

Lincoln Index for *Clethrionomys gapperi*, 1952.

Plot	Date	m	x	n	T	Approximate 95% confidence interval.	Dead (D)	Population estimate T + D
1	22/VII	--	--	6	--	--	--	--
	23/VII	6	4	7	11	7-26	--	11
	24/VII	9	5	8	14	10-27	--	14
	25/VII	11	9	16	20	14-33	1	21
	26/VII	17	9	11	21	19-29	2	23
	27/VII	19	11	12	21	20-27	2	23
Accumulative		19	38	54	27	23-38	2	29
Final 3 days		19	29	39	26	22-40	2	28
2	19/VIII	--	--	2	--	--	--	--
	21/VIII	2	2	19	19	7-66	--	19
	22/VIII	16	7	14	32	25-50	1	33
	23/VIII	20	10	19	38	31-56	3	41
	24/VIII	28	12	16	37	35-48	4	41
Accumulative		28	31	68	61	48-85	4	65
Final 3 days		28	29	49	47	40-62	4	51
2	1/XI	--	--	4	--	--	2	--
	2/XI	2	1	6	12	5-100	2	14

$T = m\,n/x$ where T = total population
m = number originally marked
n = size of sample
x = marked animals in the sample

TABLE VII

Lincoln Index for <u>Microtus</u> <u>pennsylvanicus</u>, 1952.

Plot	Date	m	x	n	T	Approximate 95% confidence interval	Dead (D)	Population estimate T + D
2	9/VII	--	--	8	--	--	3	--
	10/VII	8	2	8	32	18-67	3	35
	11/VII	12	4	7	21	15-35	5	26
	12/VII	15	7	12	26	19-40	5	31
Cumulative		15	13	27	31	22-50	5	36
2	15/VII	17	4	13	55	38-89	8	63
	16/VII	25	8	14	44	34-64	9	53
Cumulative		25	12	27	47	46-83	9	56

TABLE VIII

Lincoln Index for <u>Sorex</u> <u>cinereus</u>, 1953.

Plot	Date	Time	m	x	n	T	Approximate 95% confidence interval	Dead (D)	Population estimate T + D
2	21/XI	2400	--	--	2	--	--	--	--
		100	2	1	3	6	3-30	--	6
		200	3	2	6	9	4-42	1	10
		300	5	3	7	12	7-38	2	14
		400	6	3	5	10	7-23	5	15
	22/XI								
	23/XI	2400	6	4	7	11	7-26	7	18
		100	8	5	7	11	9-21	8	19
		200	9	7	8	10	9-17	9	19
		300	10	6	8	13	10-23	9	21
Cumulative			10	31	51	17	12-28	9	26
Final 3 hours			10	18	23	13	10-22	9	22

When the Lincoln Indices have been calculated, a decision must be made as to which value is the most accurate. Upon examination of Tables VI, VII, and VIII it appears that the accumulation of the final three determinations gives the least variation in confidence intervals and it will, therefore, be used in further work on populations.

In some cases, the numbers were too few to compute a Lincoln Index, so the number of individuals captured was used as the number of individuals living on the "effective trapping area".

When trapping on small plots there are often considerable "border effects" caused by animals residing mainly off the plot wandering onto the plot and being captured in the outside lines (8,60). In order to calculate the "effective trapping area", a boundary strip is added to the plot. This strip is the average cruising radius for the species concerned. Table IX gives the effective trapping area for the species encountered on the various plots.

TABLE IX

Effective Trapping Area for Small Mammal Species.

Plot	Species	Cruising radius	Authority	Effective trapping area
1 and 3	Clethrionomys	89 feet	Calculated(P1)	9.4 acres
	Microtus	73 "	" (P2)	8.5 "
	Sorex	139 "	" (P2)	12.2 "
	Peromyscus	133 "	Morris (1948)	12.1 "
	Zapus	133 "	Quimby (1951)	12.1 "
2	Clethrionomys	76 "	Calculated	8.2 "
	Microtus	73 "	"	8.5 "
	Sorex	139 "	"	12.2 "
	Peromyscus	133 "	Morris (1948)	12.1 "
	Zapus	133 "	Quimby (1951)	12.1 "

The populations of the various species of small mammals on Plots 1, 2 and 3 are shown in Table X.

5.2.5 Refining techniques.

In refining small mammal population techniques it would be of advantage to dispense with live traps in favour of the more convenient snap-back traps. During the 1953 season a

TABLE X

Populations of Small Mammals Expressed as Animals per Acre.

Plot	Date	Clethrionomys	Microtus	Sorex	Peromyscus	Zapus	Total Mice	Total Shrews
1	27/VII/52	3.0	.02	.7	.8	.2	4.02	.7
	14/VI/53	.106	.236	.825	0	0	.342	.825
	16/IX/53	1.710	.706	1.320	.331	.169	2.916	1.32
2	12/VII/52		4.24					
	16/VII/52	1.10	6.59	.02	.01	0	8.70	.20
	24/VIII/52	6.22	.59	.50	.33	.01	7.15	.50
	1/XI/52	4.50	.31	.15	.15	0	4.96	.15
	12/V/53	.481	.118	.248	0	0	.605	.248
	23/VI/53	.608	.705	2.23	.165	0	1.478	2.23
	2/VIII/53	.731	.824	3.06	.165	0	1.720	3.06
	2/IX/53 *	1.09	1.17	3.31	0	0	2.26	3.31
	2/IX/53	1.09	1.29	1.89	.165	0	2.545	1.89
3	12/VII/52 *	.64	.60	2.23	0	0	1.24	2.23
	8/VI/53 *	.533	.235	3.22	0	0	.768	3.22
	20/VIII/53	.745	.000	5.28	0	0	.745	5.28

* Determined by snap-back traps in close proximity to permanent sample plots.

plot similar to Plot 2 was established (Plot 2A), and snap-back trapped before one period of live trapping on Plot 2. In addition a standard trap line consisting of 50 traps placed in groups of five (one yard apart) at 10 yard intervals along a 100 yard line was operated concurrently with the snap-back grid trapping. The results are shown in Tables XI and XII.

The analysis of variance indicates that the three methods of trapping yield similar results. However the experiment should be replicated with the three types of trapping run concurrently before final conclusions are drawn.

TABLE XI

Comparison of Small Mammal Populations per Acre Using Three Trapping Techniques.

Type of trapping	Date	Clethrionomys	Microtus	Sorex	Peromyscus
Live traps on grid	23/IX/53	1.09	1.29	1.89	.165
Snap-backs on grid	2/IX/53	1.09	1.17	3.31	.000
Snap-backs on line	2/IX/53	1.34	1.38	2.42	.000

TABLE XII

Analysis of Variance on Trapping Techniques

Source	d.f.	S.S.	M.S.	F.	$F_{.05}$	$F_{.01}$
Species	3	9.295	3.096	19.974 **	4.76	9.78
Trapping	2	.165	.083	.535		
Error	6	.947	.155			
Total	11	10.407				

5.2.6 Natural history notes.

Though the primary interest is populations, certain data were collected on the life histories of the species concerned. The vital statistics are shown in Table XIII. Figures are based upon 10 or more animals.

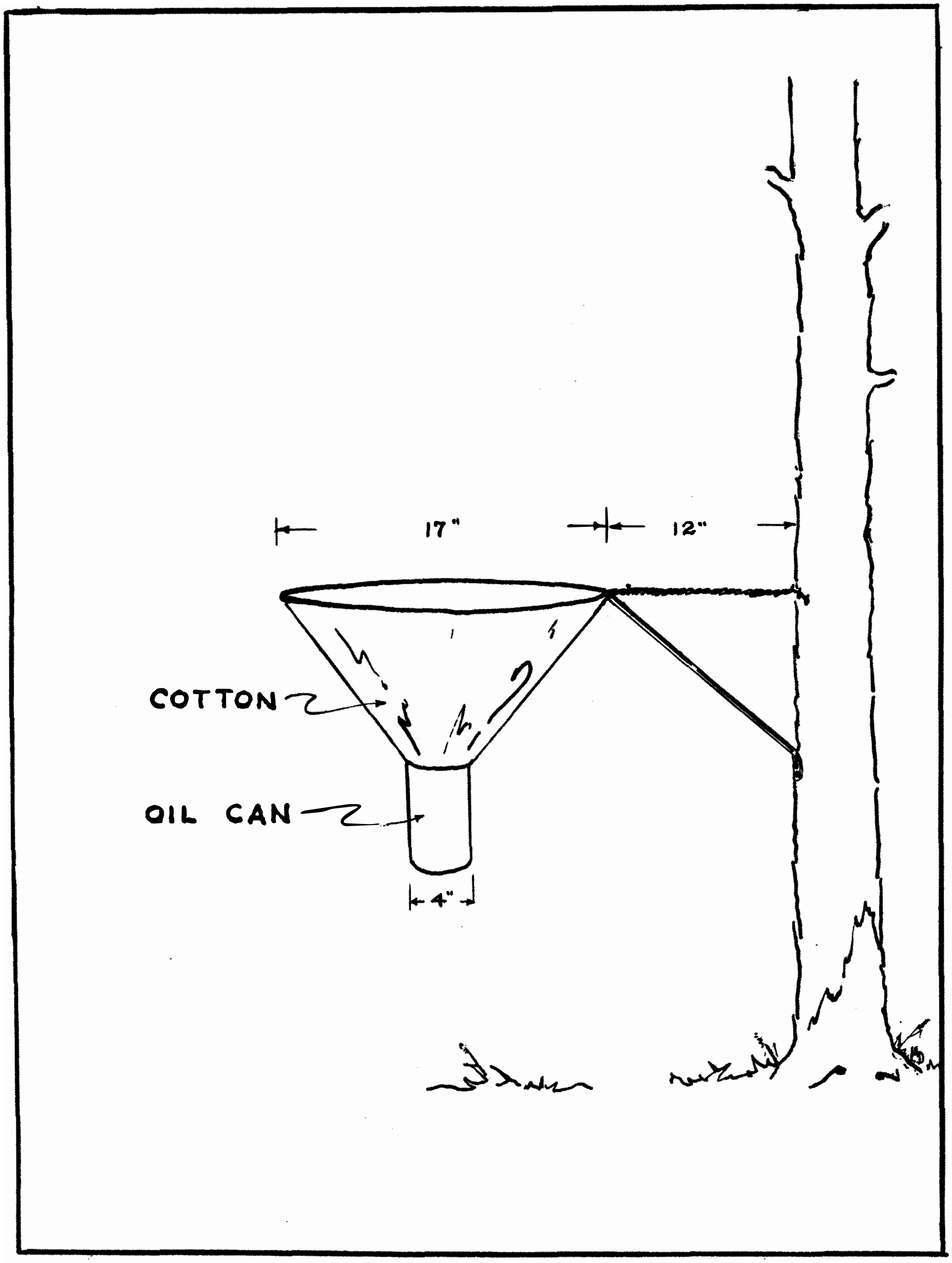
TABLE XIII

Natural History Data on Small Mammal Populations.

Plot	Date	Species	% Males	% Breeding Males	% Breeding Females	% With Ear Mites
1	27/VII/52	Clethrionomys	53	60	10	68
		Peromyscus	60	43	66	0
		Clethrionomys	56	22	29	88
		Microtus	38	33	40	25
		Sorex	64	29	75	0
2	16/VII/52	Clethrionomys	25	50	30	35
		Microtus	59	2	60	59
	24/VIII/52	Clethrionomys	57	23	22	32
		Microtus	25	0	33	25
	2/XI/52	Clethrionomys	40	0	0	0
	2/IX/53	Sorex	52	72	50	0
		Microtus	40	50	50	0
	23/IX/53	Sorex	50	0	29	0
		Microtus	64	29	0	0
3	12/VIII/52	Sorex	45	67	27	0
	8/VI/53	Sorex	69	61	13	0
	20/VIII/53	Sorex	59	41	42	0

Records of fleas were also taken but were not incorporated into the table since they are so easily missed.

There is evidence that the Microtus population experienced a "crash" during the spring or early summer of 1953. Table X indicates a relatively high population of this species in early July on Plot 2, but by August very few Microtus were captured. Five dead animals were found during late July and early August on Plot 2 and two on Plot 1. The dead animals were sub-adults and adults. There is a possibility that this sharp population decline was caused by an epizootic. Clethrionomys showed no such decline.


17"
12"
COTTON
OIL CAN
4"

The following predators were observed or captured on the permanent plots:-

(a) Marsh hawk - observed hunting on Plot 2

(b) Red-tailed hawk - observed hunting on Plot 2

(c) Broad-winged hawk - observed hunting on Plot 2

(d) Long-eared owl - five specimens were recorded roosting on Plot 2 during the week July 5-12, 1952. Two of these were still roosting on the plot on August 31, 1952.

(e) Weasel - one adult and two juveniles were captured on Plot 2 on August 19. One adult changing pelage was observed on Plot 1 on October 11. Six additional weasels were captured on Plot 2 in 1953, and one on Plot 1.

One female Microtus gave birth to three young in a trap on Plot 2. The young mice perished before the trap had been opened. Upon two subsequent captures the animal was not lactating, suggesting that suckling is necessary to produce lactation.

During the 1953 trapping sessions on Plot 1, 2 specimens of Peromyscus (male and female) and one of Zapus (female) were taken which had been marked in the 1952 season. At the time of original marking, all specimens were adults and were assumed to be a minimum of 10 months of age. This places a minimum of 23 months of age on these individuals. All three animals were apparently in good condition and the Zapus specimen was lactating. Thus the longevity of these species under natural conditions may be considerably over 2 years.

6. POPULATIONS OF THE LARCH SAWFLY

The larch sawfly, Pristiphora erichsonii (Htg.) (Order Hymenoptera, Family Tenthridinidae) is a serious pest of tamarack (23). Adults of this insect emerge from late in May to about mid-July, and deposit eggs on the new shoots of the host tree. After hatching from the eggs, the young gregarious larvae feed voraciously upon the tamarack foliage. After passing through five instars, the mature larvae drop from the trees and spin cocoons in the moss. It is while in this stadium that the insect is vulnerable to mammalian predation. The adults emerge from the cocoon in the following spring, or, in a low percentage of cases, remain in diapause until the second spring.

Since small mammal predators are primarily concerned with cocooned sawflies, no attempt was made to sample populations of eggs or larvae. However, in 1952, an effort was made to estimate cocoon populations on the ground by means of funnels to collect dropping mature larvae. These consisted of wire hoops 17 inches in diameter suspended one foot from the trunk. A cotton funnel was attached to the hoop and at the bottom of the funnel was suspended an oil can with the top removed and the bottom perforated. Damp moss was placed in the can. The funnel is shown in Figure 5. Ten of these funnels were placed on representative tamarack trees on each of Plots 1, 2, 3, and 3A. These funnels were examined weekly and the cocoons or larvae removed and tallied. The results are shown in Table XIV.

TABLE XIV.

Larval Drop Expressed as the Average Number of Larvae per Funnel.

Plot	July 23	July 30	Aug. 6	Aug. 13	Aug. 20	Seasonal Average	Standard Deviation
1	1.3	3.5	7.2	1.3	0	13.3	± 6.5
2	1.2	4.8	5.7	.7	0	12.3	± 12.1
3	5.2	10.0	11.2	1.6	.1	28.1	± 10.0
3A	5.0	7.0	10.6	5.5	.1	29.0	± 8.8

From these data the cocoon population per acre was estimated in the following manner, assuming that all mature larvae spun cocoons.

Using Turnock's data (64) from experiments conducted at Prince Albert, Saskatchewan, 11% of the total larvae on a tree fall within 18 inches of the trunk and 39% between 18 and 35 inches from the trunk. Accordingly, the funnel used in this experiment should capture 1.54% of the larvae falling from the tree. Thus having an estimate of the larvae per tree and the trees per acre the cocoon populations per acre were calculated on the various plots. The results of this calculation are shown in Table XV.

During 1953 all the larvae were collected from two trees on each plot in connection with another experiment, by means of funnels which completely encircled the tree (see Figure 6).

Figure 6. Tree Funnel Used for Larval Sampling During 1953.

TABLE XV

Sawfly Populations on Small Mammal Plots During 1952 Expressed as Insects per Acre.

Date	Plot 1	Plot 2	Plot 3	Plot 3A
23/VII/52	26,300	14,600	90,000	92,000
30/VII/52	97,300	72,800	257,000	235,000
6/VIII/52	243,000	142,000	445,000	431,000
13/VIII/52	269,000	150,500	473,000	531,000
20/VIII/52	269,000	150,500	475,000	533,000

Taking the average of these and knowing the number of trees per acre, the sawfly cocoon population was calculated. The results are shown in Table XVI.

TABLE XVI

Sawfly Populations on Small Mammal Plots During 1953 Expressed as Insects Per Acre.

Date	Plot 1	Plot 2 *	Plot 3
15/VII/53		4,100	322,400
24/VII/53	26,200	56,900	657,400
29/VII/53	79,100	128,300	899,500
4/VIII/53	81,300	170,700	963,500
19/VIII/53	92,800	180,100	972,400

* Only one tree was used since the second was obviously larger than the general stand type.

These two methods of estimating cocoon populations are rather crude, but show reasonably good agreement on per acre estimates. Therefore, it is felt that they are justified rather than attempting relative populations, since any comparison between predation and sawfly populations become so vague that conclusions are limited.

7. THE EFFECT OF SMALL MAMMAL PREDATION ON LARCH SAWFLY POPULATIONS

7.1 The Role of the Predator.

The role of the predator has received considerable attention in the literature. Allee et al (2) define two major types of predation -- canibalism and interspecies predation. Both types have been shown to be important in reducing populations in certain instances. Leopold (41) in a treatise on game management has outlined the following variables that influence the mortality of a prey species from predation effects:

1. Density of "game" populations
2. Density of predator population
3. Food preferences of the predator
4. Physical condition of "game"
5. Abundance of buffer species (i.e. alternative prey)

The author considers the interpredation between predator species as an additional factor which is important in assessing predation losses from a prey species.

The first two factors influencing predation intimate that the effects of predation are density dependent. Hartley (26) has found that sparrow hawks preying upon song birds follow this rule within certain limits. These limits are defined by Errington (19) who states that any habitat can support only a given number of individuals. When the population of prey species is lower than this limit, little predation is experienced, but once the population rises above its threshold of security this biological surplus is heavily preyed upon.

From the concepts advanced in the literature it seems evident that the following major lines of investigation should be initiated:-

(a) a detailed list of all the known predators of the prey species involved

(b) 'he food preferences and capacities of the predators

(c) population studies of both predator and prey

(d) effect of predators upon the prey species population

(e) defenses of prey species against the predator

(f) interpredator effects

7.2 Known Predators of the Larch Sawfly.

The mammalian species occurring in tamarack bogs of Eastern Manitoba have been listed earlier in this paper. In all, 14 species were noted but it was suggested that few of these could be considered important as predators of the larch sawfly. By virtue of their low occurrence it is possible to eliminate the chipmunks, squirrels, and weasels as significant cocoon predators. Similarly, *Peromyscus* and *Zapus* were taken only in the peripheral regions of the bogs and might also be omitted. Of the shrews, *Sorex cinereus* was the only one that maintained reasonably high population levels, and so from the standpoint of larch sawfly cocoon predation, only *Sorex cinereus*, *Clethrionomys gapperi*, and *Microtus pennsylvanicus* appear to be important. Observations on caged *Peromyscus* indicate that if these animals invaded the bogs more extensively, they too would merit attention.

7.3 Feeding Experiments.

In order to ascertain the food capacities and preferences of small mammals, feeding experiments were conducted on caged animals. Preliminary experiments in 1952 using 18 inch cube cages with sphagnum covered floor showed that the cage was too small to assess adequately the normal feeding habits of *Clethrionomys*. Cocoons and normal vegetation were supplied.

A male, sub-adult, *Clethrionomys* was caged for 24 hours with 60 cocoons as follows:

Apparently sound	30	opened	30
Dead	20	opened	18
B. harveyi emerged	10	opened	5

The experiment was repeated, using 150 cocoons and a fe ale sub-adult Clethrionomys.

Sound	75	opened	75
Dead	60	opened	11
B. harveyi emerged	15	opened	6

Following this, 500 apparently sound cocoons were placed in the cage with an adult male Clethrionomys. Of these, 493 were recovered and found to be opened. The experiment was discontinued because of cocoon shortages.

The experiment was repeated during 1953 using a cage with about 36 square feet of floor space covered to a depth of about four inches with sphagnum moss. Natural food was also inserted so that the animals would not feed upon the cocoons through starvation. The following cocoon types were then scattered under the moss:

(a) sound cocoons of P. erichsonii.

(b) cocoons containing living B. harveyi parasite larvae.

(c) cocoons attacked by a fungal growth.

(d) cocoons from which B. harveyi had emerged.

(e) sound cocoons wired onto tree tags.

The cocoon categories were obtained by rearing field collections of fifth instar larvae. Thus the sound cocoons were produced by apparently normal larvae, and similarly, those containing living larvae of the dipterous parasite B. harveyi were produced by larvae harbouring the parasite eggs.

In addition to the previously mentioned sawfly cocoons, five B. harveyi puparia, five emerged B. harveyi puparia, and two large undetermined dipterious puparia were placed in the feeding cage. These remained untouched throughout the experiment.

The following animals were admitted to the cage individually for 12 hours.

(a) adult male Clethrionomys.
(b) sub-adult female Clethrionomys.
(c) adult female Microtus.
(d) two adult Sorex.

Table XVII shows the results of the experiment, tested by means of individual 2 x 2 Chi-square tests. From the table it is postulated that:

(a) the tags do not attract or repel the animals. This conclusion is significant since predation is assessed in the field by means of cocoons attached to tags and later examined for predation.

(b) all species can distinguish to some degree between sound and parasitized cocoons. In the case of Microtus the difference obtained is significant at the 3% level. Since none of the dipterious puparia were touched, it is postulated that these are unpalatable to small mammals.

(c) Sorex is able to detect to some degree if a parasite has emerged, the others cannot. This minimizes the overlap of natural controls determined by cocoon collections, and suggests that the selection found in (b) is dependent upon olfaction.

(d) all species can detect to a great extent whether or not the sawfly has emerged. Sorex is unerring in this respect.

(e) all species unerringly reject fungused cocoons.

The preliminary experiment also indicates that Clethrionomys can distinguish to a limited extent sound and dead cocoons. In the field this would eliminate some of the overlap in controls.

The ability of determining moused and shrewed cocoons is important if any degree of accuracy is to be obtained in assessing predation by means of cocoon plants. Cocoons opened by shrews have serrated edges and often have a cap or "lid" over the opened end. Cocoons opened by mice have scalloped edges. Shrews usually make only one opening in the cocoon, but sometimes a second opening is made. Mice however may open a cocoon in as many as three or more places. Figure 7 shows a moused, shrewed, and sound cocoon.

Graham (22) has suggested that it is possible to determine whether a cocoon has been opened by a mouse or by a shrew by examining the opening made by each. Morris (50) however, has claimed that this is not possible with cocoons of the European spruce sawfly. In order to test this possibility, 20 cocoons known to be moused and 10 cocoons known to be shrewed from the preceding experiment were examined by 25 independent observers including one housewife, one

Table XVII

Feeding Experiments Conducted on Three Species of Small Mammals

Species	Cocoon type	Opened	Unopened	Total	% Opened	Chi-square	d.f.	P.
Clethrionomys	Sound	114	42	156	73	--	--	--
	Sound on tags	54	26	80	68	.802	1	.40 approx.
	Living *Bessa*	11	27	38	29	26.03	1	less than .01
	Bessa emerged	33	9	42	79	.422	1	.50 approx.
	Sawfly emerged	9	33	42	21	65.15	1	less than .01
	Fungus	0	38	38	0	67.86	1	less than .01
Microtus	Sound	56	22	78	72	--	--	--
	Sound on tags	31	9	40	78	.444	1	.50 approx.
	Living *Bessa*	9	10	19	47	4.124	1	.03 approx.
	Bessa emerged	14	7	21	67	.210	1	.70 approx.
	Sawfly emerged	4	17	21	19	20.62	1	less than .01
	Fungus	0	19	19	0	30.90	1	less than .01
Sorex	Sound	142	14	156	91	--	--	--
	Sound on tags	75	5	80	94	.531	1	.50 approx.
	Living *Bessa*	11	27	38	29	71.13	1	less than .01
	Bessa emerged	7	35	42	20	98.12	1	less than .01
	Sawfly emerged	0	42	42	0	133.28	1	less than .01
	Fungus	0	38	38	0	131.95	1	less than .01

Figure 7. Comparison of Sound Cocoon and Cocoons Opened by Mouse and Shrew. From left to right

(a) sound

(b) opened by a mouse showing scalloped edge

(c) opened by a shrew showing serrated edge

(d) opened by a shrew showing "cap" or "lid".

statistician, two teachers, three clerks, one stenographer, nine insect rangers and technicians, and six research officers. These were divided into three classes, and an analysis of variance was run in order to detect any differences that may occur. Table XVIII shows no significant differences between the ability of each class to distinguish between moused and shrewed cocoons. The results were then pooled, and it was found that the various classes could differentiate moused cocoons with 85% accuracy and the confidence interval of the mean at the 95% level was 84.54 - 85.46%. Similarly shrewed cocoons could be determined with 83.6% accuracy with a confidence interval of the mean at the 95% level of 82.81 - 84.39%.

Table XVIII

Test for Determining Accuracy of Classes in Differentiating Moused and Shrewed Cocoons.

Source	d.f.	M.S.	F	$F_{.05}$
Moused				
Between Classes	2	139.12	1.572	3.44
Within Classes	22	88.51		
Total	24			
Shrewed				
Between Classes	2	467.94	3.072	3.44
Within Classes	22	152.32		
Total	24			

7.4 Cocoon Predation Trends Using the "Cocoon Plant" Technique.

The predational effect of small mammals on larch sawfly cocoons was estimated in the field using the "cocoon plant" method, as previously employed by Graham (22) and Morris (50). These authors enclosed five cocoons in small cotton bags and buried the bags on various plots. The present author considered this unnatural, and in order to simulate natural conditions more closely, cocoons were wired onto small tree tags. Two cocoons about two inches apart were wired on each tag and these were buried to a depth of about two inches in such a manner that the top inch projected from the soil in order to locate the tags during subsequent examinations. One hundred sets were planted on each plot. These were examined at intervals and the individual cocoons recorded as being untouched, attacked by fungus, parasite emerged, opened by a mouse, opened by a shrew, or removed (presumably by a small mammal). Cocoons that were missing or opened were renewed after each examination.

Using this technique it was found that small mammals prey upon larch sawfly cocoons only during a definite and limited season. It was formerly supposed that this insect was particularly vulnerable to mammalian predation because it remained in the ground within the cocoon for some 10 months of the year, thus affording an extended period in which small mammals could prey upon it. However it is apparent that light predation begins in late August, reaches its greatest intensity during September, and then slowly declines until November. After this, little or no predation occurs on this population. Thus it is postulated that small mammals prey upon the larch sawfly to a limited extent in late August, reach a climax in September, and then slowly relax their pressure until the ground is frozen. This constitutes the entire predation until the following August when mammalian predators again begin to destroy cocoons. From observations it was found that small mammals prey upon cached cocoons during the winter months. However these have already been removed from the field population, and once cached are potentially destroyed.

The results of the experiment are recorded in Tables XIX, XX, and XXI. Populations of predators and prey are included in the tables since Graham (22) suggested that variations in mouse populations are reflected in the predation of the larch sawfly, and Errington (19) suggests that predation, within certain limits, is dependent upon the population density of predator and prey. In many cases, the entire cocoon was removed from the tag leaving no evidence of the predator. It was assumed that this characteristic was random for both mice and shrews. Small mammal populations were taken from the seasonal population curves for the various plots. Larch sawfly populations were estimated as outlined in Section 6, and corrected for loss through predation.

The foregoing tables indicate a substantial reduction in the larch sawfly cocoon population through the activities of mammalian predators. Shrews, especially during 1953, were particularly active as cocoon predators and their value as a natural control factor has apparently been underestimated by Graham (21). Morris (50) however, has recognized the importance of insectivore predators of the European spruce sawfly. During 1953, the cumulative predation was 94.1% on Plot 2, and 97.6% on Plot 3. Shrews accounted for 88.1 and 88.6 per cent of this respectively. Since other mortality factors, such as parasitism, operate against the

Table XIX

Predation, Small Mammal Populations and Sawfly Populations on Plot 1.

Date	% Moused	% Shrewed	% Total preda-tion	Mice per acre	Shrews per acre	Sawflies per acre	Cocoons opened per mouse per day	Cocoons opened per shrew per day
4/IX/52	21	11	32	3.85	.96	186,000	371	872
1/X/52	41	12	53	3.46	.63	130,000	53	388
15/IV/53	43	14	57	.35	.08	117,000	--	--
24/VIII/53	1.5	.5	2	1.62	.86	91,000	208	131
31/VIII/53	5	2	7	1.85	.99	86,400	284	133
7/IX/53	16	3	19	2.07	1.03	75,000	683	208
14/IX/53	39	6	45	2.27	1.28	51,000	1385	223
21/IX/53	49	10	59	2.34	1.28	38,100	519	491
28/IX/53	54	13	67	2.27	1.24	30,600	588	276
4/X/53	58	16	74	2.21	1.21	24,000	259	307
11/X/53	60	17	77	1.15	1.15	21,300	118	112

Table XX

Predation, Small Mammal Populations and Sawfly Populations on Plot 2.

Date	% Moused	% Shrewed	% Total predation	Mice per acre	Shrews per acre	Sawflies per acre	Cocoons opened per mouse per day	Cocoons opened per shrew per day
1/IX/52	12	16	28	6.41	.41	108,400	208	4058
30/IX/52	16	25	41	5.63	.30	88,700	72	1966
1/XI/52	25	38	63	4.82	.24	55,700	141	1478
15/V/53	28	41	69	.82	.51	46,700	--	--
24/VIII/53	0	4	4	2.29	3.29	173,000	--	540
31/VIII/53	0	22	22	2.25	3.35	140,000	--	1386
7/IX/53	0	36	36	2.27	3.05	115,000	--	1180
14/IX/53	0	48	48	2.33	2.52	92,900	--	1270
21/IX/53	3	75	78	2.38	2.37	39,600	198	3014
28/IX/53	5	81	86	2.27	1.74	25,300	82	1067
4/X/53	6	85	91	2.19	1.58	16,500	46	746
11/X/53	6	87	93	2.04	1.41	12,600	--	395
18/X/53	6	87.5	93.5	1.92	1.23	11,700	--	106
25/X/53	6	87.7	93.7	1.78	1.04	11,400	--	41
1/XI/53	6	88.1	94.1	1.49	.89	10,600	---	128

Table XXI

Predation, Small Mammal Populations and Sawfly Populations on Plot 3.

Date	% Moused	% Shrewed	% Total predation	Mice per acre	Shrews per acre	Sawflies per acre	Cocoons opened per mouse per day	Cocoons opened per shrew per day
3/IX/52	2	26	28	1.08	1.19	342,000	88	7185
30/IX/52	15	31	46	.95	1.06	256,000	1442	1712
15/V/53	17	32	48	.61	1.82	247,000	--	--
24/VIII/53	--	7	7	.76	5.42	677,000	--	2353
31/VIII/53	--	29	29	.74	5.56	517,000	--	4111
7/IX/53	5	36	41	.73	5.44	429,000	1174	2153
14/IX/53	5	51	56	.71	5.32	321,000	--	2900
21/IX/53	9	75	84	.70	5.21	116,500	1245	5440
28/IX/53	9	84	93	.69	5.09	50,900	--	1841
4/X/53	9	87.5	96.5	.65	4.98	25,500	--	744
11/X/53	9	88.2	97.2	.63	4.82	20,400	--	151
18/X/53	9	88.6	97.6	.60	4.73	17,500	--	88

population, it would appear that in these and similar areas, insectivorous predators might either terminate a larch sawfly infestation or decrease its intensity. Since small mammals appear to reject parasitized cocoons to some extent, the greatest effect of predation would occur, theoretically, as the infestation approached its peak in that period just prior to the parasite peak.

Upon examination of the columns "Cocoons opened per rodent per day" and "Cocoons opened per insectivore per day" in the foregoing tables, it will be noted that in one case it was calculated that over 7000 cocoons were taken by the predators per day, and in many cases about 2000 were taken. Data on caged animals do not lend support to these figures. There are three plausible explanations for this discrepancy:-

(1) Mammal populations were inaccurately measured.

(2) Sawfly populations were inaccurately measured.

(3) Sawfly larvae experienced considerable mortality after falling from the trees but before spinning cocoons, since the cocoon population was derived indirectly from mature larvae rather than cocoon counts.

The author considers that the small mammal population estimates are reasonably accurate. Furthermore, the sawfly population would have to be overestimated from four to nine times in order to bring the number destroyed per mammal per day within reasonable bounds. Therefore, the third explanation (viz: that the sawfly larvae experience heavy mortality after falling from the trees but before spinning cocoons) seems the most plausible. Such mortality may be caused by such factors as mammalian predation of transient larvae, frog predation, predation by ground feeding birds, disease, or unfavourable water relationships.

The predator and prey populations were examined, to determine whether or not predation is density dependent. The results of the analysis shown in Table XXII, indicate that there is no correlation between predation and the populations of predator and prey, although the correlation was calculated from estimates and is therefore statistically weak. Graham (22) has suggested that small mammal populations may be estimated from the results of cocoon analysis, but this portion of the study indicates that there is probably no simple relationship between the predator-prey populations and the extent of predation.

Table XXII

Correlation Coefficients on Predation, Mammal Populations and Sawfly Populations

Plot	Source	r	d.f.	$r_{.05}$
1	% Moused vs. $\frac{\text{Mouse Population}}{\text{Sawfly Population}}$	.155	8	.632
	% Shrewed vs. $\frac{\text{Shrew Population}}{\text{Sawfly Population}}$	.229	8	.632
	% Preyed upon vs. $\frac{\text{Small Mammal Population}}{\text{Sawfly Population}}$	.076	8	.632
2	% Moused vs. $\frac{\text{Mouse Population}}{\text{Sawfly Population}}$	.398	9	.602
	% Shrewed vs. $\frac{\text{Shrew Population}}{\text{Sawfly Population}}$	.171	9	.602
	% Preyed upon vs. $\frac{\text{Small Mammal Population}}{\text{Sawfly Population}}$	.226	9	.602
3	% Moused vs. $\frac{\text{Mouse Population}}{\text{Sawfly Population}}$	.165	12	.532
	% Shrewed vs. $\frac{\text{Shrew Population}}{\text{Sawfly Population}}$	.223	12	.532
	% Preyed upon vs. $\frac{\text{Small Mammal Population}}{\text{Sawfly Population}}$	.499	12	.532

The location in which the insect spins its cocoon may be in part a defense against small mammal predation. Workers in the field have noticed that there are several locations in which cocoons are almost invariably missed by small mammal predators. Using the cocoon planting technique it was found that cocoons planted beside the roots of trees and in hummocks in the bogs were heavily preyed upon by small mammals. On the other hand, cocoons in the low lying places between the hummocks were usually missed by mammalian predators especially when these locations were at or near the water table.

7.5 Saturation Trapping.

Predation by small mammals was also tested by means of a saturation trapping technique. This consisted of snap-back trapping to remove the entire small mammal population from a plot. Emerging larch sawfly adults were captured by means of emergence cages, and these numbers were compared with emergence from a similar plot containing a full complement of small mammals. The experiment was conducted on Plot 3A, and Plot 3 was used as the check plot. The plots were almost identical (see Section 4 , Tables I and II) and the larch sawfly cocoon populations were very similar (see Section 6, Table XV). The population of mammals was assumed to be the same on both plots, although no determinations could be made on Plot 3 without disturbing the small mammal population.

It is not known conclusively if it is possible to remove the entire small mammal complement from an area. Saunderson (58) found that during an extended trapping period of over 40 consecutive days, considerable numbers of small mammals were still being trapped. However in the author's experiment beginning in July 1952, animals were captured up to the sixth day, after which no further animals were captured. After an interval of two weeks, no animals were captured on the body of the plot, but a few were taken in the two outside lines. As an additional check, cocoons were planted at each trap position. By the end of May 1953, only 11 cocoons had been taken, and of these only one was on the body of the plot. In addition to these, a row of cocoons was planted around the inner square chain on the plot, and no mammalian predation had occurred on these at that time. The results of the test strongly suggest that saturation trapping is possible.

Trapping was resumed on Plot 3A in early May of the 1953 season in order to keep the mammals from the plot. The results of the experiment are summarized in Table XXIII. The initial larval index is the mean number of larvae captured per funnel, and the predation larval index is this figure corrected for small mammal predation using cocoon plants. The emergence index is the mean number of adults captured in the emergence cages which were set out in three series as follows:

(1) Series A. - Ten cages diametrically opposite larval funnels.

(2) Series B. - Ten cages randomly placed throughout the plot.

(3) Series C. - Ten cages randomly placed in the centre square chain of the plot.

Table XVIII indicates a close relationship between the per cent predation based upon cocoon plants and the surviving adult population.

Table XXIII

Relationship Between Predation and Sawfly Emergence

Plot	Treatment	Initial Larval Index	Predation Larval Index	Emergence Index Series A.	Emergence Index Series B.	Emergence Index Series C.
3	Mammals present	28.1	14.6	4.3	2.2	3.7
3A	Mammals removed	29.0	26.4	9.1	5.1	8.0
Ratio of Plot 3 and Plot 3A			.55	.47	.43	.46

Although the relationship is close, the results of this experiment should be considered indicative rather than conclusive, since it was found that the adult sawfly were able to readily escape from the base and edges of the cages. Ants were also observed removing insects from the cage. A series of six cages was set up in a bog which presumably contained no larch sawfly, and ten freshly emerged sawfly were introduced into each cage. These were examined 24 hours later and it was found that less than half the sawfly adults were recovered. The experiment should be repeated after an improved emergence cage has been constructed. Regardless of the inadequacies of the experiment, there does appear to be a good relationship between the loss due to predation assessed by means of cocoon planting and the emergence of adult sawfly the following year.

By virtue of the results of this experiment cocoon planting will be used in the future in order to estimate predation by small mammals.

8. DISCUSSION AND SUMMARY

8.1 Predator and Prey Populations.

Previous studies relating to the role of small mammalian predators of the larch sawfly have not approached the problem from a population dynamic aspect, although a density dependent relationship was suggested by Graham (22). Since this seemed to afford a promising line of investigation, considerable time was spent during the present study in refining population assessment techniques for both prey and predator species.

Because small mammal predation on the larch sawfly concerns chiefly cocooned insects in the soil, studies on sawfly populations were directed largely towards that portion of the population. It has been found by a number of workers (14, 23) that sampling cocoons directly is not only laborious to the extent of being impractical for a single operator, but also that the standard deviation of the sample is so wide that the value of the information is seriously limited. Therefore a method was adopted which attempted to estimate larval populations dropping to spin cocoons. Funnels were placed under representative trees to trap falling larvae and the number caught were related to cocoon populations on the assumption that each larva represents a cocoon. The seasonal means and standard deviations for 10 funnels on each of Plots 1, 2, 3, and 3A during 1952 were 13.3 ± 6.5, 12.3 ± 12.1, 28.1 ± 10.0, and 29.0 ± 8.8, which indicates that the estimate was reasonably accurate for the stage sampled with the notable exception of those determinations from the very small trees on Plot 2. However there is some indirect evidence to support the theorem that there is considerable mortality after the larvae have dropped to the ground but before cocoons have been spun. If this is true, there remains the problem of assessing this mortality before a fully accurate cocoon population estimate can be made. Preliminary studies on emerging adult populations were also conducted using ground emergence cages. Although the method is theoretically sound, there are several technical difficulties which must be corrected to achieve reasonable precision. The main requirement is a modification in basic design of the trap to prevent the escape of emerged insects. However useful comparisons may be derived from data collected using the unmodified emergence cage.

Small mammal populations were measured chiefly by means of live traps utilizing the mark-release-recapture technique (5). Populations on the effective trapping area were determined by means of the Lincoln Index (43) and it was concluded that a pooling of data for the final three determinations for any given trapping period gave the most accurate population value. Home ranges were calculated for *Clethrionomys gapperi*, *Microtus pennsylvanicus*, and *Sorex cinereus*; and for these, cruising radii were calculated as follows:-

Clethrionomys	89 feet (Plot 1), 76 feet (Plot 2)
Microtus	73 feet
Sorex	139 feet

The cruising radius for each species was then used as a boundary strip, which when added to the area encompassed by the traps, gave the effective trapline area for each species. Sufficient data were collected on Clethrionomys to compare the home ranges. It appears from the results of this analysis that home ranges did not differ significantly between sexes or between population densities but a significant difference was obtained between home ranges of this species on two of the habitats studied.

In addition, experiments were conducted to assess small mammal populations using snap-back traps. Although the data are meagre there is some evidence to support the view that both line and grid snap-back traplines can be used to determine absolute populations with reasonable accuracy. Should further studies substantiate this conclusion, it will enable a greater collection of information in terms of energy expended.

8.2 Coactions of Small Mammals and the Larch Sawfly.

Although 14 species of small mammals were recorded as inhabiting tamarack bogs of eastern Manitoba, few of these can be considered important predators of the larch sawfly. By virtue of their low populations, all but five of these might be excluded as cocoon predators. The species which maintain populations in sufficient numbers to reduce sawfly populations appreciably are Clethrionomys gapperi, Microtus pennsylvanicus, Zapus hudsonius, Peromyscus maniculatus, and Sorex cinereus. However Z. hudsonius and P. maniculatus occur only on the peripheral regions of the bogs and for this reason, might also be excluded as important predators, since predation in these fringe regions is probably negligible. Although all three species of important small mammals occur on all the habitats investigated, variations in the populations of these species in each habitat are evident. C. gapperi occurred in highest numbers in dense, reasonably dry sites; M. pennsylvanicus in open, moist sites; and S. cinereus in dense, wet sites. Habitat variations are important since the value of these species as cocoon predators differs.

Feeding experiments were conducted on the three important mammalian species. Although the food capacity of each appears roughly equal, S. cinereus has powers of discrimination not possessed by the other species. S. cinereus habitually rejects cocoons that have been attacked by fungus, cocoons from which sawflies or parasites have emerged, and cocoons parasitized by B. harveyi; whereas the remaining species reject these cocoons to a lesser extent. S. cinereus therefore appears to be the most useful predator from a larch sawfly control standpoint since overlapping of control factors is minimized. Morris (50) recognizes the importance of shrews as predators of the European spruce sawfly, whereas the earlier work of Graham (21) excludes them as important predators of the larch sawfly.

A modification of the earlier "cocoon planting" technique (22) was used to ascertain the extent of small mammal predation of sawfly cocoons in the field. Preliminary experiments indicated that it is possible to distinguish with reasonable accuracy between cocoons opened by mice and those opened by shrews. The technique is probably quite accurate, since it was found that decrease in spring adult emergence was proportional to predational loss as assessed by this method. The relationship between amount of predation and abundance of the predator and prey animals does not appear to be a simple density-dependent one, although this cannot be argued conclusively, as it was pointed out earlier that there may be a large discrepancy in estimates of the larch sawfly cocoon populations as determined by falling larvae. The importance of shrews is exemplified by these results, for the proportion of cocoons opened by shrews to shrew populations is considerably greater than the proportion of cocoons opened by mice to mouse populations.

The cocoon planting technique suggests that 57%, 69%, and 48% of the cocoon populations on Plots 1, 2, and 3 respectively were destroyed by small mammals during the fall of 1952, and 77%, 94.1%, and 97.6% respectively were destroyed during the fall of 1953. It was further found that the period of predation is relatively short, lasting from the beginning of September to the time the ground freezes. This is contrary to the opinion held by many workers, that predation is carried on throughout the spring period until the completion of sawfly adult emergence (22, 24, 25).

This investigation indicates that small mammals are one of the most important natural control factors operating against the larch sawfly in the study area.

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10. BIBLIOGRAPHY

1. Adams, Lowell. 1951. Confidence limits for the Petersen or Lincoln Index used in animal population studies. J. Wildl. Mgnt. 15:13-9.

2. Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt, 1949. The principles of animal ecology. Saunders & Co.

3. Anderson, R. M., 1946. Catalogue of Canadian recent mammals. Can. Dept. of Mines and Res., Nat. Mus. Can. Bull. No. 102.

4. Balch, R. E. 1939. The outbreak of the European spruce sawfly in Canada and some important factors of its bionomics. Econ. Ent. 32:412-418.

5. Bailey, N. T. J. 1951. On estimating the size of mobile populations from recapture data. Biometrica 38:293.

6. ________________ 1952. Improvements in the interpretation of recapture data. J. Anim. Ecol. 21:120-7.

7. Bess, H. A., S. H. Spurr, and E. W. Littlefield. 1947. Forest site conditions and the gypsy moth. Harvard For. Bull. No. 22.

8. Blair, W. Frank. 1941. Techniques for the study of mammal populations. J. Mammal. 22:148-57.

9. Bole, B. P. 1939. The quadrat method of studying small mammal populations. Sci. Bull. Cleveland Mus. Nat. Hist. 5:15-77

10. Borell, Adrey E. 1937. A new method of collecting bats. Jour. Mammal. 18: 478-80.

11. Buckner, Charles H., 1951. Small Mammals Annu. Tech. Rept., Green River Project, N. B.

12. Bureau of Animal Populations. Annu. Repts., Oxford Univ.

13. Burt, W. H. 1943. Territoriality and home range concepts as applied to small mammals. J. Mammal. 24: 346-52.

14. Butcher, J. W. 1952. Appraisal surveys and aerial spraying. in: Circ. No. 204. State of Minnesota, Dept. Agric., Division of Plant Industry.

15. Criddle, N. 1928. The introduction and establishment of the larch sawfly parasite, Mesoleius tenthredinis Morley, into southern Manitoba. Can. Ent. 60:51-53.

16. Davis, D. E., John T. Emlen Jr., and Allen W. Stokes. 1948. Studies on home ranges in the brown rat. J. Mammal. 29:207-25.

17. Dice, L. R. 1931. Methods of indicating the abundance of mammals. J. Mammal. 12:376-81.

18. Edwards, R. York. 1952. How efficient are snap traps in taking small mammals? J. Mammal. 33:497-8.

19. Errington, Paul L. 1946. Predation and vertebrate populations. Quart. Rev. Biol. 21:144-177, 221-245.

20. Evans, F. C. 1942. Studies of a small mammal population in Bagley Wood, Berkshire. J. Anim. Ecol. 11:182-97.

21. Graham, S. A. 1928. The influence of small mammals and other factors upon the larch sawfly survival. J. Econ. Ent. 21:301-310.

22. ____________ 1929. The larch sawfly as an indicator of mouse abundance. J. Mammal. 10:189-196.

23. ____________ 1952. Forest Entomology. McGraw-Hill Co. Inc. London and New York.

24. Hamilton, W. J. Jr., and David B. Cook. 1940. Small mammals and the forest. J. For. 38:468-473.

25. Hardy, J. E. 1939. Natural control of Diprion similis Htg. in Poland during 1936. Bull. Ent. Res. 30:237-246.

26. Hartley, P.H.T. 1947. Predation by sparrow hawk populations. Review of "De Sperver als Roofvijand van Zangvoglels", by L. Timbergen. Ecol. 28:326-328.

27. Hayne, D. W. 1949. Calculation of size of home range. J. Mammal. 30:1-18.

28. ____________ 1949. An examination of the strip census method for estimating animal populations. J. Wildl. Mgnt. 13:145-57.

29. ____________ 1949. Two methods for estimating population from trapping records. J. Mammal. 30:399-411.

30. ____________ 1950. Apparent home range of Microtus in relation to the distance between traps. J. Mammal. 31:26-39.

31. Hewitt, C. G. 1912. The large larch sawfly. Dom. Can. Dept. Ent. Bull. No. 5.

32. Hopkins, A. D. 1909. Some insects injurious to forests. Insect depredations in North American forests and practical methods of prevention and control. Bull. 58 Pt. V: 57-101. Bur. Ent. U.S. Dept. Agr.

33. Jackson, C. H. N. 1933. On the true density of tsetse flies. J. Anim. Ecol. 2:204-9.

34. ________________ 1937. Some new methods in the study of Glossina morsitans. Proc. Zool. Soc. Lond. 811-96.

35. ________________ 1939. The analysis of an animal population. J. Anim. Ecol. 8: 238-46.

36. ________________ 1940. The analysis of a tsetse fly population. Ann. Eugin., Lond. 10:332-69.

37. Kendeigh, S. Charles. 1944. Measurement of bird populations. Ecol. Monogr. 14:67-106.

38. Lejeune, R. R. 1947. Status of the larch sawfly Pristiphora erichsonii (Htg.) in the prairie provinces. Can. Ent. 79:130-134.

39. ____________ 1951. Some ecological factors governing populations of the larch sawfly, Pristiphora erichsonii (Htg.). Can. Ent. 83:152-156.

40. Lejeune, R.R. and V. Hildahl. 1954. Unpublished manuscript.

41. Leopold, A. 1933. Game management. Charles Scriber's and Sons.

42. Leslie, P.H. and Dennis Chitty. 1951. The estimation of population parameters from data obtained by the capture-recapture method. I. The maximum likelihood equation for estimating the death rate. Biometrica 38:269-92.

43. Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. Circu. U.S. Dept. Agric. No. 118.

44. Llewellyn, Leonard M. 1950. Reduction of mortality in live-trapping mice. J. Wildl. Mgnt. 14:84-5.

45. Machulick, D. A. 1937. Fluctuations in the numbers of the varying hare (Lepus americanus.) Toronto Univ., Biol. Ser. No. 43.

46. Manville, R. H. 1950. A comparison of trapping methods. J. Mammal. 31:377-83.

47. ______________ 1950. Techniques for the capture and marking of small mammals. J. Mammal. 31: 377-383.

48. Morris, R. F. 1942. Preliminary notes on the natural control of the European spruce sawfly by small mammals. Can. Ent. 74:197-202.

49. ______________ 1945-52. Small Mammals. Annu. Tech. Rept., Green River Project, N. B.

50. ______________ 1949. Differentiation by small mammal predators between sound and empty cocoons of the European spruce sawfly. Can. Ent. 81:114-120.

51. ______________ 1950. Unpublished manuscript.

52. Muldrew, J. A. 1953. The natural immunity of the larch sawfly (Pristiphora erichsonii (Htg)) to the introduced parasite Mesoleius tenthredinis Morley, in Manitoba and Saskatchewan. Can. J. Zool. 31:313-332.

53. Pearson, Oliver P.. 1948. Metabolism of small mammals with remarks on the lower limit of mammalian size. Sci. 108:44

54. Petersen, C. G. J. 1889. Fisk Beretn., Kbh.

55. ________________ 1894. On the biology of our flat-fish and on the decrease of our flat-fish industries. Rep. Danish Biol. Sta. No. 4. 146 pp.

56. Quimby, Don C., 1951. The life history and ecology of the jumping mouse, Zapus hudsonius. Ecol. Monagr. 21: 61-95.

57. Ricker, William E. 1945. Some applications of statistical methods to the fisheries problems. Biona. Bull. 1:73-9.

58. Saunderson, G. C. 1950. Small mammal populations of a prairie grove. J. Mammal. 31:17-25.

59. Schumanov, E. A., 1950. The cicada, Cicadetta montana, Scop., as a forest pest (In Russian). Dokl. Akod. Nauk SSSR (N.S.) 72:1127-1130.

60. Stickle, Lucille F. 1946. Experimental analysis of methods for measuring small mammal populations. J. Wildl. Mgnt. 10:150-159.

61. ________________ 1954. A comparison of certain methods of measuring ranges of small mammals. J. Mammal. 35:1-15.

62. Thompson, Daniel T. 1952. Travel, range and food habits of the timber wolves in Wisconsin. J. Mammal. 33:429-42.

63. Turnock, W. 1952. Annu. Tech. Rept. Forest Biology Laboratory, Winnipeg, Man.